CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

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

Edited by

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Malacochersus tornieri (Siebenrock 1903) – Pancake Tortoise, Tornier's Tortoise, Soft-shelled Tortoise, Crevice Tortoise, Kobe Ya Mawe, Kobe Kama Chapati

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Summary. – The Pancake Tortoise, *Malacochersus tornieri* (family Testudinidae), is a small, flat, and soft tortoise of up to about 17.8 cm carapace length, rarely weighing more than 500 g. It has a flat and pliable shell resulting from limited bony shell development with a covering of thin keratinous scutes. The flat shape and shell pliability are fundamental adaptations which have enabled the species to successfully utilize rock crevice microhabitats in East Africa. The species occurs widely but disjunctly in Kenya and Tanzania, and marginally in northern Zambia. It is associated with isolated rocky hills and outcrops (kopjes) within its range, where it hides in crevices between and under exfoliating slabs of pre-Cambrian rock (gneiss). Sexual maturity is reached at the age of 5–9 years, depending on sex and growth rate, and a life span of over 25 years in captivity has been reported. Normally only one egg is laid annually, and rarely two per clutch. The status of *M. tornieri* populations in the wild indicates that abundance varies from one area to another and appears to be a function of microhabitat quality and level of local exploitation. The listing of the species on CITES Appendix II, while helpful, has also added to human overexploitation abuse, as it stimulated illegal off-take to supply the international live animal trade. In 2000, a proposal to uplist the Pancake Tortoise from CITES Appendix II to Appendix I was unsuccessful, but is again being reconsidered. In Tanzania, a zero export quota for wild-caught animals and restrictions on the size and number of captive-produced juveniles that could be exported were retained. The proposal to uplist the species to CITES Appendix I is strongly recommended. The species is highly vulnerable to extinction by virtue of its restricted distribution, specialized habitat requirements, low densities and fragmented populations, reduced reproductive potential, and overexploitation for the international live animal trade.

Distribution. – Kenya, Tanzania, Zambia. Occurs disjunctly from north central Kenya southward into the southeastern part of the country. In Tanzania it occurs disjunctly from the southern shores of Lake Victoria into the Maasai Steppe and further south in the Somalia-Masai and the Zambesian Floristic Regions. In Zambia it has only been reported from a single site in northern Nakonde District.

Synonymy. – *Testudo tornieri* Siebenrock 1903, *Testudo (Malacochersus) tornieri*, *Malacochersus tornieri*, *Testudo loveridgii* Boulenger 1920.

Subspecies. – None currently recognized.

Status. – IUCN 2018 Red List: Vulnerable (VU A1bd, assessed 1996); TFTSG Provisional Red List: Critically Endangered (CR; assessed 2013); CITES: Appendix II, as Testudinidae spp.

Taxonomy. — The first description of a Pancake Tortoise by Tornier (1896), from a specimen collected by Stuhlmann in Tanzania south of Lake Victoria, caused considerable confusion (see Loveridge and Williams 1957). The soft shell, decreased ossification, and dorso-ventral flattening were thought by Tornier to be abnormal, and to represent a degenerative feature of *Kinixys belliana*. Siebenrock (1903) examined the specimen and ruled out *Kinixys* as the genus and described it as the new species *Testudo tornieri,* but concluded that the shell had a pathological defect. Lönnberg (1911), based on another specimen, concluded that the decreased ossification was not pathological, but Boulenger (1920), on obtaining a few more specimens, thought the condition represented normal osteolysis and described his series as a new species, *Testudo loveridgii*. More detailed morphological descriptions came later (e.g., Procter 1922)

Figure 1. *Malacochersus tornieri* in its habitat outside a crevice, Ruaha National Park, Tanzania. Photo by F. Schmidt.

following the collection of more specimens with similar characteristics, and the earlier theories of shell pathology or osteolysis were invalidated. Since then, the tortoise's morphology, biology, and ecology have been reviewed and updated as more information has become available, with the most recent work on its osteology by Mautner et al. (2017).

Lindholm (1929) recognized *Testudo tornieri* as the type of a new genus, for which he established the name *Malacochersus*. The genus is monotypic with only one species currently recognized. Genetic studies have demonstrated that *Malacochersus* is most closely related to Asian *Indotestudo* and Eurasian *Testudo* (Le et al. 2006; Parham et al. 2006; Fritz and Bininda-Emonds 2007). No phylogeographic studies of the species have yet been realized, but in view of its disjunct distribution, are clearly needed.

Figure 2. *Malacochersus tornieri*, Ruaha National Park, Tanzania. Photo by F. Schmidt.

Figure 3. *Malacochersus tornieri*, Ruaha National Park, Tanzania. Photo by F. Schmidt.

Description. — The largest female *M. tornieri* from Kenya had a maximum straight-line carapace length (CL) of 17.7 cm, a carapace width (CW) of 13.1 cm and a carapace depth (CD) of only 4.0 cm (Broadley 1989). The corresponding measurements for the largest male were CL 16.7 cm, CW 11.1 cm, and CD 3.6 cm (Broadley 1989). Moll and Klemens (1996) reported the largest female from Tanzania with a CL of 17.8 cm and a CW of 14.2 cm. The largest male had a CL of 17.0 cm and a CW of 12.0 cm. There are no other published reports of individuals larger than those reported by Moll and Klemens (1996). They found northern and central Tanzanian populations to be sexually dimorphic with adult females significantly longer, wider, and heavier than males. Kabigumila (2002), however, based upon measurements of captive animals from Kondoa, Tanzania, found adult females had greater CW and CD than males, but not significantly larger CL. Wood and MacKay (1997) found that adult Kenyan females had greater CD than males (as did Kabigumila [2002] with Tanzanian females), but neither they nor Malonza (2003) found sexual dimorphism in CL or mass in their Kenyan samples.

Most of the common names for *M. tornieri* simply refer to the morphology or habitat of the species. It is dorso-ventrally flattened with a soft and spongy shell making the tortoise quite vulnerable to predation and crushing which might occur if it is accidentally trampled by large herbivores. The soft shell is largely a result of unique partial ossification of the bones (Procter 1922). Continued osteological development of this tortoise is arrested before reaching adulthood, resulting in a fenestrated bony shell layer. One of the largest fenestrations is found on the plastron, and in some individual tortoises the location of this fenestration may be observed due to its overlying scutes being lighter in color than other areas of the plastron. Tortoise scutellation pattern has been described in detail by Loveridge and Williams (1957) and Broadley (1989). In most cases there are eleven marginal scutes on each side of the carapace. There is a single small nuchal scute and a supracaudal scute. There are four costals on each side and five vertebral scutes. The vertebrals reach the nuchal and supracaudal scutes. The plastron is comprised of six bilaterally symmetrical scutes: gulars (g), humerals (h), pectorals (p), abdominals (abd), femorals (f), and anals (an). The plastral formula provided by Loveridge and Williams (1957) revealed the following relationship: abd>h>p>or<f>or=g>or=an. Loveridge and Williams (1957) and more recent authors (e.g., Broadley 1989; Moll and Klemens 1996; Wood and MacKay 1997) have often reported meristic anomalies of carapacial and plastral scutes. Wood and MacKay (1997), for example, reported consistency in plastron scutes only with abd>h>p while the rest had quite variable morphologies and relational dimensions.

Adult *M. tornieri* carapacial color pattern is quite variable, but each color variant may provide a level of crypsis and often blends well with the background of the rocky habitat outside the crevice. Bonin et al. (1996) suggested that the smooth pattern often displayed by older adults could be adaptive as camouflage in rocky habitats. There

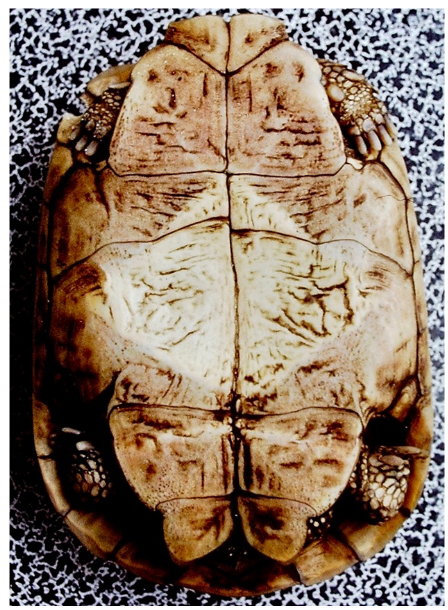

Figure 5. Adult *Malacochersus tornieri* showing the large light-colored area of the plastron covering the fenestration in the underlying bony layer. Photo by D. Moll.

Figure 4. *Malacochersus tornieri* adult. Photo by the Turtle Conservancy.

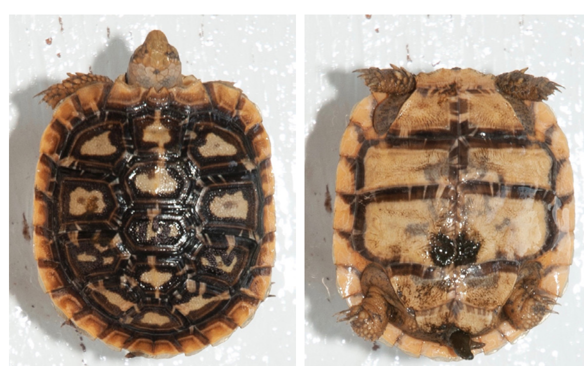

Figure 6. Hatchling *Malacochersus tornieri*. Photos by the Turtle Conservancy.

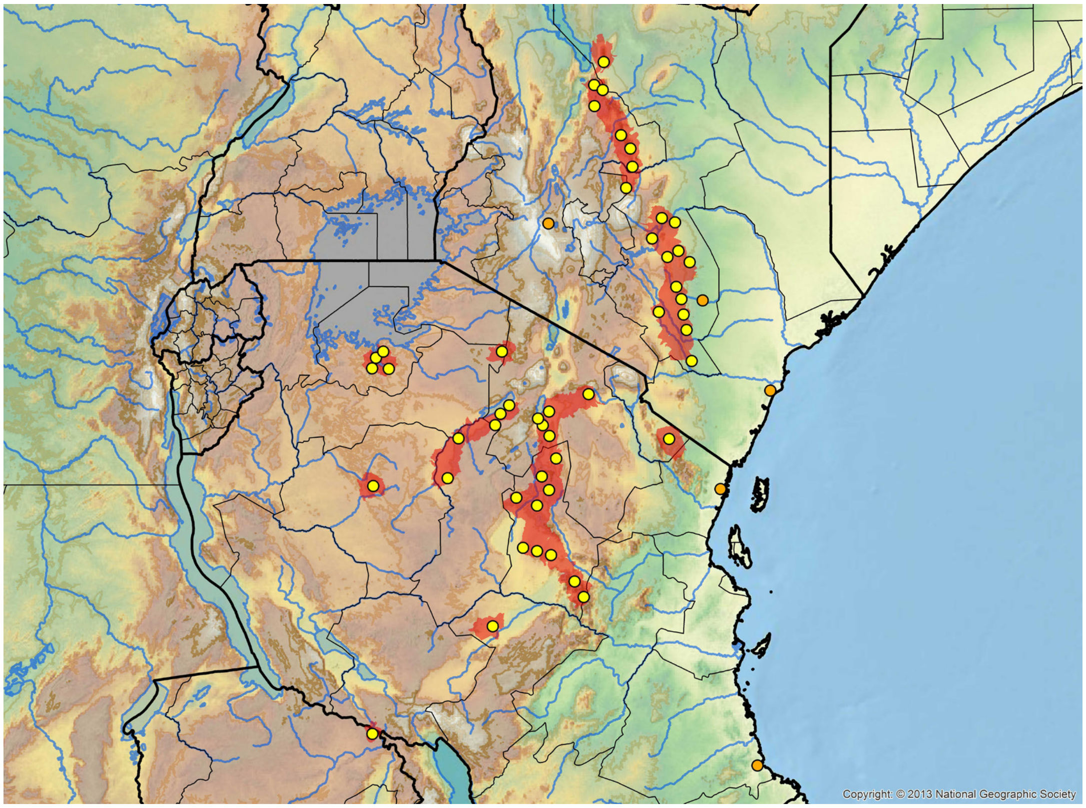

Figure 7. Distribution of *Malacochersus tornieri* in East Africa in Kenya, Tanzania, and northern Zambia. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992) plus more recent and authors' data; orange dots = uncertain native or trade or introduced specimens; red shading = projected historic distribution. Distribution based on GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009; TTWG 2017), and adjusted based on authors' subsequent data.

is no evidence of sexual color dimorphism in any of the populations that have been studied so far (Loveridge and Williams 1957; Broadley 1989; Moll and Klemens 1996; Wood and MacKay 1997; Malonza 2003). The carapacial color descriptions by Loveridge and Williams (1957), Broadley (1989), and Moll and Klemens (1996) suggest that in adults it ranges from light yellow or tan, with darker rays running across each scute to black with yellow rays across the scute. Older adults may be uniformly tan or horn-colored.

Loveridge and Williams (1957), Broadley (1989), and Wood and MacKay (1997) reported ontogenetic color changes with the carapace of hatchlings and young animals exhibiting a bold, irregular, variable pattern of deep brown and bright yellow colors which fade with age and may eventually become uniformly pale tan. Loveridge and Williams (1957), Broadley (1989), and Moll and Klemens (1996) also described variable ontogenetic changes in plastron color, ranging from pale yellow scutes, often with black margins in hatchlings to pale yellow scutes bordered by dark brown or black in juveniles and adults. Older adults may display uniform tan or horn-colored plastral scutes.

Annual growth ring zones are well-defined and conspicuous on epidermal scutes of juveniles, often displaying an annual double-ring pattern in northern Tanzania, which may be associated with the long and short rainy seasons characteristic of the region (Moll and Klemens 1996), but gradually become worn with age and largely or entirely obliterated in adults. According to Moll and Klemens (1996) ring obliteration is hastened by constant wedging and scraping against the ceiling of rock crevices; the carapacial feature which is most severely marked by wear is the hump located near the rear of the carapace. This feature is regularly used to anchor the tortoise against the ceiling of the crevice while bracing itself with its extended hind legs. In narrower crevices this wedging is often enhanced by the tortoise's ability to slightly inflate itself through inhaling and puffing out the unossified central plastron area while holding its breath, and pulling in its limbs, head, and neck (Moll and Klemens 1996). This inflation capability has also been reported by Pauler (1990) and Schmalz and Stein (1994), but disputed by Ireland and Gans (1972) and Bruekers (1994).

Distribution. — The range and distribution of *M. tornieri* in the East African region is incompletely known and is still being updated. In the past, Loveridge and Williams (1957) described and mapped the species' range from north central Kenya southward to northern Tanzania, but they also reported a probable record of its presence in the former Northern Frontier District of Kenya (bordering Somalia), undocumented by specimens. Wood and MacKay (1997) added new localities in northern and central Kenya and suggested (due to these new localities and the presence of larger expanses of suitable habitat) that the species may have a much greater distribution in Kenya than currently recognized. Malonza (2003) described and mapped its range as extending from northern to southeastern Kenya and continuing in suitable habitat in northern, eastern, and central Tanzania.

In Tanzania, the species extends from the southern shore of Lake Victoria eastward and southward through much of the Maasai Steppe and throughout the Somalia-Masai Floristic Center of Endemism into the Zambezian Center of Endemism (White 1983; Klemens and Moll 1995; Moll and Klemens 1996; Spawls et al. 2002). The southern-most populations were formerly reported to be those of Ruaha National Park in Tanzania (Spawls et al. 2002). One notable aspect of this early species geographic mapping was its eastward extension into coastal localities such as Lindi in Tanzania and Malindi in Kenya. The review by Broadley (1989) did not substantially change the existing scenario and still retained the coastal localities as part of the range. Broadley and Howell (1991), Klemens and Moll (1995), Wood and MacKay (1997), and Spawls et al. (2002) revised the range, in part, by questioning the validity of coastal localities as possibly resulting from the tortoise trade. These authors were convinced that if the two localities above were dismissed, most of the rest of the localities would fit well within the African Somalia-Masai Floristic Center of Endemism, with a few valid records from the Zambezian Floristic Center of Endemism recognized as well (White 1983).

While these recent literature records have shrunk the distribution of *M. tornieri* in the east (by excluding the coastal localities), surveys reported by Wood and MacKay (1997), Malonza (2003), and Chansa and Wagner (2006) have expanded the known distribution northward in Kenya, and southward from Ruaha National Park in Tanzania to Nakonde District in northern Zambia (a distance of about 200 km in the latter case). Much of the range appears to comprise disjunct populations occurring in suitable habitats.

Habitat and Ecology. — Within its geographical range, populations of *M. tornieri* are discontinuous and disjunct, occurring in localities having appropriate rock crevices in semi-arid climate below 1800 m a.s.l. (Broadley 1989; Moll and Klemens 1996). In Zambia the species is found at only one location, which is above 1400 m with precipitation levels exceeding 1200 mm per year (Chansa and Wagner 2006). *Malacochersus tornieri* is highly associated with ancient rocky outcrops (kopjes) of pre-Cambrian gneiss that have exfoliated long enough to provide deep and tapering

Figure 8. *Malacochersus tornieri* in its habitat entering a crevice, Ruaha National Park, Tanzania. Photo by F. Schmidt.

crevices that provide shelter for the species (Moll and Klemens 1996; Wood and MacKay 1997; Malonza 2003; Chansa and Wagner 2006). In Kenya and Tanzania the habitats where the majority of the species is found consist of scattered, irregularly spaced, rock outcrops on lower, gently undulating terrain or associated kopjes (Moll and Klemens 1996; Wood and MacKay 1997), and on gently sloping *Brachystegia* forested hillsides (Moll and Klemens 1996; Mwaya 2006).

The physical characteristics of the crevices preferred by the tortoises have been generally described by Loveridge and Williams (1957), Broadley (1989), Moll and Klemens (1996), Wood and MacKay (1997), and Malonza (2003). They are highly variable in their physical orientation with the extremes of the spectrum being vertical or horizontal and a range of angular possibilities in between. Tortoises use crevices that are deep enough to fully enclose them, and in some cases they may retreat beyond one meter deep. Inside, these crevices can be very dark, often requiring a flashlight or reflecting mirror to locate highly cryptic hiding tortoises (Moll and Klemens 1996; Mwaya 2006). The crevices also tend to taper inwards to < 5 cm in height in the sections where the tortoises reside, a property that enhances their anti-predator wedging behavior (Moll and Klemens 1996). The deep crevices also offer minimal temperature and humidity fluctuations compared to external ambient temperature and humidity, thereby ensuring optimal thermal buffering (Honegger 1968; Wilke 1984; Wood and MacKay 1997; Schmidt 2006; M. Hassanali, pers. comm.). Juvenile tortoises often hide inside crevices that are smaller than those used by adults, and they may reside closer to the crevice entrance (Moll and Klemens 1996).

Another adaptive feature of the flat shell is that, in combination with other morphological features and hard microhabitat substrate, it enables the tortoise to turn over rather quickly when it falls on its back (Ireland and Gans 1972). Kabigumila (2002) and other researchers have suggested that Pancake Tortoises may rely on their relative speed to return to their crevices to escape predation and/

or trampling rather than pulling into their shells in more typical tortoise fashion. The capacity for speed may be facilitated by the adaptations that have resulted in greater shell lightness (Kabigumila 2002), and perhaps by the greater degree of suppleness at their wrists and ankles than in most Testudinidae, as observed by Procter (1922).

Wood and MacKay (1997) described the principal vegetation of Kenyan *M. tornieri* habitat as *Acacia–Commiphora* bush which may also contain *Lannia*, *Boscia*, *Sterculia*, *Adansonia digitata,* and sometimes *Albizia* and *Euphorbia*. They also list the common climbers *Entada leptostachys* and *Adenia veneta* as frequently present.

The rocky terrain inhabited by *M. tornieri* in its northern range in Tanzania's Somalia-Masai Floristic Center is also usually dominated by *Acacia*-*Commiphora* deciduous bush land (Broadley and Howell 1991). Other frequently occurring plant genera in these habitats include *Lannia, Sterculia, Albizia, Euphorbia, Adansonia,* and *Terminalia*. Mwaya (2009) reported herbaceous species composition at a typical habitat in Tarangire National Park comprising mainly Poaceae, contributing 31% of all herbaceous species composition, followed by Papillionoidea with 7% of species composition. The southern (Zambezian) range is dominated mainly by *Brachystegia* woodland.

Most of what is known about *M. tornieri* reproduction and growth has been contributed from *ex-situ* captive breeding programs and zoos. Hatchlings of *M. tornieri* reported by Ewert et al. (2004) had an average body mass of 15.4 g and average CL of 40.7 mm (n = 30). At this stage, hatchlings

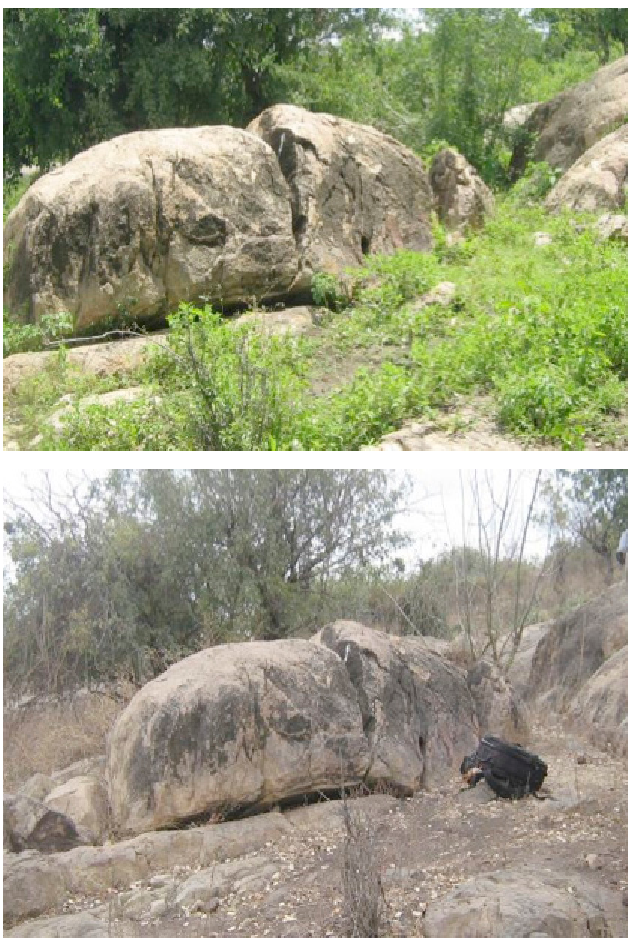

Figure 9. Typical habitat of *Malacochersus tornieri* in Vilima Vitatu, Tarangire–Manyara ecosystem, Tanzania, showing the same rocky outcropping area during the wet season (*top*) and the dry season (*bottom*); 15 tortoises were once found in the two large crevices in the boulder. Photos by R.T. Mwaya.

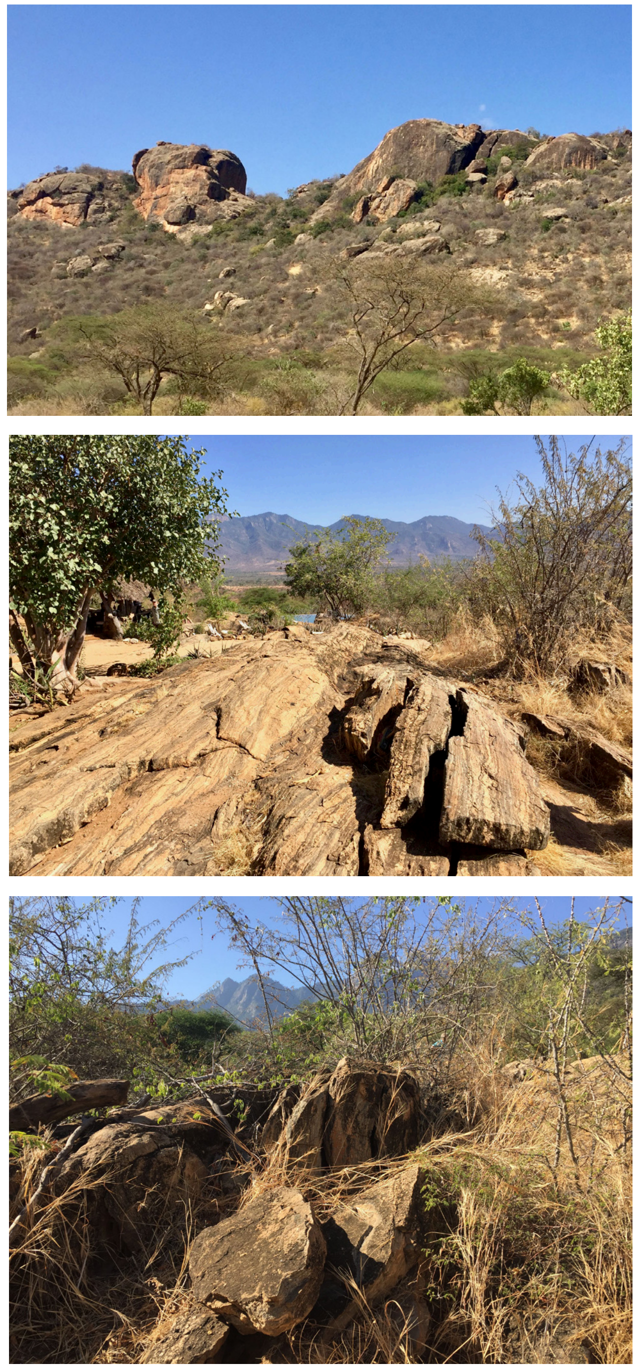

Figure 10. Typical habitats of *Malacochersus tornieri* in Namunyak Wildlife Conservancy, Samburu, northern Kenya. *Top*: Typical rocky kopje of exfoliating pre-Cambrian gneiss. *Middle and Bottom*: Sarara Camp, where tortoises have been recorded emerging from the rocky crevices. Photos by A.G.J. Rhodin.

are nearly circular in shape and not very flat; they become progressively more elongate and flatter as they grow toward maturity. Wilke (1984) described the growth process observed in the early life history of Pancake Tortoises in the Frankfurt Zoo. Hatchlings (mean mass of 11.6 g) were tightly curled at hatching, but stretched out and flattened within the first 24 hours. At that point, they had a mean carapace length and width of 38 x 38 mm and a depth of 20–22 mm. It took two to three weeks for the opening in the plastron to close after the yolk sac had been absorbed. The hatchling growth rate was rapid and after three months their mass increased about four-fold and they had grown nearly twice as long and one and a half times as wide. Ewert et al. (2004) noted that in captive males, even though they are typically the smaller sex in adulthood (at least in some locations), average CL growth rate (2.8 mm/mo ± 0.23) exceeded that of captive females (2.42 mm/mo ± 0.19) in their first 30 months. In the subsequent 12 months (30-42 mo) females overtook and exceeded the growth rate of males. In this period the CL growth in mm/mo for females became 2.47 ± 0.45 and that for males 1.37 ± 0.33.

A consequence of sexual divergence in juvenile growth rate is that adult Pancake Tortoises may become sexually dimorphic in their body mass and CL in some locations. Moll and Klemens (1996) found females were longer, wider, and heavier than males in Tanzania, although a study by Kabigumila (2002) did not. Neither Wood and MacKay (1997) nor Malonza (2003) found evidence of sexual dimorphism in length, width, or mass in Kenyan specimens. However, Kabigumila (2002) and Wood and MacKay (1997) did note that adult females were slightly deeper and more rotund in profile than males in Tanzania and Kenya – possibly as an adaptation related to egg retention. All of the above studies agreed that an adult sex ratio of 1:1 existed in these locations. Besides possible differential body mass and meristics in some adults, individuals can be sexually discriminated by the shape and size of their tails: adult males have longer and larger tails relative to the shorter and stumpier tails of females (Moll and Klemens 1996; Malonza 2003).

Pancake Tortoise age at the onset of sexual maturity is not precisely known in the wild, although this subject, and the difficulties involved in aging in the wild, were discussed by Moll and Klemens (1996). In Tanzania, males begin to mature at 9–10 cm CL and females at 13–14 cm CL (Moll and Klemens 1996). In captivity, sexual maturity may be reached in 5–9 yrs and between 9–10 cm CL (Skelton and Redrobe 2002). Using a mark-recapture technique, two Tanzanian adult females were observed to grow 2.5 and 3.0 mm CL, respectively, in a 17-mo period. However, while one increased its body mass by 20 g, the other lost 10 g in the same period of time (Moll and Klemens 1996). Shaw (1970) reported life spans between 8–9 yrs for 10 animals in captivity, while Skelton and Redrobe (2002) estimated an individual Pancake Tortoise life span to be about 20 yrs. A record of 25 yrs for one individual kept at the Bronx Zoo has been reported by Slavens and Slavens (1994).

Reproductive information for wild Pancake Tortoises is scanty and mostly anecdotal. Most of our understanding of the species' reproduction comes from *ex-situ* facilities. Loveridge and Williams (1957) observed pre-copulatory behavior of the tortoise in captive individuals in Kilosa, Tanzania, in January and February. Males were observed chasing, snapping, and clambering on females. An excited male even endeavoured to mate, albeit unsuccessfully, with a female *Kinixys belliana* placed in the same enclosure. A male chasing a female at the base of Simba Hill, near Dodoma, Tanzania, was observed by J. de Graaf (pers. comm.) and K. Howell (pers. comm.) witnessed a copulating pair at Ruaha National Park in Tanzania in December 1991. All of these behaviors occurred during the winter wet season in Tanzania.

In East Africa females are reported to be gravid in April (Loveridge and Williams 1957; Broadley 1989). Loveridge and Williams (1957) stated that a single egg is laid in July or August in East Africa, and Moll and Klemens (1996) found gravid females in June in Tanzania. In Kenya, Malonza (2003), found that mating occurs in March–May, egg laying in June–July, and egg hatching in November–December. For example, a single egg was found inside a rock crevice base in July at Namunyak Wildlife Conservancy in Samburu, northern Kenya. Schmidt (2006) observed a Pancake Tortoise egg in a crevice in Ruaha National Park, Tanzania, in September.

In captivity, breeding and egg laying have occurred almost all year round, provided there is a good food supply (Conant and Downs 1940; Shaw 1970; Darlington and Davis 1990; Skelton and Redrobe 2002; Ewert et al. 2004). Based upon laboratory observations of oviposition, Ewert el al. (2004) determined that *M. tornieri* displayed a bias toward a fall-winter pattern in its nesting season. Loehr (1997) observed very different nesting behavior in two captive females: one female sought to bury its egg in the substrate of its enclosure at laying time, while the other sought to deposit its egg in a suitable crevice. The usual nest is a shallow scrape 5 to 6 cm deep and may be dug in almost any kind of substrate by captives: sandy soil, bark mulch, and even gravel (Schmalz and Stein 1994; Skelton and Redrobe 2002; Ewert et al. 2004). Usually only one egg is laid per clutch, and rarely two, but in captivity more than one clutch may be produced annually (Shaw 1970; Schmalz and Stein 1994; Loehr 1997; Ewert et al. 2004).

The elongate egg is large relative to the adult tortoise body size. Shaw (1970) reported mean egg dimensions of 46.6 x 28.9 mm with a mean mass of 23.4 g (n = 27) at the San Diego Zoo, and Broadley (1989) reported two egg dimensions, respectively, as 42 x 26 mm and 44 x 28 mm for captive individuals in Kilosa, Tanzania. The incubation period varies inversely with environmental temperature, and is influenced by postovipositional developmental arrest (Ewert et al. 2004), but ranges from 99–237 days (Shaw 1970; Wilke 1984; Darlington and Davis 1990; Ewert et al. 2004). Like many other Testudinidae, *M. tornieri* has temperature-dependent sex determination (TSD) (Ewert and Nelson 1991; Dickson 1992; Ewert et al. 2004). The pivotal temperature is 29.8°C, with females being exclusively produced at ≥30°C; males are produced at lower incubation temperatures.

Although in the wild, Pancake Tortoises frequently occur singly or in pairs inside crevices, multiple individual assemblages are also common (Loveridge and Williams 1957; Moll and Klemens 1996; ZAWA 2000, Malonza 2003). Mwaya (unpubl. data) found 15 tortoises in a single vertically-oriented rock crevice in 2007 at Vilima Vitatu Hills, Mdori village, near Tarangire National Park. The chimney-type crevice cavity was extensive enough to accommodate that number without being crowded. However, despite frequent occurrences of pairs (Moll and Klemens 1996; Wood and MacKay 1997; ZAWA 2000), it is questionable whether the species forms stable pair bonds. Moll and Klemens (1996) observed movements of individuals (often males) between crevices occupied by other Pancake Tortoises (often females). Mwaya (2006) observed a female that occupied a crevice for three consecutive days and had a male with her when first encountered. The first male was not found the next day; instead, another male had joined the female. Current field data (Mwaya, unpubl. data) suggest higher incidences of male-female pairing than any other pairing combination. In Kenya, Malonza (2003) found male-female pairing to be seasonal, as they were found to separate after a season. Certainly, there is a clear gap in our understanding of social and breeding behavior of this species in its natural environment.

In their natural environment, Pancake Tortoises spend most of the time hiding inside deep rock crevices. The spatial behavior of this species outside the crevice is not adequately known. Sporadic field observations by Loveridge and Williams (1957) revealed some juvenile tortoises basking on top of a rock slab at 0900 hrs in the morning. Pancake Tortoises were also observed outside crevices at Tarangire and Ruaha National Parks during wetter periods in Tanzania (Moll and Klemens 1996). In April and May 2011, on different days, Mwaya (pers. obs.) observed four (3 adults and 1 juvenile) tortoises out of their crevice retreats between 0930 and 1000 hrs. When tortoises made inter-crevice movements between rock outcrops, they usually took the most direct route, except where a physical barrier, such as a fallen log, would impede movement. In such cases, they would circumnavigate the barrier if that was a possible option. The path taken was often underneath grass tussocks or along old animal trails which were sheltered by tall grasses (Mwaya 2002).

There have been no field studies of the home range of *M. tornieri*. At best, it has only been speculated upon, based on out-of-crevice movement, which is quite limited most of the time, and normally confined within a small radius around a crevice of a particular rock outcrop (Loveridge and Williams 1957; Broadley 1989). Ayoub Njalale, in Moll and Klemens (1996) made the first field observation, in Ruaha National Park, of a foraging tortoise utilizing an estimated average area of 4.2 m^2. Using a line-and-spool technique, Mwaya (2002) reported generally infrequent out-of-crevice activities. However, some individuals, especially males, occasionally made considerable daily movements between crevices, one travelling over 100 m/d.

In the captive environment, Pancake Tortoises have been fed a variety of commercial vegetable and mineral enriched pet foods (Darlington and Davis 1990; Skelton and Redrobe 2002). In the wild, the species is considered herbivorous, eating grasses and leafy vegetation (Loveridge and Williams 1957; Moll and Klemens 1996). However, neither its dietary breadth nor plant preferences are precisely known. The first report of diet in the wild was by Loveridge and Williams (1957) who observed the tortoises eating unidentified dry grass. Moll and Klemens (1996) identified dietary components from fecal samples and noted fragments mostly of the grass family Poaceae consisting of *Cynodon* sp., *Sporobolus* sp., *Themeda triandra*, and *Panicum* sp. Also, they fed on a broad-leafed *Achyranthes* (Amaranthaceae) and aloes (Liliaceae). In some localities, such as Ruaha National Park in Tanzania, the diet was inferred to have a high proportion of nuts and seeds (Raphael et al. 1994).

Probable predators of Pancake Tortoises were reported by Moll and Klemens (1996) to be White-tailed Mongoose (*Ichneumia albicauda*) and Neumann's Genet (*Genetta genetta*). Other carnivores of the rocky terrain which may become opportunistic predators include various Felidae, the White-throated Savanna Monitor (*Varanus albigularis*), and jackals (*Canis* sp.). Avian predators might also take individuals moving outside the crevices; prime suspects being Ground Hornbills (*Bucorvus leadbetteri*) Secretary Birds (*Sagitarrius serpentarius*), White-necked Ravens (*Corvus albicollis*), and Pied Crows (*Corvus albus*). All of these birds are found throughout East Africa (Williams and Arlott 1980), are known to eat small reptiles, and the latter two species, in particular, are known to be important predators of small tortoises (Uys 1966; Fincham and Lambrechts 2014).

Rocky terrain microhabitats, and the crevices in particular, are also home to a variety of other reptilian and non-reptilian small vertebrates, many of which may be encountered together with Pancake Tortoises. The common crevice microsympatrics include the Greater Plated Lizard (*Gerrhosaurus [Broadleysaurus] major*), White-throated Savanna Monitor (*Varanus albigularis*), Rock Agama (*Agama lionotus*), and various skinks (*Mabuya [Trachylepis] striata, M. quinquetaeniata,* and *M. varia*). Infrequently, geckos (*Hemidactylus squamulatus* and *Pachydactylus [Elasmodactylus] tuberculosus*) have also been found in Pancake Tortoise crevice habitats (Klemens and Nikundiwae 1995; Moll and Klemens 1996). Occasionally, snakes (*Bitis arietans, Python sebae* and *Naja nigricollis*) have been observed inside tortoise crevices (Malonza 2003; Mwaya, unpubl. data). On two occasions, and in two different rocky areas in Tarangire National Park, foraging Black Mambas (*Dendroaspis polylepis*) were seen outside, but in the vicinity of crevices used by Pancake Tortoises (Mwaya, unpubl. data). Although Wood and MacKay (1997) did not themselves encounter any snakes in Kenya, a local guide insisted that spitting cobras (most likely the Red Spitting Cobra, *Naja pallida*) were also fairly common inhabitants of the crevices.

Population Status. — The status of *M. tornieri* populations in the wild is poorly known, but many are decreasing (Ngwava, unpubl. data). Species abundance varies from one area to another and appears to be a function of habitat quality, including the presence of appropriately oriented and well-exfoliated rock crevices with suitable interior dimensions (Moll and Klemens 1996, Malonza 2003). Other aspects of microhabitat quality include the degree of herbaceous vegetation cover over rock outcrops (Mwaya 2009), and the extent of anthropogenic habitat alteration (Wood and MacKay 1997; Chansa and Wagner 2006; Kyalo 2008). Low population densities in otherwise seemingly suitable habitat also result from removal and offtake by commercial collectors (Klemens and Moll 1995; Malonza 2003).

In Kenya, recorded species densities in appropriate habitats have ranged from 8.86 tortoises /km^2 in Voo, Kitui County (Malonza 2003), to as low as 1.2 tortoises /km^2 in Nguni, Kitui County (Kyalo 2008). However, even relatively high-density populations such as those at Voo can become rapidly depleted. Ngwava (unpubl. data) found no Pancake Tortoises there when resurveying Voo in 2014. Notably, a commercial farming operation for Pancake Tortoises had been established near Voo and was still operational in 2014; it is likely that the local wild population had been harvested to provide breeding stock for the farm. A few other areas surveyed by Malonza (2003) that had good Pancake Tortoise populations at that time were also noted by Ngwava (unpubl. data) to be depleted in 2014.

In Zambia, 66 animals were found at eight sites in Nakonde District which were inhabited by 2–25 individuals per site (Chansa and Wagner 2006). Based upon a mark-recapture study conducted at eight sites in suitable habitat at Nakonde District, a population size estimate of 518 animals was obtained by ZAWA (2000) and a density of 11 individuals/km^2 (Chansa and Wagner 2006).

Published information on the Zambian population has stimulated some discussion. For example, ZAWA (2000) and Chansa and Wagner (2006) reported that the demand for the live export of Pancake Tortoises from Zambia increased from 400 in 1996 to 10,000 in 2000. The reports further pointed out that one of the significant threats to Pancake Tortoise survival in Zambia is illegal trade. Indeed, export statistics from Zambia show that from 2007 to 2016, nearly 22,000 Pancake Tortoises were exported out of the country (CITES Trade database, http://www.unep-wcmc-apps.org/citestrade/report.cfm [June 2018]).

With only a single Zambian occurrence location known, no matter how productive it might be, it is doubtful that legal or illegal collection of the species for live trade could be sustained there at the volumes reported. There are probably at least three plausible explanations for the large number of traded Pancake Tortoises exported out of Zambia: 1) the known Nakonde population could be vastly larger than estimated; 2) the range in Zambia could be more extensive and fragmented, extending into other areas not yet recognized; or 3) the high trade volume could be a result of tortoises collected in other areas (probably Tanzania) and illegally "laundered" through Zambia (and also possibly Mozambique), thereby entering the exotic animal trade in that fashion (Chansa and Wagner 2006).

Abundance estimates in Tanzania were provided by Klemens and Moll (1995) based on the number of specimens per man-hour (mh) of searching time. The greatest abundance observed was in Kondoa District, outside Tarangire National Park, with the Iyoli area having the highest abundance (8.5 tortoises/mh). This was followed by the Pahi and Kolo Mongoni areas, where in both cases the abundances were 4.0 tortoises/mh. Within Tarangire National Park, highest abundance was 1.5/mh at Ridge Road near Buffalo Pool. Populations that occur inside national parks are afforded the highest level of protection, but even they are not safe from collectors for the exotic animal trade (Klemens and Moll 1995).

Pancake Tortoises have been heavily exploited in the wild to service the international live animal trade. Thus, in Tanzania, the species was considered overexploited even prior to the implementation of a moratorium policy in 1992. Overexploitation has continued to be inferred from export volumes and intercepted consignments of illegally shipped tortoises (e.g., Luiijf 1997). According to Klemens and Moll (1995) the most vulnerable Tanzanian populations of Pancake Tortoises, as a result of live trade collection, have been those occurring near or along the African Great

North Road from Dodoma to Arusha via Kondoa. It was also suggested that populations occurring in inaccessibly remote areas would probably remain more secure from anthropogenic abuse.

Threats to Survival. — The single most serious human threat is overexploitation for the live exotic animal trade (Klemens and Moll 1995; Luiijf 1997; Goh and O'Riordan 2007; Nijman and Shepherd 2007). Habitat degradation from rock destruction that reduces available habitat is also an important threat, especially as related to illegal tortoise collection (range-wide), construction purposes and slab and ballast extraction in Kenya, and kiln building for charcoal production in Zambia (Klemens and Moll 1995; Malonza 2003; Goode et al. 2005; Chansa and Wagner 2006). Vegetation removal through slash-and-burn cultivation, wildfires and charcoal burning (Wood and MacKay 1997; Malonza 2003; Ngwava, unpubl. data) are also detrimental to the species because they are likely to negatively affect the ability to feed, and increase exposure to predation and thermal stress (Mwaya 2006, 2009). Livestock grazing does not seem to be as big a problem for Pancake Tortoises as the other various human activities, as it results in little destruction of crevice microhabitats (Malonza 2003). Apart from the women of the Hadzabe, a remnant tribe of hunters and gatherers at Yaeda Chini, near Lake Eyasi, Tanzania, who occasionally consume the tortoise to subsidize their protein requirement (Klemens 1992), no other tribes within the species' range utilize it as a source of food, and it does not seem to be affected by the global turtle meat consumption trade.

There has been no serious documentation of diseases in natural populations of the Pancake Tortoise (Klemens et al. 1997), but this possibility cannot be ruled out in the future because the species-human interface outside protected areas is becoming increasingly common and widespread (Mwaya, pers. obs.). Unfortunately, this interface is potentially a disease-prone zone for the tortoises (Jacobson et al. 1991; Brown et al. 1994; Jacobson 1997). For example, Mwaya (unpubl. data) has found higher tick and intestinal oxyurid parasite loads in tortoises outside of Tarangire National Park in Tanzania, where human-tortoise interaction is higher. Ticks are hosts to some serious diseases, including heartwater, caused by the bacterium *Cowdria ruminantium* (Fyumagwa and Hoare 2005; Okanga and Rebelo 2006; Loehr 2008). Indeed, Burridge et al. (2000a,b) and Burridge and Simmons (2003) reported potential for tortoise ticks to act as vectors of *C. ruminantium*. For example, the latter reported evidence of *C. ruminantium* infection in *Amblyomma sparsum* ticks found on tortoises imported into Florida. Ticks of the genus *Amblyomma*, first reported on Pancake Tortoises by Loveridge and Williams (1957), were found on confiscated Pancake Tortoises kept at Mweka (Mwaya, unpubl. data) and have since also been observed in wild populations (Mwaya, unpubl. data).

Conservation Measures Taken. — *Malacochersus tornieri* is currently categorized as Vulnerable on the IUCN 2018 Red List, based on an outdated assessment from 1996, but the IUCN Tortoise and Freshwater Turtle Specialist Group more recently assessed it as Critically Endangered in 2013 (TTWG 2017; Rhodin et al., in press). The species is listed on CITES Appendix II as part of all Testudinidae spp., but is currently under consideration for possible uplisting to Appendix I.

Kenya discontinued exporting this species from the wild in 1981, but a few farms are now authorized to breed for export. A significant milestone in Pancake Tortoise conservation in Tanzania emerged following imposition of an export quota moratorium in 1992 (Kabigumila 1998), and allowance for the private sector to captive-breed the species for live trade demand (MNRT 1998). Currently, at least four farms have been licensed to breed the Pancake Tortoise in Tanzania (Kabigumila 1998; Mbassa and Maganga 2002). In Zambia, international trade in Pancake Tortoises was suspended because "laundered" animals from East Africa had presumably been exported from there previously. The suspension held until the suspected presence of natural populations there was verified and its size evaluated by ZAWA (2000). However, no protection of the area known to support Pancake Tortoise populations in Zambia is provided by ZAWA (Chansa and Wagner 2006).

In Tanzania, Pancake Tortoise populations have been reported from 4 of 16 gazetted national parks, namely Serengeti, Tarangire, Ruaha, and Mkomazi. National parks in Tanzania are fairly comprehensively protected and are considered ecological benchmarks (Sinclair et al. 2002). In Kenya, about 95% of the total *M. tornieri* population occurs outside protected areas, where the best habitat also occurs. Pancake Tortoise presence has been confirmed in the following protected areas, from south to north: Tsavo East National Park (northern sector), Kitui South, Shaba, Buffalo Springs and Samburu National Reserves, and Namunyak Wildlife Conservancy (Malonza 2003). It has also been recorded in some adjacent Laikipia Conservancies.

The only discovered population of Pancake Tortoises in Zambia (Chansa and Wagner 2006) is found outside a protected area. Across its entire range, Bombi et al. (2013) estimated that only 22.6% of *M. tornieri* habitat is currently protected. The fact that a majority of the species' populations occur outside protected areas predispose them to illegal collection for live trade as well as to anthropogenic habitat disturbance.

Conservation Measures Proposed. — In 2000, during CITES CoP 11, a proposal to uplist *M. tornieri* from CITES Appendix II to Appendix I was tabled and then withdrawn during negotiations, resulting in retention of the species in Appendix II. While listing in CITES Appendix II (as part of the family Testudinidae) is helpful, we believe it may also have had the effect of increasing the desirability of the species in the pet trade. This has contributed to overexploitation of some populations to serve the needs of an expanding market. Zero export quotas for wild-caught animals, and restrictions on the size and number of captive-produced juveniles that could be exported by Tanzania were retained.

We continue to recommend that *M. tornieri* be uplisted to CITES Appendix I. Our rationale for this recommendation is supported by Congdon et al. (1993, 1994) and summarized by Klemens (1989) who said "Although the concept of sustainable management of species has been highly promoted, there are many...who question whether such long-lived animals as turtles and tortoises can be managed on a sustained-yield basis." Listing the Pancake Tortoise on CITES Appendix I would be the most precautionary option, especially if illegal trade and "laundering" animals through other countries continues to be a threat, or if range countries' moratoriums on trade in wild Pancake Tortoises should ever be lifted. As collecting for commercial trade (essentially the only motive for collecting wild Pancake Tortoises) has already caused catastrophic reduction in some populations (Klemens and Moll 1995; Ngwava, unpubl. data), and since natural repopulation of these habitats is unlikely due to the specialized ecology and isolation of suitable habitats of this species, the elimination of all motivation for future legal collecting would be the best protection possible for the Pancake Tortoise.

In the meantime, while the species is still listed under CITES Appendix II, a strict control of captive breeding operations should be exercised by the Tanzanian government, which advocates for sustainable exploitation and nature-based economic enterprises (MNRT 1998). There should be close and regular monitoring of the breeding stocks, hatchlings, and market-ready individuals. This would limit illegal acquisition of extra breeding stock from the wild as well as potentially allowing for the identification of captive-bred hatchlings and their differentiation from illegally acquired individuals. This suggested procedure would necessitate the assignment of ethical wildlife officers to take on the suggested responsibilities. As a long-term strategy, however, DNA fingerprinting and microchipping of the wild populations and the breeding stocks are highly recommended so as to be able to easily identify and therefore limit "laundering" of poached animals (Beebee and Rowe 2004; Ogden et al. 2009).

The ultimate goal of captive breeding programs above and beyond the objective of establishing a legal and sustainable trade should be to re-establish (or establish) viable populations in depleted but still suitable habitats in the wild, preferably in areas where populations could be protected and monitored (e.g., Zug 1993; Malonza 2003). The Tanzanian national parks containing suitable habitat where previous poaching has depleted populations (e.g., Tarangire), and especially Saanane N.P. in Lake Victoria (Harmon 2000 and below), which has suitable habitat but no known natural populations, would seem to provide such opportunities.

We further suggest involvement of local communities in the conservation of the species, especially in habitats outside national parks or other protected areas across the species' range. Apparently, most *M. tornieri* populations and habitats in all known range countries occur outside protected areas (Klemens and Moll 1995; Malonza 2003; Chansa and Wagner 2006; Bombi et al. 2013). Presumably, people will be most likely to support conservation efforts because of two main incentives. First, they may be motivated by the love of what they know and in which they can take pride. This knowledge is usually enhanced by education, and according to Klemens (1997), "Education is an important component for success of any conservation program." Second, local people in developing nations will support conservation efforts when and where there are tangible economic benefits. Consequently, we further recommend the introduction of education programs for local communities, and the general public, intended specifically to sensitize them to the values and inclusive benefits of the species. An education program focusing specifically on the uniqueness and limited distribution of the Pancake Tortoise may help to instill local pride and interest in its conservation, especially if the input of tourist dollars into the local economy may be realized as an associated gain.

Ecotourism programs, such as establishment of wildlife (including tortoise)-based nature walking trails, might provide an approach where monetary incentives to local communities could be realized. This proposed intervention is especially attractive in at least two areas in Tanzania: the Vilima Vitatu (Three Hills) village in Babati District and Jenjeluse village in Kondoa District. The former is situated near the highly visited wildlife-based tourism sites of Tarangire, Lake Manyara, and Serengeti national parks where tourists could conceivably be influenced to stop by the Pancake Tortoise habitats en-route to the Serengeti, for example. In this way the area could generate some support to the village governments while also providing local employment. If such a program became successful, it could be scaled up to include other potential areas and hopefully provide a solid base for local conservation support.

Captive Husbandry. — The Pancake Tortoise has been a common species in captive breeding facilities and/or zoos in the range countries of Tanzania and Kenya (Kabigumila 1998; Kyalo 2008) and abroad (Europe and North America; e.g., Eglis 1960; Shaw 1970; Wilke 1984; Pauler 1988, 1990; Darlington and Davis 1990; Hatcher 1997; Sanz and Valverde 2002). Because of its relatively small size, a properly designed small enclosure is adequate to house a limited number of tortoises. Skelton and Redrobe (2002) recommended enclosure dimensions of at least 2 x 1 m for a pair of tortoises. The enclosure design has almost always been improved by including rockwork with appropriate crevice dimensions. However, Darlington and Davis (1990) used 1.2 m square plywood cages with wooden hide boxes instead. The enclosure substrates have varied among facilities. For example, Darlington and Davis (1990) used 50/50 sand and potting soil enriched with live *Euphorbia* and *Sansevieria*. The species also does well in such enclosures with the right temperature regime and photoperiods (Darlington and Davis 1990; Pickering 1990; Highfield 1996).

Because the species is mostly or completely herbivorous, a vegetable and fruit diet supplemented with vitamins and minerals has been successful in maintaining it in captivity (Darlington and Davis 1990; Kabigumila 1998; Mbassa and Maganga 2002; Skelton and Redrobe 2002). Blake et al. (1996) recommended food plants of high fiber and low protein. This diet prevents excessive growth and development of morphological deformities of the shell (Skelton and Redrobe 2002). Generally, Shaw (1970) testified to the fact that the Pancake Tortoise is a hardy species, comparatively resistant to diseases, and does very well in captivity if properly maintained.

On a larger scale, Harmon (2000) has proposed the use of an island such as Saanane (recently upgraded from a game reserve to a national park) in Lake Victoria, Tanzania, as a possible translocation site and maintenance area for confiscated Pancake Tortoises in the future. The island has the advantage of containing suitable habitat, but probably no Pancake Tortoises are currently resident. Separated from mainland populations, the spread of disease to natural populations from translocated individuals would be unlikely, and protection from poachers heightened.

Current Research. — A field ecological study to understand effects of anthropogenic habitat degradation and alteration on the species viability in Tanzania is in progress by Reginald Mwaya as part of his Ph.D. research. In the future, field research should focus on determining a more exact species range within eastern Africa and elucidate population dynamics and genetic structure of this species. Stanford and Tuma (2013) proposed field research across the range of this species which would contribute knowledge in these areas. Genetic fingerprinting, in particular, will help identify illegal live trade and authenticate that traded individuals came from licensed breeding facilities. At the moment, efforts are underway by Michael Tuma, Day Ligon, Denise Thompson, and Mwaya to initiate genetic studies.

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