CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

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Rhinoclemmys annulata (Gray 1860) – Brown Wood Turtle, Montañero, Bambera

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Summary. – The Brown Wood Turtle, *Rhinoclemmys annulata* (family Geoemydidae, subfamily Rhinoclemmydinae), is a medium-sized turtle (maximum straightline carapace length [SCL] to 226 mm), that is largely terrestrial and primarily occurs in rainforest areas in Caribbean drainages of Central America from Honduras to northern Colombia, and in Pacific drainages from eastern Panama south to Ecuador. In Ecuador, the species occurs in dry forest areas as well. The known elevational range is from sea level to 920 m. The species is monotypic, without subspecies, and demonstrates substantial variability in carapace coloration within populations. There is modest sexual size dimorphism, with males reaching a maximum SCL of 202 mm, and females up to 226 mm. Females lay one large elongate egg measuring approximately 71 x 37 mm and 48–49 g, with a mean hatchling SCL of 63.9 mm. The ecology of *R. annulata* is poorly studied, and its population status is unknown. The greatest threat faced by this species is habitat destruction, although the degree and impact of this threat remains unknown. It is also sometimes utilized as a local pet and food source by several indigenous and rural populations. Trade into the international pet market appears to be minimal. The species has been recorded from several protected areas within its range, but assessments of its threats, conservation status, and population trends are needed.

Distribution. – Colombia, Costa Rica, Ecuador, Honduras, Nicaragua, and Panama.

Synonymy. – *Geoclemmys annulata* Gray 1860*, Clemmys annulata, Rhinoclemys annulata, Rhinoclemys (Callopsis) annulata, Chelopus annulatus, Rhinoclemmys annulata, Nicoria annulata, Geoemyda annulata, Callopsis annulata, Chelopus gabbii* Cope 1875*, Emys gabbii, Nicoria gabbii, Geoemyda gabbii, Rhinoclemmys gabbii, Testudo mercatoria* Vaillant 1911 *(nomen nudum).*

Subspecies. – None recognized.

Status. – IUCN 2022 Red List: Near Threatened (NT; assessed 1996); TFTSG Provisional Red List: Data Deficient (DD; 2011, 2018); CITES: Appendix II as *Rhinoclemmys* spp. (2023); Colombia Red List: Least Concern (LC; 2015); Costa Rica Red List: Least Concern (LC; 2014); Ecuador Red List: EN (Endangered; 2005); Nicaragua: Least Concern (LC; 2017).

Taxonomy. — This species was described as *Geoclemmys annulata* by Gray (1860) based on a small series of specimens from Esmeraldas, Ecuador. Cope (1875) later described specimens of the same species from Costa Rica as *Chelopus gabbii*. Other than a variety of generic name combinations, the specific epithet *annulata* has experienced relative stability in usage for all populations since shortly after its description (Boulenger 1889; Wermuth and Mertens 1961; Ernst 1980; Fritz and Havaš 2007; TTWG 2017, 2021). Although a great deal of variability has been noted, e.g., in carapace coloration (Mittermeier 1971b), this variation appears in many populations and, therefore, subspecies have never been proposed (Ernst 1978, 1980).

Hirayama (1985) conducted a phylogenetic analysis of a morphological data set for all Geoemydidae, including six species of *Rhinoclemmys*. He concluded that *Rhinoclemmys* is polyphyletic and indicated that the two terrestrial species, *R. annulata* and *R. rubida,* were more closely related to Old World geoemydids and testudinids than the other species of *Rhinoclemmys*. Gaffney and Meylan (1988) adopted this phylogeny and placed these two terrestrial *Rhinoclemmys* in a separate clade from the other monophyletic clade of four *Rhinoclemmys* species. Yasukawa et al. (2001) re-analyzed a smaller morphological dataset than Hirayama (1985) and recovered much the same topology, indicating a polyphyletic genus *Rhinoclemmys*, providing justification for the taxonomic placement of *R. annulata* and *R. rubida* in the genus *Chelopus* Cope, with *C. rubidus* designated as the type species. However, studies that have included a combination of morphological and genetic data (Carr 1991), or genetic data alone, have consistently identified a monophyletic genus *Rhinoclemmys* (Spinks et al. 2004; Le and McCord 2008). As a result, *Chelopus* is not currently accepted as a separate genus and most phylogenetic studies

Figure 1. Adult female *Rhinoclemmys annulata* from Tortuguero National Park, Costa Rica. Photo by Michael Redmer.

involving DNA sequencing are consistent in recognizing *R. annulata* as the sister taxon of *R. pulcherrima* (Spinks et al. 2004; Le and McCord 2008; Guillon et al. 2012; Pereira et al. 2017; Colston et al. 2020; Thomson et al. 2021).

Description. — *Rhinoclemmys annulata* is a medium-sized species with a maximum straight-midline carapace length (SCL) of 226 mm. It has an ovate to quadrangular carapace in dorsal outline that varies in coloration from a straw yellow-brown to almost entirely black, often with a distinctly yellow-colored, low, broad vertebral keel. The plastron is usually dark brown to black, except around the periphery, which is yellow; however, the intensity of the black coloration is variable. Head coloration usually involves a number of pale white or yellow stripes on the lateral surface, surrounded by a dull olive to brownish ground color. The upper jaw is slightly hooked, a characteristic shared within the genus only with *R. rubida*. There is little to no webbing between the toes of all four limbs. The species is distinguished from all other *Rhinoclemmys* species by the following combination of shell features: the ventral portion of marginals 4-8 contact plastral scutes (pectoral and abdominal) across the bridge; the anterior margin of costal scute 2 contacts the posterior of marginal 5; the anterior margin of costal 4 contacts the middle or posterior of marginal 9; the 7th marginal scute is consistently 5-sided in dorsal outline; and the interhumeral seam is longer than the intergular seam.

Mittermeier (1971b) noted that males have a narrower shell than females, longer tails, and a concave plastron. The slightly concave and narrower, shorter plastron in males was mentioned by Grünewald (2015). Ernst (1980) also described the males as having a longer tail than females,

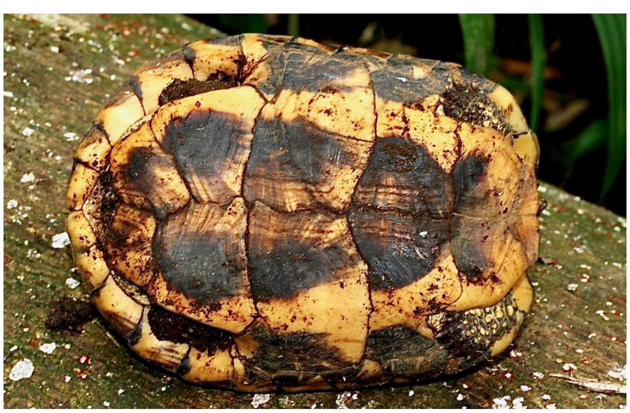

Figure 2. Adult female *Rhinoclemmys annulata* from Tortuguero National Park, Costa Rica. Same individual as in Fig. 1. Photo by Michael Redmer.

Figure 3. Adult female *Rhinoclemmys annulata* from Tortuguero National Park, Costa Rica. Same individual as in Fig. 1. Photo by Michael Redmer.

Figure 4. Adult female *Rhinoclemmys annulata* from Isla Palma, Valle del Cauca, Colombia. Photo by John L. Carr.

Figure 5. Adult female *Rhinoclemmys annulata* from Isla Palma, Valle del Cauca, Colombia. Photo by John L. Carr.

but reported no sexual dimorphism in carapace length. However, females appear to achieve slightly larger sizes than males, with the largest male recorded at 202 mm SCL, and the largest female at 226 mm SCL (Ernst 1978; Giraldo et al. 2012; *n* = ca. 110 museum specimens rangewide). In a more geographically restricted Panamanian sample, Mittermeier (1971b) reported mean male size as 160 mm SCL and mass of 533 g (*n* = 3) and mean female size as 177 mm SCL and mass of 770 g (*n* = 6).

Distribution. — *Rhinoclemmys annulata* is distributed from eastern Honduras (McCranie 2018) to northern Colombia in Caribbean drainages (Medem 1962a,b); Castaño-Mora and Medem 2002; Giraldo et al. 2013), and from the Province of Panamá, Panama (Mittermeier 1971b) to western Ecuador in Pacific drainages (Carr and Almendáriz 1990). The range extends to at least southern Guayas Province (ca. 2.7°S) in western Ecuador (Arteaga 2022). The possible origins of erroneous out-of-range localities for *R. annulata* in Amazonian Ecuador and Venezuela were discussed by Carr and Almendáriz (1990).

Habitat and Ecology. — This species is largely terrestrial according to Dunn (1945) and Medem (1962a,b). Specimens were found in dry leaf litter of the Tropical Moist Forest of Barro Colorado Island, Panama (Allee 1926), and McCranie (2018) reported usually finding them on the forest floor, active during the day, in both the rainy season and during dry times of the year in Honduras. The species is said to easily negotiate high hills and uneven terrain (Allee 1926; Medem 1962a; Acuña Mésen 1993). In addition, individuals have been found sitting or soaking in shallow water (Medem 1962a; Giraldo, pers. obs.), or buried in mud of a backwater or along a stream bank (McCranie

Figure 6. Adult male *Rhinoclemmys annulata* from western Ecuador. Photo by Ferry Grünewald.

Figure 7. Adult female *Rhinoclemmys annulata* from the vicinity of Guayaquil, Ecuador. Photo by Ferry Grünewald.

2018; Cárdenas-Arévalo et al. 2019). Ramos Galdamez et al. (2019) found two *R. annulata* in Honduras, one ca. 30 m from the water and one in a stream. The report of Abellá et al. (2008) is unique in indicating that *R. annulata* was common in bodies of water (canals, lagoons, ponds) in the Pacuare Nature Reserve, Costa Rica.

The ecological distribution of *R. annulata* consists of forested areas, specifically Tropical Rain Forest (TRF), Tropical Moist Forest (TMF), and Tropical Dry Forest (TDF) in terms of global ecozones (FAO 2012). These three forest types are distinguished by the number of dry months each year, with a dry month defined as having total precipitation in mm ≤ 2 times the mean monthly temperature in °C (FAO 2012)—the tropical, lowland areas inhabited will typically have a mean monthly temperature >18°C. Tropical Rain Forest has the wettest climate, with 0–3 dry months per year, and the corresponding numbers of dry months for Tropical Moist Forest and Tropical Dry Forest are 3–5 and 5–8, respectively (FAO 2012). Although altitude and climate have typically factored in these potential vegetation classifications (Holdridge 1967; FAO 2012), annual precipitation in these forest types have often been distinguished by a range of approximately 1000–2000 mm for dry forest, 2000–4000 mm for moist forest, and >4000 mm for (wet) rain forest (Savage 2002). The distribution of *R. annulata* includes the world's rainiest area in the Chocoan region of Pacific Colombia (12,000–13,000 mm/yr; Poveda and Mesa 2000) and the precipitation drops off north and south of there. Around the equator in coastal Ecuador, the change is compressed as forest types change over short distances and altitudes from TRF to TMF to TDF between ca. 1°N and 2°S, and this region of southwestern and southern Ecuador is the only place the species is found in dry forests.

Although the FAO (2012) ecozones are somewhat based on Holdridge (1967) life zones that have been widely used in tropical America, specific application of terms will not necessarily correspond with those used in the literature associated with this species. For example, Meyer and Wilson (1973) recorded the ecological distribution of *R. annulata* in eastern Honduras as confined to the Tropical Moist formation, also referred to as Lowland Moist Forest (McCranie 2018); however, as mapped by FAO (2010), the ecozone with distributional records of *R. annulata* in Honduras is Tropical Rain Forest. Similarly, in Costa Rica, Savage (2002) referred to the occasional presence of this species in Premontane Wet Forest in addition to the Tropical Wet and Moist Forest formations, but all these forest areas below ca. 1000 m are mapped as the Tropical Rain Forest ecozone (FAO 2010, 2012).

Figure 8. Adult male *Rhinoclemmys annulata* from vicinity of La Virgen, Heredia Province, Costa Rica. Photo by Michael Redmer.

Habitat used by *R. annulata* has been most thoroughly studied by Moll and Jansen (1995) in Tortuguero National Park, Costa Rica, within the TRF ecozone (Tropical Wet Forest life zone of Holdridge 1967). There, the dominant rain forest habitat is composed of diverse evergreen tree species with well-developed canopy (ca. 45–55 m), subcanopy (ca. 30–40 m), and understory (10–25 m) layers. Light intensity is low and ground vegetation is sparse, except in scattered tree-fall zones where increased light penetration supports abundant growth of early successional plant species. Within the dominant rain forest matrix, the species is also found in swamp forest characterized by different tree species that develop where soil drainage is poor (Moll and Jansen 1995). At a site in Esmeraldas Province, Ecuador, *R. annulata* was reported in proximity to a forested stream and swamp (Ortega-Andrade et al. 2010a).

Rhinoclemmys annulata inhabits lowland forests from near sea level up to ca. 920 m elevation (Savage 2002; Leenders 2019). An older reference to an upper elevational limit of 1500 m for *R. annulata* in Costa Rica by Ernst (1983), repeated by Ernst and Barbour (1989) and Acuña Mésen (1993, 1998), is considered erroneous due to mistaken georeferencing of an old locality description (Savage 1970, 2002).

The movements of three adult males and three adult females were monitored in Tortuguero National Park, Costa Rica, for four weeks between February and March (the dry season) in 1991 by Moll and Jansen (1995). These six animals inhabited overlapping home ranges that included portions of tropical wet forest, swamp forest, and tree-fall areas (described above). The mean home range area was 2.86 ha, and the total area encompassed by the home ranges collectively covered 8.42 ha. Of the total home range area, 63.4% was characterized as tropical wet forest, 33.9% as swamp forest, and 2.7% as tree-fall area. In 504 encounters with telemetered turtles, 42.1% were located in tropical wet forest, 20.2% were in swamp forest, and 37.7% were in tree-fall areas. All individuals were encountered in all three habitat types, and in more than one of the three tree-fall areas present within the study area. Multiple individuals were sometimes present at the same time in the latter areas. Fruit juice stains on the jaws of some of these individuals in the tree-fall areas suggested frequent use of this habitat. In addition, there were abundant *R. annulata* feces found on the substrate in this habitat. Stomach contents obtained by flushing also contained fruits and vine seedlings found growing in tree-falls (see Diet below). Collectively, these observations suggested tree-fall areas were frequently and preferentially used, and were important as foraging habitat for Costa Rican populations of *R. annulata* during the dry season (Moll and Jansen 1995).

Courtship and Reproduction. — Observations of courtship behavior in captivity are fragmentary and scattered across multiple range countries: Panama (Mittermeier 1971b), Colombia (Castillo Flor et al. 2013), and Ecuador (Grünewald 2015). Other authors presumably also made observations of captives in Costa Rica (Acuña Mésen 1993, 1998; Leenders 2019). In addition, Pritchard (1979) reported additional observations by Mittermeier that were not included in Mittermeier (1971b). Courtship and mating usually takes place on land (Grünewald 2015, Leenders 2019), although Castillo Flor et al. (2013) reported courtship in the water during observations at the Cali Zoo. The timing of courtship has been associated with rainfall and the rainy season (twice/year in some locations), but most authors did not specify the time of year. Mittermeier (1971b) noted that copulatory attempts among captives on Barro Colorado Island, Panama, were especially common during heavy rains while there from September–December. Captive observations in Guayaquil, Ecuador, a part of the range with a drier, more seasonal climate, noted that males were particularly active in attempting to mate after a rain towards the end of the rainy season (ca. April–May; Grünewald 2015).

Figure 9. Captive-hatched and raised *Rhinoclemmys annulata* in Guayaquil, Ecuador—a near-hatchling on the right with two 1-year-olds to the left. Photos by Ferry Grünewald.

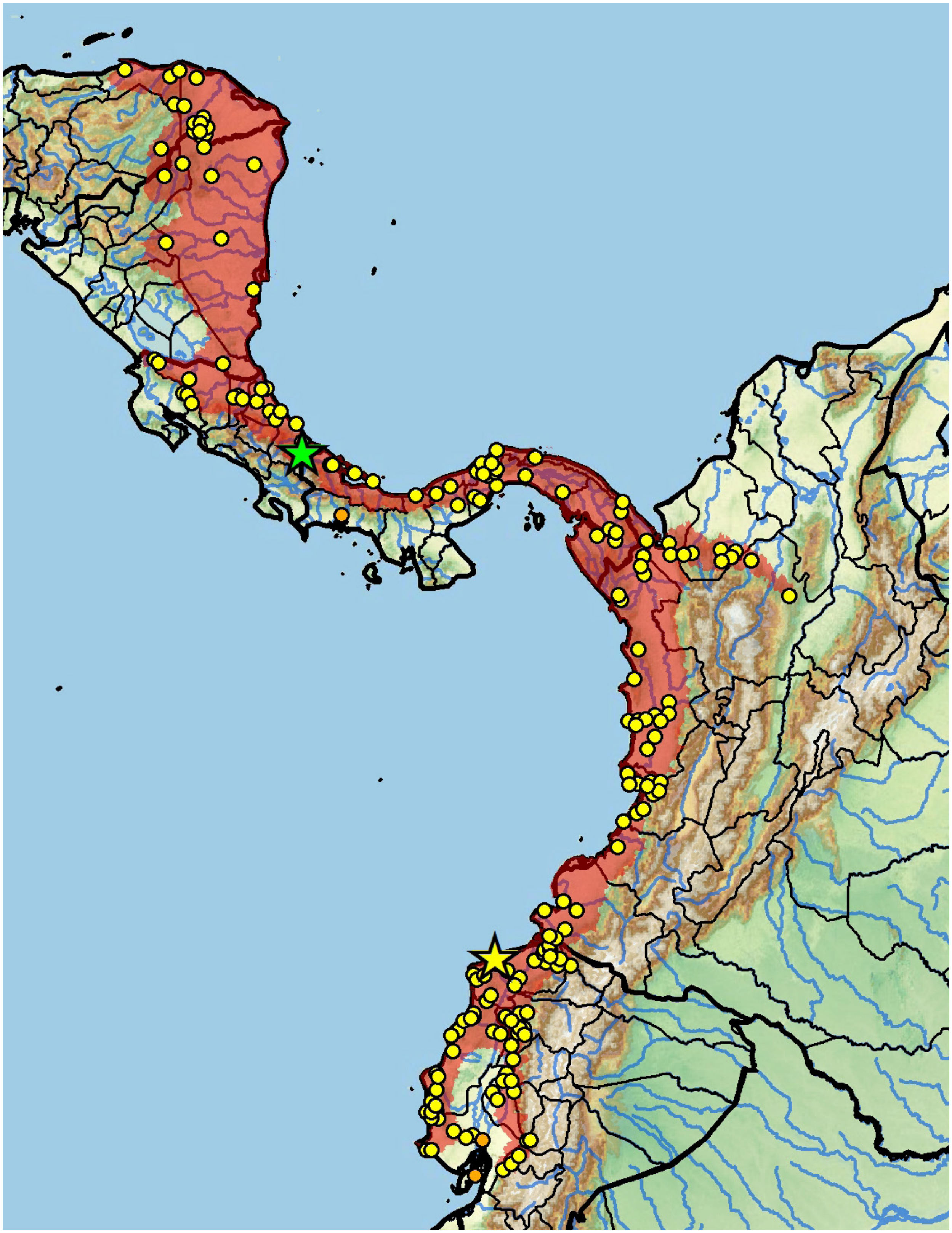

Figure 10. Distribution of *Rhinoclemmys annulata* in southern Central America and northern South America (Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador). Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), other more recent literature records (see TTWG 2021), and authors' additional data; orange dots = possible trade or translocated specimens; yellow star = *Geoclemmys annulata* Gray 1860 type locality; green star = *Chelopus gabbii* Cope 1875 restricted type locality. Distribution based on fine-scaled 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 based on Buhlmann et al. (2009), TTWG (2017, 2021), and data from authors and other sources.

Figure 11. Habitat of *Rhinoclemmys annulata* in Tortuguero National Park, Costa Rica. Photo by Michael Redmer.

Figure 12. Treefall habitat in Tropical Rain Forest, Isla Palma, PNN Uramba Bahía Malaga, Valle del Cauca, Colombia, admitting abundant sunlight after this large tree blew down, creating a shallow depression over the rocky substrate, the shallow root disk sticking up vertically ca. 5 m, and the tree stem extending to the right. Photo by John L. Carr.

Courtship starts with the approach of a male toward the female. Acuña Mésen (1993, 1998) noted that during courtship, a male may follow a female for long distances. Castillo Flor et al. (2013) reported a significant amount of social behavior time devoted to exploratory sniffing (27%) and chin resting (16%), but did not specifically associate the behaviors with courtship (9%). When the male mounts the female, he tries to bite her head and insert his tail under her carapace (Pritchard 1979; Acuña Mésen 1993, 1998). Grünewald (2015) mentioned the male mounting the female and biting her head and neck so she would stop moving, then attempting copulation. Castillo Flor et al. (2013) also reported the male biting the female during copulation. Leenders (2019) reported wounds to the female's neck and anterior carapace due to the male biting and hanging on with his claws while copulating. After several minutes of attempted copulation, the male may "froth at the mouth" (Pritchard 1979:178) or salivate (Ernst and Barbour 1989; Acuña Mésen 1993, 1998) over the female's head.

Figure 13. Disturbed, Tropical Dry Forest habitat in the Chongón-Colonche Hills west of Guayaquil, Guayas Province, Ecuador. *Left*: wet season, *right*: dry season, same location. Photos by Ferry Grünewald.

Grünewald (2015:fig.19) has a photo showing a male and female in copula that looks much like the 2-legged support stance illustrated by Liu et al. (2013), which is found in two other *Rhinoclemmys* species (*R. areolata*, Pérez-Higareda and Smith [1988], and *R. pulcherrima incisa*, Hidalgo [1982]).

Oviposition was reported by field informants to occur throughout the year (Medem 1962a,b), and many have followed this source (Pritchard 1979; Ernst and Barbour 1989; Acuña Mésen 1993, 1998; Savage 2002; Leenders 2019). Females excavate a small nest, or simply lay an egg on the ground and sometimes cover it with leaves (Medem 1962a,b; Moll 2010; Leenders 2019). Castillo Flor et al. (2013) recorded that a captive laid one clutch of one egg in March without digging a nest or covering the egg. Supposedly, one or two eggs are laid at a time (Medem 1962a,b; Pritchard 1979; Ernst 1983; Ernst and Barbour 1989; Acuña Mésen 1993, 1998; Savage 2002; Rueda-Almonacid et al. 2007; Leenders 2019). Medem (1962a,b) was clear in stating that his reproductive information came from local inhabitants—his own observations of specimens (n = 3 females) were presented in more detail and did not include any shelled eggs, only measurements of enlarged follicles in the ovaries (Medem 1962a).

We are not aware of any actual clutches of two eggs in *R. annulata*. Grünewald (2015) reported three 1-egg clutches laid by captives in Guayaquil starting 27 July (dry season), and the two that hatched did so in the subsequent rainy season (January–February). Similarly, Ewert (*in* Clark et al. 2001) reported 11 one-egg clutches by a single captive *R. annulata,* but not the frequency of oviposition. Ewert (1979) reported the size of an egg as 71 x 37 mm, with a mean SCL of 63.9 mm (n = 9) for hatchlings. This appears to be the source of the oft-cited hatchling size of 63 mm (e.g., Ernst and Barbour 1989; Acuña Mésen 1993, 1998; Savage 2002). Ewert (1985) later placed *R. annulata* in the group of species with a high egg-to-body mass ratio, with variation between 3.9 and 5.0% and maximum egg mass reported as 48.8 g. Iverson and Ewert (1991) reported on two eggs averaging 71.5 x 31.6 mm (and average mass of 46.8 g), the most elongate dimensions of any turtle eggs they measured (length/width ratio = 2.26).

Growth and Longevity. — There is no information available on growth in this species, but one captive individual maintained in Paraguay lived at least 30 years (H.D. Philippen, pers. comm.).

Behavior. — This species is diurnal (Park et al. 1940; Medem 1962a; Moll and Jansen 1995; Moll 2010; McCranie 2018), mainly active from 0700 to 1200 hrs (Medem 1962a), specifically with an earlier peak from 0700–1000 hrs (Mittermeier 1971b). Park et al. (1940), in a study in captivity, also reported a morning peak, but there was fairly sustained activity between ca. 0900 to 1500 hrs. Only in Ecuador has there been a mention of nocturnal activity in the field, but with no further details (Ortega-Andrade et al. 2010a). In Colombia, Castillo Flor et al. (2013) reported the peak of diel activity at 2000 hrs in the Cali Zoo; however, the entire diel activity cycle was not presented, nor were the methods of observation after dark explained. Several authors have reported increased activity associated with and immediately following heavy rain (Mittermeier 1971b; Moll and Jansen 1995; McCranie 2018). In addition, McCranie (2018) reported instances of activity on the forest floor associated with rain in May, July, August, October, and December, as well as activity during dry periods in February and May. Piles of dead leaves and vine tangles or weedy vegetation were chosen as resting places when not active (Mittermeier 1971b; Ortega-Andrade et al. 2010b). The species may also choose locations between the buttresses of large trees where leaf litter accumulates (Medem 1956; Whitfield and Pierce 2005), or hidden around tree falls (Ortega-Andrade et al. 2010b).

In captive circumstances in Colombia and Ecuador, respectively, Castillo Flor et al. (2013) and Grünewald (2015) reported a significant amount of time spent basking, particularly during the morning hours. There was also an observation of a wild caught animal basking on a small log surrounded by water in Honduras (McCranie 2018). Castillo Flor et al. (2013) recorded a substantial proportion of time spent resting or standing in water in a zoo enclosure; however, the extent to which this reflects the zoo being located in a much drier, more strongly seasonal climatic zone than where the turtles originated, is not known.

Diet. — *Rhinoclemmys annulata* is considered strictly herbivorous (Medem 1962a). Mittermeier (1971b) observed free-ranging adults on Barro Colorado Island, Panama, and identified a number of plants eaten, including ferns, shrub seedlings, and vines; all were seedlings or small plants up to about 20 cm in height.

The species was also found to be completely herbivorous in Tortuguero National Park, Costa Rica, by Moll and Jansen (1995). They identified a variety of small pteridophytes, vines, fruits and seeds, tree seedlings, tree leaves, and miscellaneous unidentified vegetation in the diet during the dry season. The plants utilized were characteristic species of the three habitats (i.e., tropical wet forest, swamp forest, and tree-fall areas) represented in the study area.

Rhinoclemmys annulata eats fallen fruits in small banana plantations, thereby possibly reducing the proliferation of flies and other insects (Acuña Mésen 1993, 1998). Moll and Jansen (1995) determined that seeds from the fruits of several plants characteristic of tree-fall areas (*Jacaratia dolichaula*, *Solanum siparunoides*, *Faramea suerrensis*, and *Miconia affinis*) and from *Ficus* spp. of tropical wet forest were capable of germination after passage through digestive tracts of *R. annulata* (passage of ingested foods usually took 24–48 hrs). These data and regular movements between suitable habitats (see above) suggest that *R. annulata* probably functions as a seed disperser for these species of plants (Falcón et al. 2020).

Parasites. — There have been two observations of a leech on specimens of *R. annulata*; one collected in Panama (Ernst and Ernst 1977) and identified as *Placobdella* sp. and the other in Costa Rica, specifically *P. ringueleti* (Oceguera-Figueroa and Pacheco-Chaves 2012).

The species has also repeatedly been observed with ticks. The association between carapace pits and *Amblyomma* sp. ticks in *R. annulata* has been known for nearly a century on Barro Colorado Island, Panama (Allee and Allee 1925; Allee 1926). Schmidt (1946) reported all Panamanian specimens were parasitized by ticks, or had been, as evidenced by the pitting on the carapace. Similarly, Mittermeier (1971b) found all specimens on Barro Colorado Island were parasitized by ticks on the shell, with some also on the soft tissue of the limbs. Ernst and Ernst (1977) reported the tick *Amblyomma sabanerae* from *R. annulata* in Panama and Colombia, and Evans (1947) reported *A. humerale* (as *A. humerli* Koch) from Panamanian specimens. Also, Fairchild et al. (1966) reexamined material previously identified as *A. humerale* by Fairchild (1943) and corrected the identification to *A. sabanerae*. *Rhinoclemmys annulata* from Tortuguero, Costa Rica, also carried *A. sabanerae* (Moll, unpubl. data). Medem (1956, 1962a,b) reported ticks found primarily near the first two costal scutes and referred them to *A. crassum*. Garcés-Restrepo et al. (2013) reported *A. sabanerae* from *R. annulata* in the Department of Valle del Cauca, Colombia. López Valencia (2017) referred to specimens of *A. sabanerae* from *R. annulata* from the departments of Chocó and Antioquia. Acevedo-Gutiérrez et al. (2020) recently reviewed these records of *A. sabanerae* in Colombia. Unidentified ticks were found on the carapace of all Honduran adults of *R. annulata* reported by McCranie (2018). However, as detailed in Guglielmone et al. (2021), the tick species *A. crassum*, *A. humerale*, and *A. sabanerae* are very similar, which makes it seem doubtful that there are any legitimate records of *A. crassum* and *A. humerale* for the host *R. annulata*. Adult specimens in particular of *Amblyomma sabanerae* are closely associated with numerous species of *Rhinoclemmys* as hosts (Guglielmone et al. 2021).

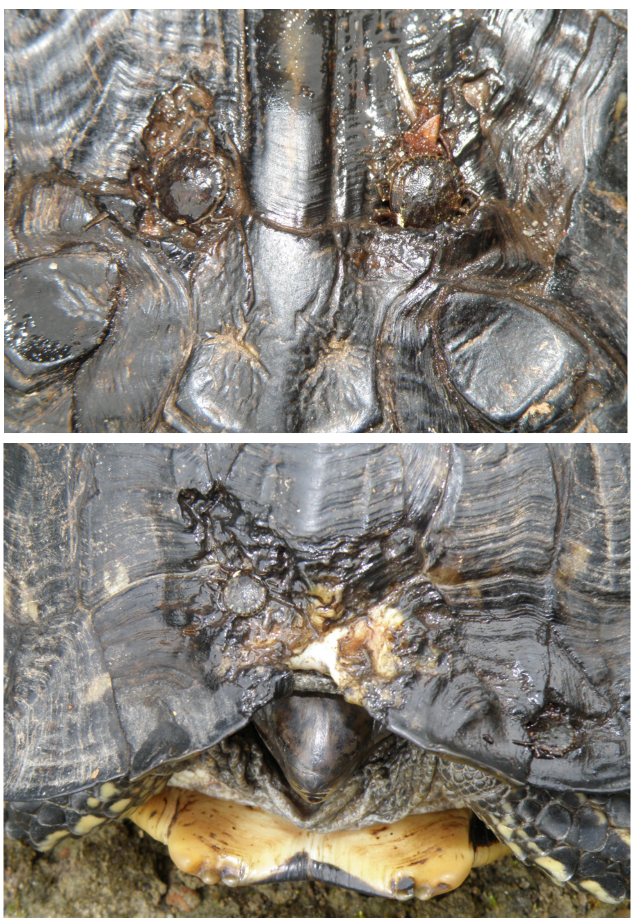

Figure 14. Adult female *Rhinoclemmys annulata* from Isla Palma, Valle del Cauca, Colombia with 3 embeded *Amblyomma sabanerae* ticks on its carapace with resultant carapacial pitting and bone exposure. Photos by John L. Carr.

Endoparasites of *R. annulata* include nematodes and protozoans. Dyer and Carr (1990) reported two helminth species of Nematoda from *R. annulata* in Ecuador: *Falcaustra tikasinghi* (Kathlaniidae) and *Atractis caballeroi* (Atractidae), now reclassified as *Klossinemella caballeroi* (Bursey and Flanagan 2002). The same two species of nematodes were reported from *R. annulata* in Costa Rica, as was *Sauricola sauricola* (Strongylidae) and the new species *Falcaustra guanacastensis* (Bursey and Brooks 2011). Two other nematodes were reported from *R. annulata* in a wildlife rescue center in Cali, Colombia: a *Strongyloides* sp. (Strongylidae) and a species of Ancylostomatidae (hookworm) (Copete Sierra et al. 2013). Protozoan parasites identified from the feces of a single Costa Rican *R. annulata* were ciliates (Ciliophora), *Isospora* sp. (Apicomplexa: Eimeriidae), and trichomonads (Metamonada: Trichomonadida) (Hartdegen et al. 1999).

Predators. — Falcons, hawks, and vultures have been reported as predators of *R. annulata* eggs or hatchlings (Acuña Mésen 1993, 1998).

Population Status. — There are only limited population data from surveys of this species across its range. Acuña Mésen (1993) considered *R. annulata* one of the rarest turtles in Costa Rica; however, Moll and Jansen (1995) considered it to be common in Tortuguero National Park, Costa Rica, although cryptic and difficult to observe. A study of the leaf litter herpetofauna at the La Selva Biological Station in Costa Rica presented data from a tropical moist forest site; extrapolating the number of *R. annulata* encountered in their plots yielded a density of 11.2 specimens per hectare (Whitfield and Pierce 2005).

Several authors have presented categorical indications of abundance for a number of sites where *R. annulata* is present. In Honduras, both Wilson and Townsend (2006) and Ramos Galdamez et al. (2019) categorized the species as "infrequent" in the respective areas studied. Guyer (1994) considered *R. annulata* in the "rare abundance" category at La Selva in Costa Rica. Two different assessments are available for the central region of Panama: Rand and Myers (1990) placed the species in the "infrequent abundance" category and Ibáñez et al. (1994) used a different categorization as "usually found if you look in the right habitat at the right time." In Ecuador, Yánez-Muñoz et al. (2010) reported the frequency of encounters as *bajo* (low), and Arteaga (2022) referred to the species as rare.

Threats to Survival. — Modern-day indigenous groups in Costa Rica apparently do not consume *R. annulata* or use its shell as an ornament (Acuña Mésen 1993, 1998) as may have occurred in the past. Mittermeier (1971a) reported specimens of *R. annulata* kept as pets in the San Blas archipelago of eastern Panama by indigenous Kunas, and that they apparently only rarely ate this species. Rural Afro-Hispanic and indigenous populations along the Pacific coast of Valle del Cauca, Colombia, utilized this species as a food source, although in lesser numbers than other turtle species (Corredor et al. 2007). Using *R. annulata* as pets and an occasional food source by local Afro-Hispanic and indigenous populations was also reported for Esmeraldas Province in Ecuador (Altamirano-Benavides et al. 2010; Ortega-Andrade et al. 2010b). Within Esmeraldas, Carr et al. (2014) reported on capture techniques and uses of *R. annulata* and the entire turtle fauna by rural Afro-Hispanic and indigenous communities in the Río Cayapas-Santiago basin. Two additional threats identified with respect to *Rhinoclemmys* species in general in the department of Valle del Cauca, Colombia, were the pet trade and the use of shells to make handcrafted ornamental objects (Corredor et al. 2006, 2007). An inventory of a wildlife rescue center in Cali, Colombia, in 2004, where much of the pet turtle traffic ends, registered only one *R. annulata* as compared to 150 of each of the two most-commonly trafficked species, *R. melanosterna* and *Kinosternon leucostomum* (Corredor et al. 2006). Using turtle shells to handcraft ornamental objects for sale to tourists was a common practice in the Pacific coast port city of Buenaventura, Colombia, although of the five local turtle species, including three *Rhinoclemmys* spp., *R. annulata* was the only turtle species not found in ornament form (Corredor et al. 2007).

In country-wide surveys of seizure data for non-marine turtles in Colombia, *Rhinoclemmys* was reported as the fifth most trafficked genus; making up 2.7% (of 6,214) for the 7 years 2003–2009 (Bonilla et al. 2012) and 2.9% of the number (5,882) identified for 2005–2009 (Arroyave Bermudez et al. 2014). Numbers of individuals were relatively stable by month over the course of each year, but there was a 22-fold increase in *Rhinoclemmys* traffic interdicted between 2005 and 2009 (Arroyave Bermudez et al. 2014). These percentages and the quality of the underlying data (Arroyave Bermudez et al. 2014) do not permit estimation of the numbers of *Rhinoclemmys* internally trafficked within Colombia, but based on the Valle del Cauca data it would be expected that *R. annulata* would form but a tiny portion of the entire *Rhinoclemmys* trade (Corredor et al. 2006, 2007).

Similarly, in Ecuador, limited information on domestic trade is available from two areas in the Pacific coastal region of Ecuador. Subía-Ramos (2018) reported the presence of *R. annulata* in a wildlife rescue center in Guayas Province, but no numbers, and Pozo Rosales (2021) recorded three *R. annulata* of 328 reptiles in a wildlife rescue center in Santa Elena Province. Trade figures by the Ministry of Environment (Ministerio del Ambiente) for *R. annulata* in Ecuador vary annually out of the total number of recovered reptiles (5 of 132 in 2003, 4 of 92 in 2006, 7 of 155 in 2007, 1 of 62 in 2008, 1 of 879 in 2011 (MAE 2012), and 22 of 436 in 2014 (MAE 2015); however, the use of many different common names for the same species in their reports causes some concern about identification. Also, *R. annulata* was the only one of five Pacific coastal plain turtle species not included in the identification guide for animals in the wildlife trade within Ecuador (MAE 2017).

In recent reviews of the international reptile and turtle trade, *Rhinoclemmys* usually does not appear because it was not listed on CITES (Herrel and van der Meijden 2014, Auliya et al. 2016, Luiselli et al. 2016). The study by Ceballos and Fitzgerald (2004) mentioned imports into the United States (Texas) of *Rhinoclemmys* spp. and Marshall et al. (2020) listed seven species of *Rhinoclemmys* in international trade, but not *R. annulata*. Only in the recent proposal to list the genus *Rhinoclemmys* on CITES Appendix II (CITES 2022) was there a mention of *R. annulata* in trade — six specimens offered for sale in Germany out of 125 total *Rhinoclemmys* listings (5%) online. We also learned of a recent importation of *R. annulata* into the USA from a range country that was apparently mislabeled as another species of *Rhinoclemmys*.

Tropical forests that covered most of the range of this species have been heavily impacted by human activities, particularly over the last 50–60 years. Deforestation in Costa Rica and western Ecuador was particularly extensive and rapid up to about 1990 (e.g., Dodson and Gentry 1991; WRI 1992). Since 1990, regular updates at a global scale have focused attention on forest losses and made data more readily available (FAO 2020, FAO and UNEP 2020, GFW 2023). From 1990 to 2020, Costa Rica had a net increase in forest cover of 4.4% since the 1990 baseline and the other five range countries experienced tree cover loss of 8.5 to 46.7% (FAO 2020); however, these figures are for the countries as a whole, not specific to the forests within the range of *R. annulata*. One range area in the TRF ecozone, the Darién-Chocó Forest extending south from southeastern Panama to Ecuador, has been recognized as a deforestation hotspot for the period 2004–2017 (Pacheco et al. 2021). In Colombia, conversion of the rainforest habitat in areas occupied by this species has increased as a consequence of cattle ranching, small farms, proliferation of illegal crops, effects of uncontrolled mining activities, and planting of extensive oil palm monocultures (Arboleda Montaño 2008; Andrade 2011; Bermúdez Rivas et al. 2014; Otálora Sechague 2021, Pacheco et al. 2021).

A recent quantitative study of deforestation in Ecuador focused on protected areas and found proximity to agriculture was the most significantly correlated factor related to deforestation (Kleemann et al. 2022) in coastal Ecuador, just as it was for the entire country. In a study specifically of tropical dry forest in western Ecuador, Rivas et al. (2021) found a reduction of 27% in the area of TDF from 1990 to 2018 and a deterioration in the degree to which forest patches were fragmented. Both recent studies in Ecuador found increased deforestation and patchiness occurring in protected areas, although usually less so than in areas outside of protected areas (Rivas et al. 2021; Kleemann et al. 2022). In general, human population growth and economic circumstances are drivers of the environmental changes of habitat destruction and degradation.

The two most important drivers of deforestation for Latin America as a whole were commercial scale agriculture (ca. 67%), such as livestock ranching and African oil palm plantations, and second was small scale, subsistence level farming (ca. 25%) (FAO and UNEP 2020). The specific effects of deforestation and forest fragmentation due to conversion to anthropogenic activities such as farming and ranching on populations of *R. annulata* are unknown, but probably highly impactful and in need of additional study.

An Environmental Vulnerability Score (EVS) has been advocated by some as an alternative to the IUCN Red Listing process for a conservation assessment that is fast, simple, and inexpensive (Wilson and McCranie 2004). In a reassessment of Central American reptile species, Johnson et al. (2015) listed *R. annulata* with an EVS score of 12, which they considered a Medium value (scale = 3–20). The score represents the sum of three species attributes: geographic distribution (scores of 1–6), ecological distribution (1–8), and the degree of persecution (1–6). The component scores yielding a total score of 12 for *R. annulata* were: 2 (most of the geographic range is in Central America), 7 (found in 2 ecological formations), and 3 (a terrestrial species usually ignored by humans). Later, McCranie (2018) reassessed the species with the same overall score, but with component scores of 1, 8, and 3, respectively.

Conservation Measures Taken. — *Rhinoclemmys annulata* undoubtedly benefits from general measures against domestic commercial-scale collecting in some range countries, e.g., in Colombia, Costa Rica, and Ecuador. All *Rhinoclemmys* spp., including *R. annulata*, were recently (November 2022) adopted by the CITES Parties for inclusion in Appendix II, which came into effect in February 2023. The species did not receive a rating in the first IUCN/SSC Action Plan (TFTSG 1989), but was assessed as Near Threatened (NT) for the IUCN Red List by the TFTSG (1996) and then provisionally assessed by the TFTSG as Data Deficient (DD) in 2011 and again in 2018 (Rhodin et al. 2018; TTWG 2021).

National-level Red List exercises have resulted in several different assessments among the four countries where completed. The first Colombian Red List status for *R. annulata* was Data Deficient (DD) (Castaño and Medem 2002), but the more recent list assessed it as Least Concern (LC) (Morales-Betancourt et al. 2015). In Costa Rica, the species is listed as LC with stable populations by Chaves et al. (2014). The Ecuador Red List status is Endangered (EN) (Carrillo et al. 2005; Torres-Carvajal et al. 2019). The Nicaraguan Red List status is LC (Robleto-Hernández and Gutiérrez-Rodríguez 2017).

Protected areas with populations of *R. annulata* should contribute significantly to conservation of the species. For Colombia, Forero-Medina et al. (2014) listed two national parks with confirmed presence of this species, with the possibility of occurrence in seven national parks based on distributional modeling. The species is present in at least two Colombian Pacific coast parks, PNN Utría (Ferwerda 2008) and PNN Uramba Bahía Málaga (Giraldo et al. 2012, 2014).

In Costa Rica, the species is known from Tortuguero National Park (Moll 2010), Area de Conservación Guanacaste (Bursey and Brooks 2011), La Selva Biological Station (Scott et al. 1983, Guyer 1994), La Suerte Biological Field Station (Lewis 2001), and Pacuare Nature Reserve (Abellá et al. 2008).

Within Ecuador, distributional records indicate that this species is likely present in Machalilla National Park (Almendáriz and Carr 2012), Cotacachi-Cayapas Ecological Reserve, Bilsa Biological Station (Ortega-Andrade et al. 2010a), and several smaller biological stations and private reserves (Arteaga 2022).

In Honduras, *R. annulata* is reported from PN Patuca (Nicholson et al. 2000; McCranie 2018) and the Río Plátano Biosphere Reserve (McCranie 2018; Ramos Galdamez et al. 2019).

In Nicaragua, the species is recorded from the Bosawas Biosphere Reserve (Köhler 1999) and Reserva Biológica Indio Maíz (FUNDAR-SERBSEN 2002).

For Panama, *R. annulata* has been reported from several national parks, including PN Chagres (Ibáñez et al.1994), PN Altos de Campana, PN Portobelo (Fuentes Magallón et al. 2021), and Barro Colorado Nature Monument (Schmidt 1946; Mittermeier 1971b).

Conservation Measures Proposed. — In a review of the state of knowledge of Colombian turtles (Forero-Medina et al. 2016), *R. annulata* was found to be in the lower quartile of the range of values with respect to basic data pertinent to conservation biology (e.g., population, reproductive, and spatial ecology). Other areas of research and actions that have been proposed for continental turtles in general would also apply to *R. annulata*. Virtually all information on this species is anecdotal in nature and comes from non-targeted herpetofaunal surveys and inventories of particular sites, or entire countries. There is a lack of surveys in any range country explicitly targeted for assessing the status of the species, such as population density in optimal, protected habitat. We suggest identification of a small number of prospective sites for survey work in order to identify a site or sites that would be suitable for population monitoring via a capture-mark-recapture study to begin to understand demographic characteristics of a population, and that could serve as the site of a spatial ecology study to contribute to knowledge of its specific habitat use and movement patterns in different habitat types and in relation to transformed habitats. Additional work on the species' trophic ecology would help understand how it might adapt to modified habitat, if at all, given its heavy reliance on low-growing forest floor and understory vegetation. Field work should also include evaluation of the commercial and subsistence use of turtles via survey instruments (Corredor et al. 2006; Forero-Medina et al. 2016).

Other essential research areas to better assess the conservation status of *R. annulata* include reproductive biology, genetics, and behavior in an *ex situ* setting. Genetics work based on field collected samples would assist in understanding whether or not there is any genetic structuring within the species' large distribution area. Reproductive biology and aspects of behavior could be studied in a controlled, captive situation such as at the Cali Zoo in Colombia where a captive colony has been maintained for more than a decade (Corredor et al. 2007; Castillo Flor et al. 2013). Also, the Parque Histórico Guayaquil in Ecuador had a plan to reproduce the species for possible conservation efforts in the Pacific coastal region (Grünewald 2015; Ampuero Falquez and Molina Moreira 2018). Any such efforts should have close monitoring of individuals in order to acquire the maximum possible information on reproductive periodicity, mode of sex determination, and other unknown aspects of the species life history that would be more difficult in the field. Other countries are certain to have interested zoos as well. These aspects of the biology and threats to populations of *R. annulata* are largely unknown throughout the six range countries.

This species does not appear to be common in the international pet trade (see above); however, it does enter into local trade at least in Colombia and Ecuador (e.g., Corredor et al. 2007; Subía Ramos 2018; Pozo Rosales 2021). Now that all *Rhinoclemmys* are listed on CITES Appendix II, *R. annulata* will be subject to international trade monitoring. The prudent move would be for management authorities in range countries to set export quotas to zero.

Captive Husbandry. — *Rhinoclemmys annulata* is inoffensive and even recently captured individuals will not bite (Medem 1962a; Mittermeier 1971b; McCranie 2018). Captive specimens are known to consume banana, plantain, papaya, apple, raspberry, mango, guava, tomato, avocado, cacao fruit, cantaloupe, pepper, lettuce, endive, malanga leaves (Aracaeae), bread, and cat food (Medem 1962a,b; Mittermeier 1971b; Acuña Mésen 1993; Grünewald 2015). Ewert (1985) reported that reproductively active *Rhinoclemmys* spp. did well with a dietary supplement of 200 IU/g of Vitamin A. He successfully maintained and reproduced *R. annulata* in captivity in an aquarium tilted so that part of it was dry while the lower end contained a shallow pool of water. A potential problem with reproductive females is the large size of the egg (Pritchard 1979). Ewert (1985) reported upon a specimen in which an egg broke in the cloaca during an attempt to hormonally induce oviposition.

Current Research. — We are not aware of any current field research taking place on this species.

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