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Podocnemis erythrocephala (Spix 1824) – Red-headed Amazon River Turtle, Irapuca

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Summary. – The Red-Headed Amazon River Turtle, *Podocnemis erythrocephala* (Family Podocnemididae), is the smallest species in its genus, with a maximum straight carapace length of 322 mm in females and 244 mm in males. It inhabits primarily smaller blackwater streams and flooded forests rather than main river channels. It is primarily herbivorous and nests on sandy beaches associated with open shrub or grassland along black or clearwater rivers, streams, and lakes. Females produce up to four clutches per year, with 2–18 eggs per clutch. The species is threatened by unregulated hunting of adults and egg gathering at the nesting beaches for food and black market sales, in spite of national laws protecting the species in each of the three countries where it occurs.

Distribution. – Brazil, Colombia, Venezuela. Occurs primarily in the Rio Negro Basin of Brazil and neighboring Venezuela and Colombia, but also in the lower Rio Solimões and upper Rio Amazonas basins of Brazil and the upper Orinoco Basin of Venezuela and Colombia.

Synonymy. – *Emys cayennensis* Schweigger 1812 (partim, misidentified type), *Chelys (Hydraspis) cayennensis*, *Chelys cayennensis*, *Hydraspis cayennensis*, *Podocnemis cayennensis*, *Emys erythrocephala* Spix 1824, *Podocnemis erythrocephala*, *Hydraspis expansa erythrocephala*, *Chelys (Hydraspis) erythrocephala*, *Chelys erythrocephala*, *Emys bitentaculata* Cuvier *in* Gray 1830 (nomen nudum et dubium), *Hydraspis bitentaculata* Gray 1831 (nomen oblitum et dubium), *Podocnemis agassizii* Coutinho *in* Göldi 1886, *Podocnemis coutinhii* Göldi 1886 (nomen novum).

Subspecies. – None currently recognized.

Status. – IUCN 2014 Red List: Vulnerable (VU A1bd; assessed 1996); TFTSG Draft Red List: Vulnerable (VU, assessed 2011); Brazil: Near Threatened (NT); Colombia: Vulnerable (VU A1acd+2cd); CITES Appendix II (as *Podocnemis* spp.).

Figure 1. Adult male *Podocnemis erythrocephala* from Rio Jufari, a tributary of the Rio Negro, Amazonas, Brazil. Photo by Richard C. Vogt.

Figure 2. Adult female *Podocnemis erythrocephala* from Rio Jufari, a tributary of the Rio Negro, Amazonas, Brazil. Photo by Richard C. Vogt.

Taxonomy. — *Podocnemis erythrocephala* was first described as *Emys erythrocephala* by Spix (1824) from a specimen obtained along the Rio Solimões, Brazil. Vanzolini (1983) believed that the specimen was not from the Rio Solimões, and since no one has ever collected a specimen from the mainstream Solimões, the locality record is perhaps an error. However, the original type locality recorded by Spix (1824) when he visited Tefé and the Rio Solimões was "*Habitat in aquis ripariis fluminis Solimoens, Jurura Campeva cognominata*", indicating that the native Kambeba (= Campeva) tribespeople that lived along the upper Solimões near Tefé at the time, had a vernacular name for the species (*jurura*), and it probably occurred in smaller regional blackwater tributaries of the Solimões.

The Red-headed Amazon River Turtle, now locally known in the vernacular as the *irapuca*, is a monotypic species that was previously widely and erroneously referred to as *Podocnemis cayennensis* (Schweigger 1812) until its nomenclatural status was clarified by Mittermeier and Wilson (1974). Neither of its other unequivocal synonyms, *Podocnemis agassizii* Coutinho *in* Göldi 1886, or *P. coutinhii* Göldi 1886, were ever widely used for this species.

Frair et al. (1990), using serum electrophoresis, first demonstrated the close relationships of the currently recognized species of *Podocnemis*, separating out *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* from the *Podocnemis* clade. Iverson

Figure 3. Plastron of male *Podocnemis erythrocephala* from Rio Unini, Amazonas, Brazil. Photo by Virginia C.D. Bernardes.

Figure 4. Adult male *Podocnemis erythrocephala* from Rio Itú, a tributary of the Rio Negro, Amazonas, Brazil. Photo by Richard C. Vogt.

Figure 5. Adult female *Podocnemis erythrocephala* from Amazonas, Brazil. Photo by Russell A. Mittermeier.

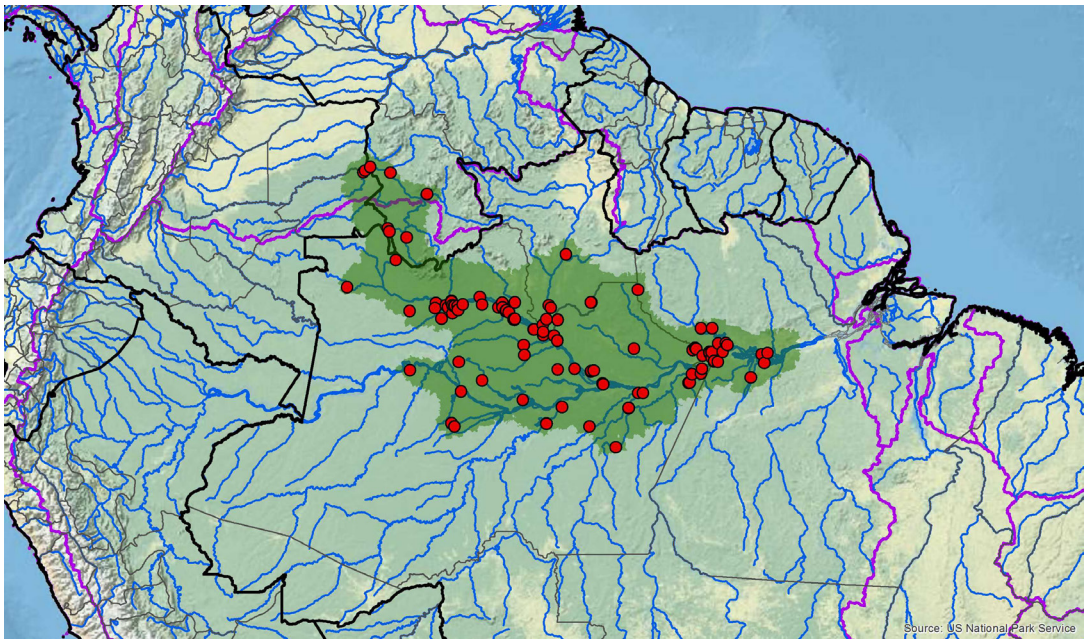

Figure 6. Distribution of *Podocnemis erythrocephala* in Brazil, Colombia, and Venezuela in northern South America. Purple lines = boundaries delimiting major watersheds (level 3 hydrologic unit compartments – HUCs); red dots = museum and literature occurrence records based on Iverson (1992) plus more recent data, and the authors' personal data; green shading = projected historic native distribution based on GIS-defined level 10 HUCs 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 2014), and adjusted based on authors' subsequent data.

et al. (2007) presented a proposed phylogeny of the Podocnemididae based on morphology and genetics. A molecular phylogeny of the Podocnemididae (Vargas-Ramírez et al. 2008) proposed that in the genus *Podocnemis*, *P. unifilis* + (*P. erythrocephala* + *P. lewyana*) were supported as a clade. Reid et al. (2011), using molecular DNA barcoding, also found *P. erythrocephala* and *P. lewyana* to be sister taxa. These results are in striking contrast to the relationship proposed using skull morphology: *P. vogli* (*P. lewyana* (*P. uniflis* (*P. erythrocephala* (*P. sextuberculata*) (Gaffney et al. 2011). The karyotype of *P. erythrocephala* is 2N = 28 chromosomes, of which 6 are large to medium sized, metacentric and submetacentric, and larger than 50% of the largest chromosome; 4 are large to medium subtelocentrics; 16 are small to very small metacentric and submetacentric; 2 are small acrocentric and subtelocentric (Rhodin et al. 1978).

Figure 7. Adult female *Podocnemis erythrocephala* from Rio Unini, Amazonas, Brazil. Photo by Virginia C.D. Bernardes.

Figure 8. Hatchling *Podocnemis erythrocephala* from Amazonas, Brazil. Photos by Rafael Bernhard (top) and Virginia C.D. Bernardes.

Figure 9. Flooded blackwater habitat of *Podocnemis erythrocephala* in Rio Itú, a tributary of the Rio Negro, Amazonas, Brazil. Photo by Richard C. Vogt.

Description. — *Podocnemis erythrocephala* is the smallest species in its genus, and females are larger than males. Females reach 322 mm and males 244 mm straight carapace length (CL). A series of 2342 adult females and 1077 adult males from the middle Rio Negro, Amazonas, Brazil, were captured and measured; mean CL was 258 ± 18 mm for adult females and 207 ± 15 mm for adult males, mean mass was 1490 ± 314 g for females and 786 ± 150 g for males (Bernhard and Vogt 2012). The carapace is convex, and extends posteriorly in individuals greater than 100 mm CL. There is a slight vertebral keel on the 2nd and 3rd vertebral scutes. The intergular scute is always larger than the gulars (Mittermeier and Wilson 1974). Males have a deeper and more rounded anal notch, as well as longer and thicker tails than females. Sexual dimorphism is evident once juveniles have reached 130 mm in CL (Bernhard 2010). Hatchlings of both sexes have a distinctive bright red or reddish-orange color pattern on the head. The coloration persists into adulthood in males, but in females the reddish coloration begins to fade to a dull brown at a size between 120–150 mm CL. There is a broad band of red stretching across the top of the head between the tympanic membranes, and the nostrils are similarly colored. Carapacial coloration is chestnut brown and the plastron is yellowish.

Distribution. — The center of distribution for this species is the Rio Negro basin of northwestern Brazil, with additional localities from tributaries of the Rio Amazonas, Rio Uatumã, near Manaus, to the mouth of the Rio Trombetas and Rio Tapajós near Santarém in Brazil (Mittermeier and Wilson 1974; Hoogmoed and Ávila-Pires 1990; Rebêlo 1991; Vogt et al. 1991; Basto-Neves and Nobuo Yuki 2000). There is also a record from the Rio Solimões, from Tefé, MCZ 3413, which is suspect, since Tefé was well known as a turtle commercial center so the turtle could have come from somewhere else. We have spent over 20 years doing field research with turtles in the area and have never seen or talked to anyone who has ever seen *P. erythrocephala* in this region. Localities are also known in eastern Colombia and in the Rio Casiquiare and upper reaches of the Orinoco basin in southern Venezuela (Mittermeier and Wilson 1974; Pritchard and Trebbau 1984; Iverson 1992; Castaño-Mora 1997; Castaño-Mora et al. 2003; Vogt 2008; Páez et al. 2012).

Figure 10. White sand beach nesting habitat of *Podocnemis erythrocephala* on the blackwater Rio Negro, 30 km above Barcelos, Amazonas, Brazil. Photo by Richard C. Vogt.

Habitat and Ecology. — Most known localities for *P. erythrocephala* are blackwater rivers and their affluents. Although at least one whitewater locality, Rio Branco, Roraima, Brazil, has been recorded (Mittermeier and Wilson 1974), the records for the Rio Branco are actually from blackwater tributaries (Rueda-Almonacid et al. 2007; Vogt 2008). This species also inhabits clearwater lakes and streams (Hoogmoed and Ávila-Pires 1990; Rebêlo 1991; Vogt et al. 1991). Within the Rio Negro basin, the species is most commonly found in small streams and lakes, rather than the main river channels.

Reproduction. — *Podocnemis erythrocephala* has a polyandric reproductive behavior, with multiple paternity found in 5 of 6 nests analyzed by microsatellite markers (Fantin et al. 2010). Courtship has not been observed in the wild but was described for captive animals; see Captive Husbandry below. Up to four clutches per reproductive season were laid in the Rio Itú, a tributary of the Rio Negro in Amazonas, Brazil. Estimation was made by gonadal analysis, counting and measuring oviducal eggs, vitellogenic follicles, and corpora lutea (Vogt 2001).

Nesting occurs between August and November along the Rio Negro (Mittermeier and Wilson 1974; Batistella

and Vogt 2009), and from November to January in the Rio Tapajós, Pará, Brazil (Carvalho et al. 2011). In Venezuela, in Amazonas state, the species nests in October and November (Barrio-Amorós and Narbaiza 2008), and in December along the Rio Atabapo in Venezuela (Groombridge 1982). In Colombia it nests in November-January (Castaño-Mora 1997; Castaño-Mora et al. 2003).

Nesting takes place at night during the dry season on sandy beaches covered with grass and shrubs, known locally as *campinas (*Mittermeier and Wilson 1974; Batistella and Vogt 2009). Females emerge to nest singly or in small groups (Vanzolini 1977; Castaño-Mora et al. 2003; Rueda-Almonacid et al. 2007). In the Rio Negro the first nests are dug on open white sand beaches. As the water continues falling, the turtles move farther inland, nesting in *campinas* — grassy areas with scattered shrubs and low trees up to 100 m from the river. Rarely they will nest in black soil (Bernhard, unpubl. data). Black soil in the Amazon is characterized by black color, formed from archeological middens, high in nutrients and texture from medium to high clay content (Kern et al. 2009).

Nests of *P. erythrocephala* have an elliptical shape, with one of the walls more concave than the others. The opening of the nest is circular and smaller than the egg chamber (Batistella and Vogt 2009). The depth to the first egg varies from 3 to 100 mm, and to the bottom of the nest from 70 to 225 mm (n = 119) (Batistella and Vogt 2009).

Eggs are elongate and brittle-shelled or slightly flexible (Mittermeier and Wilson 1974). Mean length of eggs is 41.5 mm (range, 30.0–49.9 mm, n = 1084), mean width is 27.4 mm (range, 19.0–33.2 mm, n = 1084), and mean mass 16.6 g (range, 9.0–23.3 g, n = 1034) (Vogt 2001; Castaño-Mora et al. 2003; Batistella and Vogt 2009). Reported clutch size is 4–8 eggs in Venezuela (Barrio-Amorós and Narbaiza 2008), 5–12 in Colombia (Castaño-Mora et al. 2003), and 2–18 in Brazil (Vogt 2001; Novelle 2006; Batistella and Vogt 2009; Carvalho et al. 2011).

Mean carapace length, plastron length, and weight measurements of 16 hatchlings from two clutches by three females from the Rio Cuieras, Rio Negro, were 38.0 mm, 31.7 mm, and 11.7 g (n = 7) and 39.7 mm, 34.4 mm, and 13.1 g (n = 9), and relative clutch mass for the three clutches was 8.9%, 9.4%, and 9.4% (Mittermeier and F. Medem, unpubl. data). Mean clutch mass of the eggs in 88 nests from the middle Rio Negro, Amazonas, was 153 ± 50 g (Batistella 2003).

The mean daily nest temperature for three nests monitored in the lower Rio Inírida in Colombia ranged from 24.6–33.17ºC in the upper part of the nest and 25.9–31.2ºC in the lower part; daily extremes of temperature were 18.1–45.2ºC (Castaño-Mora et al. 2003). In the Rio Negro, two monitored nests had mean temperatures of 29.5 and 30.4ºC, with a range of 20.1–41.1ºC (Vogt 2001). Nests incubated in the laboratory produced 100% males at an incubation temperature of 27.5 ± 0.6ºC, demonstrating that this species has temperature-dependent sex determination (Vogt 2001). Drajeske (2011) reported that incubation at the threshold temperature (30.7°C) had an effect on subsequent courtship behavior.

Incubation duration in the middle Rio Negro, Amazonas, varies from 65 to 87 days, with a mean of 76.1 days (n = 19, Novelle 2006). In the Rio Inírida in Colombia, hatchlings emerge after a mean of 90 days (range, 81–102 days, n = 24, Castaño-Mora et al. 2003). It is important to note that the number of days of incubation to the hatching of the first egg and the emergence of the first hatchling from the nest are two different measurements; the difference in the incubation times reported by Novelle (2006) and Castaño-Mora et al. (2003) could be in part due to the number of days that the hatchlings remained in the nest before emerging. Hatchlings in these two studies measured 29.5–47.4 mm in CL (n = 60) and 24.8–37.1 mm in carapace width (n = 60), and had a mass of 7.9–15.3 g (n = 59) (Castaño-Mora et al. 2003; Novelle 2006).

Diet. — Adults are primarily herbivorous, consuming aquatic plants and fallen fruits in flooded forests, but specimens have been caught with hook and line using fish as bait (Mittermeier and Wilson 1974). Rhodin et al. (1981) reported that juveniles utilize neustophagia (Belkin and Gans 1968) to harvest the fine floating particles on the surface of the water. Vogt (2001) observed that in Rio Itú, a tributary of the Rio Negro, *P. erythrocephala* feeds principally on plant material, with more than 50% of their diet composed of periphyton. They also consumed a vast number of seeds, while less than 5% of their diet was material of animal origin. Thomé-Sousa (2005) evaluated carbon isotopes ($\delta^{13}C$) in *P. erythrocephala* from the Rio Itú, finding that about 71% of the carbon assimilated came from the trees of the flooded forest (*igapó*) and 29% from filamentous algae. Sousa and Vogt (2008) studied the diet in the Rio Itú, finding 88% of the diet to be composed of seeds and plant material, and the rest made up of fish, crustaceans, insects, and unidentified matter. Stomach flushing from 11 adults in the Rio Uatumã had 96.8% plant material and 3.1% animal material by volume, 88.7 % of the plant material was fruits and seeds (Lima 2013).

The diet of *P. erythrocephala* varies along with the cycle of the dry and rainy seasons. During the dry season the species feeds predominately on periphyton, while in the high water season it feeds on fruits and seeds, principally from the families Fabaceae, Sapotaceae, Rubiaceae, Loranthaceae, and Poaceae (Vogt 2001; Santos-Júnior 2009; Bernhard unpubl. data). Animal material composed less than 5% of its diet (Vogt 2001; Santos-Junior 2009). The flooded forest is important in providing the seeds and fruits that represent 48% of the total volume of food consumed by both males and

females in the Rio Jaú (Santos-Junior 2009). One mollusk, Ampularidae sp., was found in the stomach flushing of a female, representing 0.03% of the total volume of food consumed. Although fish parts were found frequently within the stomach contents of 76% of the females and 24% of the males, this represented only 1.08% and 0.28% of the volume of food consumed by females and males, respectively. Scales, spines, and bones of the fish orders Characiformes, Siluriformes, and Perciformes were the fish parts most often found in the stomach contents. Crustaceans were found in 28% of the females and 35% of the males, representing only 0.51% and 1.03% of the volume, respectively. Even though insects occurred in 32% of the stomach contents of females and 12% of the males, this only represented 0.51% and 0.28% of the total volume, respectively. Animal material occurred in 71% of the *P. erythrocephala* studied, but represented only 3.85% of the total volume of food consumed. These small amounts of animal material may be important for contributing particular nutrients to the diet of these turtles that are lacking in the plants they consume (Santos-Junior 2009). Wetzel et al. (2012) found a new species of epizoic diatom, *Tursiocola podocnemicola*, in the stomach contents of this species from the Rio Negro.

The concentration of mercury in *P. erythrocephala* throughout the Rio Negro basin was low, similar to that of herbivorous fish, demonstrating that most of the food ingested by this species is of plant origin (Schneider et al. 2009; Burger et al. 2009).

Growth and Sexual Maturity. — Growth rates in the Rio Ayuanã, as measured by CL, were 44.11 ± 6.04 mm/yr for juveniles (n = 11), 1.47 ± 1.33 mm/yr for adult males (n = 53), and 2.57 ± 3.52 mm/yr for adult females (n = 138) (Bernhard 2010). Females reached maturity at 221.8 mm CL and males at 161 mm. Age at sexual maturity in both males and females was nine years (Bernhard 2010).

Predators and Parasites. — Natural predators of eggs and hatchlings are: red ants (*Solenopsis* sp.), termites (*Nasutitermes* sp.), fox (*Cerdocyon thous*), ocelot (*Leopardus* sp.), jaguar (*Panthera onca*), grey-headed tayra (*Eira barbara*), white-fronted capuchin (*Cebus albifrons*), paca (*Agouti paca*), agouti (*Dasyprocta agouti*), opossum (*Didelphis marsupialis*), ocaracará (*Daptrius ater*), caracaraí hawk (*Polyborus plancus*), giant ameiva lizard (*Ameiva ameiva*), crocodile tegu (*Crocodilurus lacertinus*), and tegu (*Tupinambis* sp.) (Castaño-Mora et al. 2003, Novelle 2006, Batistella and Vogt 2009). Adults are eaten by black caiman (*Melanosuchus niger*) (De La Ossa et al. 2010).

Junior-Santos (2009) found nematodes in 100% of the stomachs analyzed from the Rio Unini, and Silva (2007) found them in 89% of the *P. erythrocephala* in the Rio Ayuanã, comprising 37% of the average volume of the stomach contents. The high prevalence of nematodes may indicate their importance in the digestion of plant material (Bjorndal and Bolten 1990). Trematodes were also observed in individuals from the Rio Unini (Junior-Santos 2009). Lima (2013) found trematodes present in 27% of the individuals of *P. erythrocephala* and 14.6% of *P. expansa* in the Rio Uatumã, while nematodes were found in 61.1% of the *P. unifilis*, 54.5% of the *P. erythrocephala*, 26.8% of the *P. expansa,* and 5.3% of the *P. sextuberculata*.

Population Status. — The Rio Negro, the principal area of occurrence of this species, has at least two dozen small blackwater tributaries, all of which should have populations of *P. erythrocephala*. However, population size estimates are available for only two tributaries: Rio Ayuanã and Rio Unini. The Rio Ayuanã was studied from 2003 to 2008, capturing 4432 *P. erythrocephala*, of which 523 were recaptured. The low index of recaptures, 11.8%, indicates that a small proportion of the existing population was captured (Bernhard and Vogt 2012). During the entire study the capture rate had a mean of 0.59 turtles/hr/trammel net [how long?], ranging from 0.26 to 0.8 (Bernhard and Vogt 2012). During 2009–2010, 352 *P. erythrocephala* (162 males, 150 females, 40 juveniles) were captured in the Rio Unini in 4752 trammel net hours, representing a sex ratio of 1.08:1. The capture index varied between 0.05–0.12 turtles/hr/trammel net for the four sites collected. The carapace length of males was 210 ± 14.02 mm CL (range, 163–262 mm), with females 251 ± 17.75 mm CL (range, 221–303 mm) (Bernardes et al. 2014). Even though the sex ratio was essentially 1:1, there appeared to be low levels of recruitment, since few juveniles were found in the study in the Rio Unini compared to the Rio Ayuanã. This result is related to the high number of turtles captured for food in the Rio Unini by the people in the communities residing within Jaú National Park. They consume approximately 10,000-15,000 turtles annually, with 4 to 5 turtles eaten per family per month (Victoria Amazônica Foundation, unpubl. data).

The greater capture index in Rio Ayuanã is perhaps due to the fact that there are no riverine communities along the river, while there are four communities on the Rio Unini. In the Rio Ayuanã only occasional ornamental fish collectors utilize the river for a part of the year when the water is at its lowest, thus the population of turtles is less likely to be exploited. Despite there not being heavy exploitation pressure on the turtles in the Rio Ayuanã today, long term residents in the area, as well as turtle collectors, note that the population is not as robust as it used to be 20 years ago. It is now more difficult for them to capture *P. erythrocephala* by diving or by using nets or baited hooks (Bernhard and Vogt 2012). Contrary to the data available for *P. expansa*, there are no historical accounts for the utilization of *P. erythrocephala* and their eggs for human use or an indicator of the historic size of populations of this species. It is urgently necessary to undertake population

surveys throughout the species' range to verify its actual conservation status.

Threats to Survival. — In spite of its small size, *P. erythrocephala* is hunted for its meat and eggs, primarily for subsistence purposes, throughout its range in Brazil (Mittermeier and Wilson 1974; Hoogmoed and Ávila-Pires 1990; Rebêlo 1991; Vogt et al. 1991). The same has also been reported for Venezuela, where it is a major component of indigenous diets (Groombridge 1982). Specimens are captured on hook and line, in nets, and by harpooning while in the water; in addition, females are captured on nesting beaches and nests are poached for their eggs (Mittermeier and Wilson 1974). *Podocnemis erythrocephala* is one of the three species of turtles most consumed in the middle Rio Negro of Brazil (Pezzuti et al. 2004, De La Ossa 2008). Adult females were sold live for food in 1997–2002 at prices of US$ 1.00–1.50 in Novo Airão, on the lower Rio Negro (Pezzuti 2003). Since *P. erythrocephala* feeds predominately on fruits and seeds, it is a species highly dependent on the flooded forest to survive; clear-cutting forests will have drastic consequences for this species by removing the major source of food, thus *P. erythrocephala* may serve as an indicator species for the state of the flooded forest habitat.

Conservation Measures Taken. — All *Podocnemis* species have been listed on CITES Appendix II since 1975, requiring that any exports be permitted and shown to be non-detrimental. *Podocnemis erythrocephala* has been assessed as Vulnerable on the IUCN Red List since 1996, a category also recommended in 2011 by the IUCN Tortoise and Freshwater Turtle Specialist Group in its draft updated Red List account (TTWG 2014). Brazil listed the species as Near Threatened (NT) in 2012; Colombia listed it as Vulnerable (VU A1acd+2cd) (Castaño-Mora 2002). There are national laws protecting *P. erythrocephala* in each of the three countries where it occurs (Mittermeier 1978); however, there appears to be little enforcement.

In Brazil, outside protected reserves throughout the Amazon region, it is illegal to capture, kill, sell, buy, or eat freshwater turtles or their eggs, except those purchased from legal commercial farms, or in case of starvation, when no other food is available. Generally, this law is only enforced in city markets, on public riverboats and airline transportation, and in urban restaurants, not in rural areas where turtles are taken for home consumption. Within biological reserves such as National Parks, turtles are protected by law, and people living within these reserves are not allowed to eat turtles. However, people who live in Sustainable Development Reserves, such as Amanã and Mamirauá, are allowed to consume turtles, but they are not allowed to sell them commercially. In the Rio Unini Extractive Reserve, the inhabitants have permission to use the natural resources of the forest and rivers in a sustainable manner, including *P. erythrocephala,* for both commercial and sustenance purposes.

In Brazil there are six main protected areas where the habitat of *P. erythrocephala* is protected: 1) Jaú National Park (3,844,514 ha), the largest rainforest preserve in the world, a UNESCO World Heritage Site, along with the Central Amazon Biosphere Reserve and Rio Unini Extractive Reserve; 2) Rio Negro Forest Reserve (37,900 km^2); 3) Las Anavilhanas Ecological Reserve on the Rio Negro (350,000 ha), with 400 islands; 4) Amazonas National Park (10,000 km^2); 5) Viruá National Park (2,291 km^2) in Roraima; and 6) Mariuá Archipelago, Barcelos, Rio Negro, the largest fluvial archipelago on earth, with more than 700 islands.

Brazil also shares reserves with its neighbors: with Colombia, the Forest Reserve of the Rio Negro and Indigenous Areas Iaurete and Pari-Cachoeira, and Capau Area, with Colombia and Venezuela, the Rio Negro-Atabapo-Vihada Area, and with Venezuela, the Serranía de Neblina National Park.

In Venezuela *P. erythrocephala* occurs in the Yapacana National Park (3200 km^2). In Colombia the species is protected in the Puinawai National Natural Reserve (10,925 km^2), the Cahuinarí National Park (575,500 ha) on the Rio Caquetá, and the Reserva Natural La Pedregoza on the Rio el Bita in Vichada, near Puerto Carreño on the Orinoco.

Conservation Measures Proposed. — Enforcement of existing laws that protect the species will need to be improved. A study of fishing practices in the Rio Negro and tributaries and how these practices affect *P. erythrocephala* populations is needed. Programs to stimulate local community involvement with conservation of nesting beaches rather than consumption of adults and eggs would be beneficial.

Captive Husbandry. — Collection of this species for living zoological collections, or for the exotic pet trade, does not appear to have caused significant impact on wild stocks. Nevertheless, comparatively modest numbers of hatchling specimens entered the pet trade in 1971–73 with large (and illegal) shipments of *P. expansa* and *P. unifilis* hatchlings that were imported into the United States during those years. Unlike the larger species, *P. erythrocephala* did not prosper in captivity and few of these imports survive today.

Zoos and private collectors rarely keep this species. Slavens and Slavens (1993) listed the Bronx and Columbus zoos as having a total of seven adult specimens. A few additional adult specimens are in private collections in the United States, and the Tennessee Aquarium has been breeding the species. The Bronx Zoo's two male and single female adult specimens, acquired in 1978 and 1980, are believed to be from those animals imported in the early 1970s. Fertile egg clutches were deposited 9 April 1990, 15 January 1991, and 3 January 1992; 16 individuals hatched from the latter two clutches (P. Taylor, pers. comm).

Courtship has not been described in the wild, but was observed in a pair of the Bronx Zoo's 20-yr old captive specimens during the three months prior to egg deposition in January 1992 (P. Taylor, pers. comm.). The male (CL = 181 mm, PL = 143 mm, mass = 0.66 kg) was observed to approach a hovering female (CL = 270 mm, PL = 220 mm, mass = 1.9 kg) from directly below in a nearly perpendicular, plastron-to-plastron orientation, and repeatedly nip her throat. She then settled to the bottom of the tank and copulation was attempted.

Behavioral observations were made on *P. erythrocephala* in captivity from individuals collected on the Rio Negro near Barcelos (Ferrara 2007; Ferrara et al. 2009). Stereotyped behavioral patterns were initiated by males searching for females, but had different sequential patterns, depending on the receptivity of the females. Three phases of courtship were observed: searching, precopulation, and copulation. The studies indicated that females were initially receptive only 14% of the time, but most males (86%) continued their pursuit, and they were successful 51% of the time. Larger females were able to avoid the male by moving away initially or during any subsequent pursuit, or they could be aggressive. However, even males initially rejected by females biting them aggressively, continued their pursuit.

Captives accept a wide assortment of green leafy vegetables, non-citrus fruit, crustaceans, mollusks, annelids, insects, freshwater fishes, and commercial pelleted and flaked fish and turtle diets.

Current Research. — Jan Michels and collaborators are performing genetic analyses of different populations in Venezuela and Colombia. Iris de Fátima Guerreiro Bastos is continuing to study this species in Lago Sapucuá near Oriximiná and the mouth of the Rio Trombetas; this population is the farthest downstream population known. The Pé-de-Pincha project of Paulo Andrade is protecting nesting beaches with the rural communities in the Barcelos region, Rio Negro, focusing on the community of Daraquá on the Rio Itú. He has convinced the people to transfer the nests to a controlled beach rather than eating or selling the eggs. In 2013 they produced 8000 hatchlings. The project has been ongoing there for 6 years.

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