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Ecological Characteristics of the Pancake Tortoise, *Malacochersus tornieri*, in Tanzania

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ABSTRACT. – *Malacochersus tornieri* is an inhabitant of rocky outcrops and kopjes located below 1800 m, primarily in the Somalia-Masai floristic region of Tanzania and Kenya. Crevice-rich rock outcrops with well-vegetated substrates separated by intervals of Masai steppe or *Brachystegia* woodland are favored. The species is very specialized in its microhabitat requirements, particularly with regard to the internal dimensions and configuration of crevices in which individuals, pairs (many of which are composed of adult males and females), and occasionally larger assemblages reside. Suitable crevices that provide protection from predators, overheating, and desiccation are limited in number and therefore may regulate population size. Several grass species, leafy vegetation, and aloes that grow in or near these outcrops were identified as food items. Tortoises were observed foraging and moving outside of crevices in November and February, although observations by others and indirect evidence indicate that outside activity also occurs at other times of the year. Tortoises move between crevices, and limited data suggest that males may be more wide-ranging than females. Five females collected in June were determined to be gravid, but we found no evidence of reproduction at other seasons. Considerable variation in ontogenetic and adult color patterns and meristic scute characteristics was observed. Most pancake tortoises display distinct growth zones, which probably represent growth episodes in wet periods and growth cessation during dry periods. Our data suggest that females may attain sexual maturity at approximately 130 mm carapace length, and males mature at 90–100 mm carapace length. Adult males are on average smaller than females.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Malacochersus tornieri*; tortoise; ecology; habitat; growth; kopje; Somalia-Masai floristic region; East Africa; Tanzania

The pancake tortoise, *Malacochersus tornieri*, is a small dorso-ventrally flattened testudinid characteristic of the Somalia-Masai floristic region in Kenya and Tanzania (White, 1983; Broadley and Howell, 1991). This is an arid, semi-desert region characterized by *Acacia-Commiphora* deciduous bushland and thicket, with grasslands on the Serengeti plain and *Brachystegia* woodland in some upland localities. *Malacochersus tornieri* may also be found in the relatively moister Zambezian floral region (White, 1983), where suitable microhabitat is present. The pancake tortoise inhabits crevice-rich rock outcrops and kopjes below 1800 m (Broadley, 1989), its flattened shape and flexible body allowing it to use even very narrow crevices for shelter and protection.

Despite the pancake tortoise's bizarre appearance, which has made it a favorite in the pet trade, it has received relatively little attention from researchers, especially in the field. Procter (1922) published a detailed account of the anatomy of this species, and Loveridge and Williams (1957) published information concerning its distribution, habitat, and systematics, with notes on status and ecology. Loveridge (1944) provided an anecdotal account of its discovery and status in the Dodoma District of Tanzania. Mertens (1942) reported on the behavior of captives. Popular accounts of this tortoise were given by Eglis (1960, 1964, 1967), of its climbing ability by Juvik (1971), and of its captive behavior, care, and reproduction by Shaw (1970). An anecdotal account of aggressive behavior of a captive adult male toward a juvenile was provided by Beattie (1971). More recently, available information concerning the status, distribution, ecology, and conservation of this species has been summarized by Honegger (1979), Pritchard (1979), Groombridge (1982), Broadley (1989), and IUCN/SSC (1989). Darlington and Davis (1990) reviewed the reproduction of captive *Malacochersus*. Ireland and Gans (1972) studied the adaptive significance of the flexible shell.

There has been very little recent field research concerning this species. Alex Duff-McKay and Roger C. Wood conducted surveys for pancake tortoises in Kenya in 1987 (Pritchard, 1987). Their preliminary results indicated that the Kenyan range of *Malacochersus* is more extensive than previously thought and that, despite past exploitation (now banned), viable populations still exist. However, they expressed concern that ongoing habitat alteration for agriculture posed a threat to the species. They stressed the need for further field studies to assess population status. In 1987 they marked 33 tortoises near Samburu, and Pritchard (1987) found three tortoises, one marked, while surveying the same habitat several months later. Wood and MacKay (1993) provided natural history information concerning this population. Broadley and Howell (1991) listed the species as present in Serengeti and Ruaha national parks. Moll et al.

(1993) and Klemens and Moll (1995) previously documented the status and exploitation of pancake tortoises in Tanzania. We now provide additional field observations of the ecology of this species in Tanzania.

METHODS

In June and July (the early dry season) of 1992, we conducted field investigations of the status and effects of commercial exploitation of the pancake tortoise in the Arusha and Dodoma regions of northern and central Tanzania (Moll et al., 1993; Klemens and Moll, 1995) and at the same time collected ecological and natural history data (see Klemens and Moll, 1995, Figs. 1–2, for maps of our study area). Additional field work in February 1992 (Arusha and Dodoma regions) and November 1992 (Ruaha National Park) by field assistant Ayoub Njalale, as well as in February 1993 (Tarangire and Ruaha national parks) and July 1994, March 1995, and September 1995 (Tarangire National Park) by Klemens yielded additional data. These different observation periods allow comparisons of natural populations during seasonal climatic extremes.

Potentially suitable pancake tortoise habitats were located from literature records, by inspection of topographic maps, and through interviews with knowledgeable local persons. Deep rock crevices were searched for pancake tortoises with the aid of flashlights. Macro- and microhabitat characteristics (i.e., configuration, dimensions, and placement of crevices) were recorded in both occupied and unoccupied habitats. The number of tortoises found in each occupied crevice was recorded, and if not extracted (because of inaccessibility or permit constraints), their size and sex was estimated. More exact sex and age data as well as color descriptions, measurements, and reproductive data were obtained from extracted tortoises, from those encountered outside crevices, and from individuals we examined that were obtained by commercial collectors. Most individuals handled were individually marked by notching the carapacial marginals before release. Shell measurements and weights of female and male tortoises were compared using a Student's t-test. Diet was determined from analysis of fecal material obtained from occupied crevices, from newly caught specimens, and from direct observation of foraging animals. Timing and duration of diurnal out-of-crevice activity and extent of movement of tortoises away from crevices was obtained by extended, continuous, daily observation of selected crevices and surrounding areas (0630–1800 hrs) in Ruaha by A. Njalale from 21 to 25 November 1992. The observer was concealed and used binoculars when necessary to aid observations of active tortoises. Additional data on patterns of crevice use, out-of-crevice movements, and crevice fidelity in Tarangire and Ruaha in February 1993 and in Tarangire in July 1994 were also recorded. Growth characteristics were observed in two recaptured individuals in Tarangire between February 1993 and July 1994 and in another individual from Tarangire marked in February 1993 and recaptured in July 1994, March 1995, and September 1995.

RESULTS AND DISCUSSION

Habitat Characteristics and Utilization

Pancake tortoises were found only in rock crevices of suitable dimensions in rock outcrops and kopjes, mainly in arid grassland, *Acacia-Commiphora* bushland, and *Brachystegia* woodland (Fig. 1). Tortoises spend most of their time hiding within crevices, and all those encountered during the February 1992, June–July 1992, and July 1994 surveys were found in crevices.

The orientation of inhabited crevices varied from horizontal to vertical (Fig. 2). The measured distances from entrance to nearest tortoise, entrance width, height of crevice opening at its entrance, and height of crevice opening above the ground were extremely variable (Table 1, Fig. 2). These characteristics probably had little influence on the habitability of crevices. However, crevices inhabited by tortoises generally shared certain similarities, including rock floors (although a few tortoises were found in cave-like crevices at the base of boulders or at the base of vertical crevices on soil substrates) and entrances that were relatively clear of ob-

Figure 1. Typical pancake tortoise habitat in *Acacia-Commiphora* bushland at Tarangire National Park (**left**) and in *Brachystegia* woodland near Kolo (**right**).

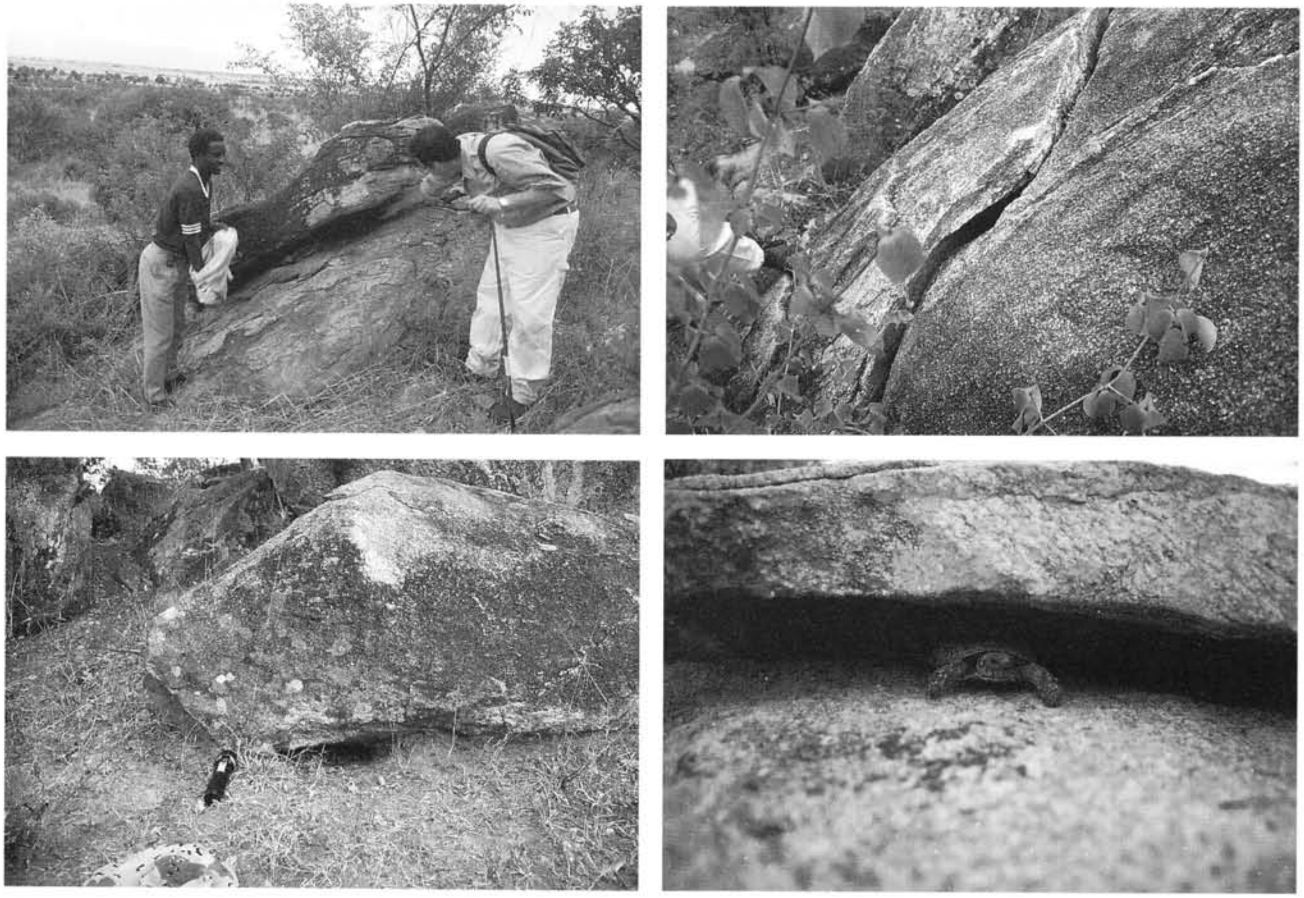

Figure 2. Several representative crevice configurations, all of which contain one or more pancake tortoises.

structions (e.g., soil and detritus other than tortoise droppings, vegetation, spider webs, etc.). Inhabited crevices are apparently kept clear by the regular movements of tortoises within the crevice as well as by frequent passage through the entrance opening. The most definitive characteristic of tortoise-inhabited crevices was that they taper at some point to a height of approximately 5 cm or less. This narrow section of the crevice, especially if it is deep within the crevice, is the location to which pancake tortoises retreat (see "distance to tortoise" in Table 1).

In these narrow areas tortoises are able to wedge themselves tightly between the floor and ceiling of the crevice and are extemely difficult to dislodge. Wedging is accomplished by two different behaviors. In wider crevices tortoises can extend and brace the hind legs to force the ossified rear (fifth vertebral) dorsal carapacial projection against the ceiling, usually while facing away from the crevice entrance. The function of this carapacial hump also is suggested by its often relatively greater degree of wear compared to other areas of the carapace. With slightly narrower crevices, where the tortoises can contact the floor and ceiling without leg extension, a different wedging mechanism is employed. We observed that by withdrawing their legs tightly, tortoises forced out a balloon-like unossified area of their plastron (Fig. 3) which, by increasing the shell height of the tortoise, wedged them even more tightly into the crevice. The observation of this balloon-like area contradicts the report by Ireland and Gans (1972), based on laboratory observations of pancake tortoises, which discounted their ability to inflate themselves. Our observations support the original account of this behavior by Loveridge and Williams (1957).

Another general similarity of the inhabited crevices above ground level is usually a relatively gentle descent point from the crevice entrance to the soil substrate at the base of the rocks that contained the crevice. This allows the tortoises easy access to and from edible vegetation growing at the base of the rocks. Their occasional presence in less accessible crevices atop rock faces with steep slopes to the ground, in some cases approaching 45°, suggests remarkable rock climbing ability. Juveniles also often inhabited smaller crevices and were often nearer to crevice entrances than were adults (Table 1).

The rocky areas that contain the crevices the tortoises inhabit were mainly outcrops of exfoliating granite interspersed along hillsides of varying slope from nearly flat to as steep as 45°. In the areas covered in our surveys, the best habitats were low, gently rolling hillsides with numerous granite outcrops that provided many large crevices of the configurations detailed above. These outcrops were separated by small grassy areas (as in Tarangire) or along *Brachystegia*-wooded slopes (such as in upland habitats near Kolo, Dodoma Region) (Fig. 1). We had little success in single, isolated kopje-type habitats, although we have reliable personal communications of the presence of pan-

Table 1. Distance (cm) from entrance to nearest pancake tortoise and selected crevice dimensions (cm) of rock crevices occupied by one or more adult (Ad) or juvenile (Juv) pancake tortoises in Tarangire National Park (TNP) (6/92 and 2/93) and Ruaha National Park (RNP) (2/93). Means, one standard deviation, and ranges of measurements (in parentheses) are provided.

Age, Location, Time Period	No. of Crevices	Distance to Nearest Tortoise	Entrance Height	Entrance Width	Distance to Ground
Ad, TNP Jun 92	7	85.3±31.0 (76–137)	>46.1* (3.8–>244)	>78.0* (7.6–>244)	34.8±38.3 (0–99)
Ad, TNP, RNP Feb 93	14	119.5±55.0 (20–190)	>30.8* (5–>244)	>114.7* (19–>480)	76.6±100.9 (0–345)
Juv, TNP Jun 93	2	25.4±18.0 (13–38)	5.1±0 (0)	14.0±9.0 (8–20)	20.3±28.7 (0–41)
Juv, TNP, RNP Feb 93	7	44.1±20.9 (18–74)	45.0±85.1 (3–235)	41.9±42.3 (3–109)	91.7±72.1 (0-175)

*Means are estimated as some dimensions could not be measured precisely with equipment available.

cake tortoises from or near such habitats in the Dodoma area (J. de Graaf), Seronera (P. Moehlman), and the Moru Kopjes of Serengeti National Park (A. Sinclair).

Our observations suggest that optimal pancake tortoise habitat is usually provided by rock outcrops and kopjes that have been exposed long enough for weathering and erosion to produce suitable crevices and collect substrates capable of sustaining vegetation. Older areas that have degraded into sparsely vegetated rubble are not suitable as pancake tortoise habitats. The frequency and location of these "middle-aged" rocky habitats must ultimately determine the abundance and distribution of the pancake tortoise in East Africa. We also intensively searched some apparently suitable habitats without finding tortoises (Moll et al., 1993; Klemens and Moll, 1995). Some of these had been depleted by commercial tortoise collectors or, perhaps at one site (Yaedachini Game Controlled Area near Lake Eyasi) by a hunter-gatherer tribe (Hadza) whose women use the tortoise as a source of food (Klemens, 1992). The absence of tortoises in some areas searched could be due to altitude. We found no pancake tortoises in apparently suitable habitats above 1800 m, which Broadley (1989) reported as the maximum elevation recorded for this species. The location of suitable habitats in relation to possible source populations may also be important. Although pancake tortoises leave their crevices to forage and mate in the immediate vicinity (see below), the extent to which they disperse from their home crevices and the distances they can travel are unknown, but dispersal distances are probably limited.

Predation

At least seven pancake tortoises encountered in field surveys in Tarangire in 1992 and 1993 had been killed by predators. We were informed by a tortoise collector that the *quicheche* (probably either the large grey mongoose, *Herpestes inchneumon*, or a genet) is a regular predator of this tortoise in the Sangaiwe Hills. We observed a white-tailed mongoose, *Ichneumia albicauda*, a potential tortoise predator, on a kopje at Tarangire. While the crevice environment undoubtedly provides protection from overheating and desiccation, the microhabitat requirements of pancake tortoises could be the result of intense selection pressure imposed by small, agile predators such as these. The number of crevices of suitable dimensions, which is often limited in even large expanses of suitable rock outcrop macrohabitat, may limit population size in any given habitat. The population could be further limited by social behavior

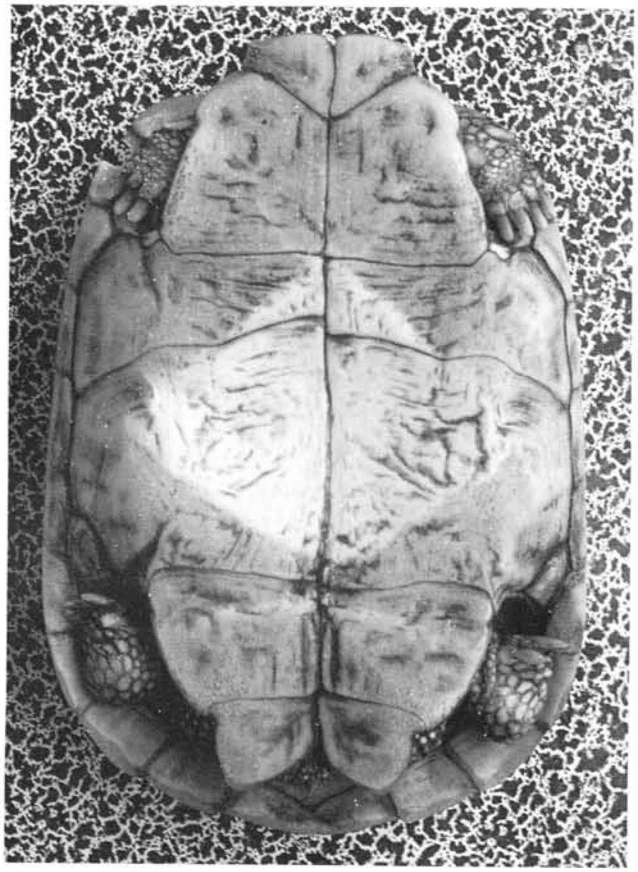

Figure 3. Unossified area (central lighter colored area of plastron) which can be distended slightly to allow the tortoise to more tightly wedge itself against crevice walls.

Table 2. The occurrence of 115 pancake tortoises observed in solitary or grouped assemblages in crevices and their known or estimated composition by sex and state of maturity (ad = adult, subad = subadult, juv = juvenile). Data were collected from surveys in June and July 1992 and July 1994 in Tarangire and various localities in northern Tanzania (e.d. = early dry season), in Ruaha in November 1992 (l.d. = late dry season), and in Tarangire and Ruaha in February 1993 (w. = wet season).

Number and Composition of Tortoises Observed per Crevice	Total No. of Occurrences	When Observed and No. of Occurrences (in parentheses)	Percentage of Total Tortoises Observed
10 - mainly ad, some juv	1	e.d.	8.7
5 - 1 ad, 4 juv	1	l.d.	4.4
4 - 1 ad ♀, 3 juv (l.d.); 1 ad ♂, 1 subad ♂, 1 ad (sex?), 1 juv (w.)	2	l.d., w.	7.0
3 - 3 ad (e.d.); 2 juv, 1 ad (sex?) (l.d.)	2	e.d., l.d.	5.2
2 - ad (sex?)	9	e.d. (3), l.d. (1), w. (5)	15.7
2 - ad ♀	1	e.d.	1.7
2 - 1 ad ♀, 1 ad ♂	11	e.d. (4), w. (7)	19.1
2 - 1 ad (sex?), 1 juv	1	l.d.	1.7
1 - solitary ad ♂	10	e.d. (3), l.d. (1), w. (6)	8.7
1 - solitary ad ♀	5	e.d. (1), w. (4)	4.3
1 - solitary ad (sex?)	10	e.d. (8), l.d. (1), w. (1)	8.7
1 - solitary juv	17	e.d. (8), w. (9)	14.8

that apparently limits the number of tortoises inhabiting any given crevice (see below). We found no evidence of predation on tortoises by domestic or feral species in habitats near settlements.

Patterns of Assemblage and Crevice Fidelity

In habitats considered unexploited by commercial tortoise collectors (Moll et al., 1993; Klemens and Moll, 1995) multiple assemblages as well as single tortoises often were present in suitable crevices in both dry and wet season surveys (Table 2). Pancake tortoises were usually encountered in pairs or as single individuals (38.3 and 36.5% of total tortoises encountered in crevices, respectively), but larger assemblages of tortoises (up to 10) were also occasionally observed. Loveridge and Williams (1957) described an association of 11 individuals under one slab of rock at Dodoma in January. Whereas both adults and immature tortoises were frequently found in larger assemblages, all but one pair of tortoises were composed of two adults (21 of 22 pairs, 96%). Of these adult pairs, we were able to confirm that 11 (52.4%) were male and female, and we suspect most of the others were also (we were not always able or permitted to extract individuals to confirm identifications). Male-female pairs were particularly common in crevices during the wet season (64% of occurrences). Solitary adult males and females were regularly encountered, and juveniles were most frequently encountered singly within crevices.

While our data are limited, we have obtained information on movement of marked individuals between crevices and on crevice fidelity in Tarangire. A subadult male, which was part of a four-tortoise crevice assemblage in February 1993 (Table 2), had moved 36 m to inhabit another crevice in the vicinity by July 1994 (the original crevice still housed several adults). A crevice inhabited by a solitary adult male

Table 3. Tortoise activity patterns observed outside six clustered crevices at Ruaha National Park, Tanzania in late dry season (November 1992). The weather was hot, sunny, and dry during the five-day survey. All observations by A. Njalale (*pers. comm.*).

Date	Crevice Number	No. of Tortoises Within	Maturity	Emergence Time	Re-entry Time	Total Time of Outside Activity (min)	Activity	Estimated Area of Movement (m^2)
Nov. 21	1	1	adult	1352	1412	20	foraging for grass	1
Nov. 22	1	3	adult	1513	1537	24	foraging for grass	3
			juv.	?	1541	?	foraging for grass	?
			juv.	–	–	–	did not emerge	–
Nov. 22	2	5	small juv.	1040	1126	46	foraging for grass; inactive for 6 min	4
			small juv.	1045	1123	38	foraging for grass; inactive for 7 min	4
			small juv.	?	1216	?	foraging for grass	?
			adult female	1305	1340	35	foraging for grass	8
			juv.	1308	1343	35	foraging for grass	8
Nov. 23	3	4	juv.	1214	1217	3	inactive	1
			adult female	?	1220	?	foraging for grass	?
			juv.	1340	1420	40	foraging for leaves	5
			small juv.	1342	1410	28	foraging for grass; inactive ca. 15 min	2
Nov. 24	4	2	adult	–	–	–	did not emerge	–
			juv.	–	–	–	did not emerge	–
Nov. 24	5	1	adult male	1405	1434	29	foraging for leaves and grass	6
Nov. 25	6	2	adults	–	–	–	did not emerge	–
Means						$\bar{x} = 29.8$		$\bar{x} = 4.2$

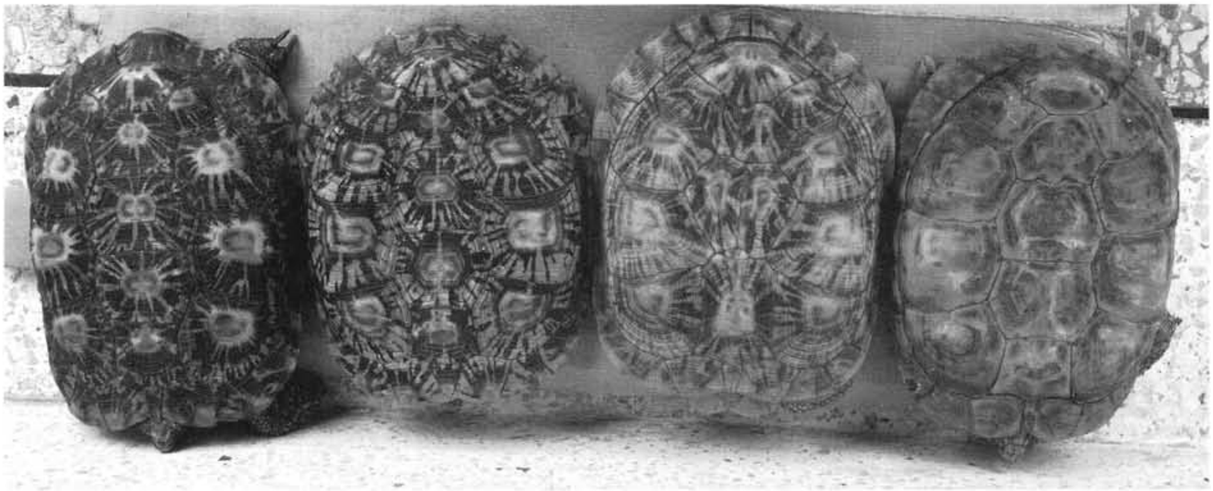

Figure 4. A selection of four adult pancake tortoises from the Sangaiwe Hills, Tanzania, illustrating variation in carapacial color and pattern.

marked in February 1993 was inhabited by an unmarked male-female pair in July 1994. A crevice inhabited by a male-female adult pair marked in February 1993 was inhabited by the same female in July 1994, but the male was no longer present. Similarly, the female of another adult male-female pair observed and marked in February 1993 was still resident in the same crevice in July 1994, but the male was again not present (though another unmarked female was present). In another case, although not based upon marked individuals, an adult that was observed alone in a crevice at Ruaha in November 1992 was probably the same adult joined by two juveniles in the crevice the next day (see Table 3). These observations suggest that pancake tortoises exhibit complex social behavior with more wide-ranging males possibly circulating among crevices inhabited by relatively sedentary females — an aspect of their life history that warrants further investigation.

Commensals

Other reptiles usually associated with pancake tortoises in rocky habitats examined in Tarangire were agama lizards (*Agama agama elgonis*), gekkos (*Hemidactylus squamulatus* and *Pachydactylus tuberculosus*), skinks (*Mabuya striata* and *Mabuya v. varia*), and plated lizards (*Gerrhosaurus m. major*) (Klemens and Nikundiwe, 1995). These often occurred microsympatrically in crevices inhabited by pancake tortoises. *Gerrhosaurus* was especially useful as an "indicator species" of suitable pancake tortoise microhabitat, although its absence did not necessarily indicate unsuitable habitat because it, like the pancake tortoise, had often been removed from outcrops for the commercial animal trade (Moll et al., 1993; Klemens and Moll, 1995).

Activity Outside Crevices

Loveridge and Williams (1957) recorded young individuals basking on top of a rock slab at 0900 hrs, and prior to our study we received reliable personal communications of pancake tortoises observed outside crevices. Job de Graaf observed a male chasing a female across a dirt road near the base of Simba Hill in Dodoma, Patricia Moehlman saw a pancake tortoise crossing a vehicle track at the Serengeti Wildlife Research Center, and Kim Howell reported a few active tortoises, including a copulating pair on rocky ground near the Ruaha River Camp (Ruaha National Park) in December 1991.

Although we encountered no tortoises outside their crevices in June or July, animals in the crevices were alert and produced fecal matter containing fragments of fresh vegetation, indicating recent foraging activity. Extended observations between 0630 and 1800 hrs for five days at six crevices clustered in a rocky area near Mwayangi River Camp at Ruaha in November (by A. Njalale) and our intensive field surveys conducted at Tarangire and Ruaha in February also confirmed regular out-of-crevice activity during these months.

Pancake tortoise adults and juveniles at Ruaha were observed leaving crevices from mid-morning to late afternoon to forage upon grasses and leafy vegetation. Occasionally tortoises remained inactive in the vicinity of the crevice before returning to it (Table 3). The mean activity time outside the crevice was 29.8 min ($n = 10$ animals), and the mean estimated area covered during foraging activity was 4.2 m^2.

In the February 1993 wet season at Tarangire, an adult male tortoise was collected at 1600 hrs as he moved quickly toward a crevice from lush, shaded, herbaceous riverside vegetation about 70 cm away. Also in February, at Ruaha, three young tortoises and one adult male-female pair were encountered outside crevices at 0900, 1120, 1200, and 1500 hrs, respectively.

Loveridge and Williams (1957) suggested that pancake tortoises probably emerge from crevices only during the early morning hours, but our observations indicate that outside activity may occur any time of the day.

Diet and Access to Water

Plants growing near the crevices inhabited by pancake tortoises were apparently the main dietary source. Feces

Table 4. Mensural characteristics of 40 adult female and male pancake tortoises from three combined north-central Tanzanian localities (Sangaiwe Hills, Tarangire N.P., and Ruaha N.P.). Means, one standard deviation, and ranges (in parentheses) are provided. Length and width are expressed in mm and mass in g.

Measurement	Females (*n* = 22)	Males (*n* = 18)
Carapace Length	146.2 ± 36.5 (131.0–178.4)	140.1 ± 20.7 (90.0–170.4)
Carapace Width	113.2 ± 9.5 (96.0–142.0)	101.6 ± 11.9 (76.0–120.2)
Plastron Length	147.1 ± 24.1 (129.0–176.2)	136.4 ± 20.1 (86.0–162.3)
Mass	380.0 ± 118.5 (220.0–600.0)	260.4 ± 94.0 (75.0–380.0)

obtained from pancake tortoises near Iyoli Village in the Dodoma Region in June 1992 consisted of fragments of grasses, including star (*Cynodon* sp.), drop seed (*Sporobolus* sp.), and red oat grass (*Themeda triandra*). Small pieces of aloe were present in most of the fecal pellets analyzed. These were common plant species in the kopjes and outcrops inhabited by the tortoises. At Ruaha, tortoises were foraging upon the grass *Panicum* sp. (Poaceae) and the leaves of *Achyranthes aspera* (Amaranthaceae). Loveridge and Williams (1957) observed one individual feeding on dry grass near Tabora. Raphael et al. (1994) observed differences in the levels of gamma-tocopherol in the blood samples collected at Tarangire and Ruaha in February 1993. These differences reflected a diet high in seeds and nuts at Ruaha.

Although tortoises often voided relatively large amounts of pungent fluid when handled during dry season surveys, we saw no readily accessible sources of water near most tortoise-inhabited outcrops. However, some crevices observed during the wet season contained pools of standing water, which were used by resident tortoises.

Reproduction

Loveridge and Williams (1957) stated that pancake tortoises produced a single egg in July or August, and Shaw (1970) recorded that in captivity a female may lay several eggs in a year. While Darlington and Davis (1990) said that the presence of oviductal eggs could not be determined by palpation of pancake tortoises, we found this technique valid, although somewhat more difficult than with most chelonians. We judged that five females from the Sangaiwe Hills collected in June were gravid. Palpation of females collected at other times produced no evidence of oviductal eggs. Hatchlings and very small juveniles were observed in all seasons we surveyed. Although adult male and female pairs were definitely associated with one another in both dry and wet seasons, we observed no copulatory behavior. Both accounts of mating behavior stated above (J. de Graaf and K. Howell, *pers. comm.*) were observations during the wet season, as were Loveridge and Williams' (1957) observations of precopulatory behavior in captive individuals (in January and February).

Coloration, Size, and Growth

The Tanzanian pancake tortoises observed in this study conform largely to the general physical description, characteristics of ontogenetic color change, and extensive degree of adult color and pattern variation described for the species by Broadley (1989) and Loveridge and Williams (1957).

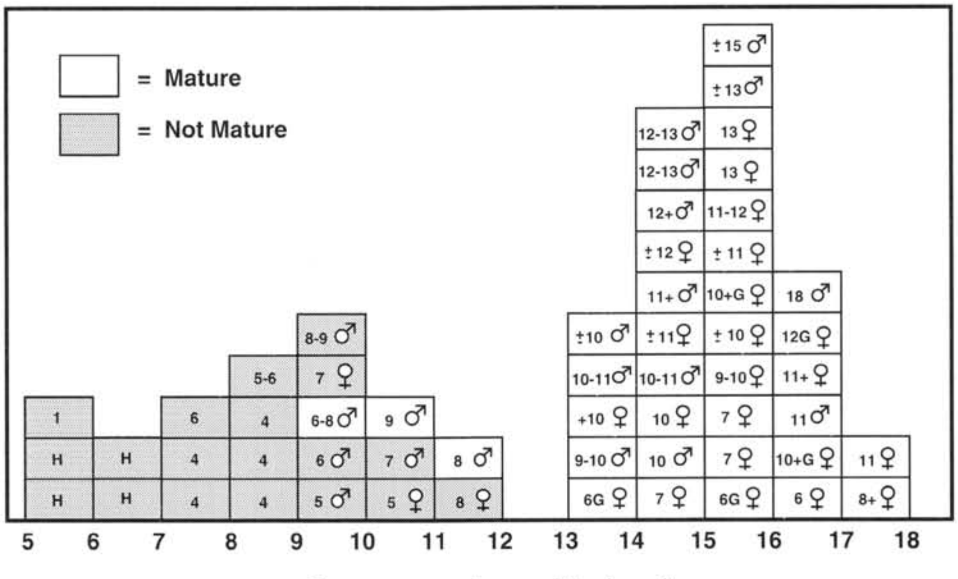

Figure 5. The carapace lengths of 57 pancake tortoises collected from several Tanzanian localities in relation to their degree of maturity, sex, and number of annuli displayed. In the boxes, the letter "G" = gravid females, "H" = hatchlings, and numbers = annuli. As no specimens were killed, the sex and maturity designations between 9 and 12 cm carapace length should be considered subjective. Decisions were based upon a combination of tail morphology and color patterns which change with maturation (see text).

Hatchlings and small juveniles have yellow carapacial scutes with broad brown borders, and vertebrals and costals usually contain a medial brown blotch or spot. The marginals are usually bordered with brown proximally and along their lateral margins. The plastron is pale yellow. Hatchlings are nearly circular but become increasingly elongated and rectangular as they mature. The ontogenetic changes in color that occur are quite variable. Generally, the brownish scute borders and sutures and the medial scute blotches become more irregular and interrupted with yellow rays. The yellow plastral scutes become increasingly bordered by dark brown sutures interrupted by light rays. Adult carapacial color patterns are extremely variable, ranging from light yellow or tan with darker rays running through each scute to black with yellow rays running through the scutes (Fig. 4). Some individuals, presumably the oldest ones, have lost the carapacial pattern entirely and are horn colored. The plastral pattern of most adults remains much as described for juveniles, but in some individuals the soft unossified central area of the plastron is sometimes much lighter in color than the surrounding areas (Fig. 3). In older individuals the plastron may also become horn colored and unpatterned. As Loveridge and Williams (1957) found, we also noted frequent divergence from standard meristic carapacial scute patterns, and scute shapes were quite variable in individuals from our study areas.

Measurements of 40 adults (22 females, 18 males; sex ratio 1.2:1) from Tanzania are provided in Table 4. Carapace length in females ranged from 131.0–178.4 mm with a mean of 146.2 mm and in males 90.0–170.4 mm with a mean of 140.1 mm. The largest female recorded by Loveridge and Williams (1957), a 177.0 mm specimen from Kenya, was slightly smaller than our largest. Our largest male exceeded the largest male recorded by Broadley (1989) at 167 mm carapace length. In general, Tanzanian females were significantly longer, wider, and heavier than males in our sample ($P < 0.05$) for each mean measurement. These physical differences and distinctive sexual differences in tail morphology (males have longer, thicker tails than females) often allowed us to qualitatively recognize males and females *in situ* without extraction from crevices. Similarly, we could usually differentiate between adults and juveniles in crevices based upon size (and sometimes color pattern), as individuals over 120 mm carapace length were always adults (Fig. 5).

We observed up to 18 distinct growth rings on the plastral scutes of 57 tortoises examined (Fig. 5). The factors that influence the development of growth rings and boundaries (indicating growth cessation) are not absolutely clear. We observed a characteristic "double ring" pattern in many specimens from northern Tanzania (especially evident in earlier growth periods) where a relatively wide area of growth was separated from a very narrow area by a demarcation line. The narrow area was then bordered by another line, followed by another wider area, etc. We suggest that this pattern indicates that two growth periods typically occur each year. These may be correlated with the "long rains" (approximately February to June) and the "short rains" (approximately October to November) which characterize northern Tanzania's weather (Norton-Griffiths et al., 1975; Sinclair, 1977; Sinclair and Norton-Griffiths, 1979). In central Tanzania, which is usually characterized by single wet and dry seasons annually, the "double ring" growth pattern was not evident in the small pancake tortoise sample observed. We believe young individuals here probably produce only one growth ring annually. Age determination of pancake tortoises by growth rings is less reliable as age increases. Not only are growth areas progressively narrower and increasingly subject to misinterpretation and miscounting, but a variable number of growth rings may be accumulated or lost by individuals within the same time period (Table 5). Three marked individuals from Tarangire examined in both February 1993 and July 1994 had accumulated approximately four, three, and two additional rings, respectively, in the interim 17 months. One of these individuals recaptured twice in 1995 had lost three or four rings since 1994. The reasons for this variation are unknown. Germano and Fritts (1994) have also noted instances in which annuli counts do not match known ages in desert tortoises, *Gopherus agassizii*.

Table 5. Growth of three recaptured pancake tortoises in Tarangire National Park.

Tortoise	R-3	L-1, L-2	L-3, R-3
Sex	female	female	male
Carapace Length			
Feb 93	151.0	144.0	117.0
Jul 94	153.5	147.0	132.5
Mar 95		148.5	
Sep 95		148.5	
Plastron Length			
Feb 93	148.0	149.5	116.5
Jul 94	152.0	152.0	128.5
Mar 95		153.5	
Sep 95		153.0	
Carapace Width			
Feb 93	106.0	102.0	90.5
Jul 94	110.5	102.5	97.0
Mar 95		103.5	
Sep 95		102.5	
Weight			
Feb 93	390.0	365.0	165.0
Jul 94	410.0	355.0	200.0
Mar 95		385.0	
Sep 95		400.0	
Annuli			
Feb 93	± 13	± 12	8
Jul 94	17	± 15	± 10
Mar 95		11–12	
Sep 95		12	

We observed a correlation between increasing numbers of growth rings and increasing carapace length of tortoises (Fig. 5). Based upon the onset of adult color patterns, secondary sex characteristics of mature individuals (i.e., mainly the presence of longer, thicker tails in adult males), and the presence of oviductal eggs in some females, we estimated that sexual maturity may be attained by some males at 90–100 mm carapace length and by some females at approximately 130 mm carapace length. Recaptures of three animals in July 1994 (which had been originally measured and marked in February 1993 with one of them subsequently recaptured again in March 1995 and September 1995) provide our only direct observations of growth (Table 5). One adult female had grown 2.5 mm in carapace length and 20 g heavier during the 17 months. An adult male had grown 15.5 mm in carapace length and 35 g heavier in the same 17-month period. Another adult female had increased 3.0 mm but lost 10 g over the same 17-month period, but gained 1.5 mm and 45 g over the next 14 months, for a total gain of 4.5 mm in carapace length and 35 g in mass over 31 months.

Opportunities for comparisons of our data with other pancake tortoise populations and with other crevice-dwelling tortoise species are limited due to the paucity of such studies. However, Wood and MacKay (1993) studied a pancake tortoise population in the Kitui District of Kenya. Their findings were generally similar to ours in most respects. Kenyan pancake tortoises were found only in crevices in low, irregularly spaced exfoliating granite rock outcrops, set in *Acacia-Commiphora* bush, and they were often encountered in adult male-female pairs. They encountered adults in an approximately 1:1 sex ratio and considered tail morphology to be the only notable sexually dimorphic character. More data based on larger sample sizes should be collected to resolve this issue. Bayoff (1995) found another crevice-dwelling tortoise, *Homopus signatus*, only in crevices (primarily east-facing) in dolomite kopjes in South Africa during December–January surveys. He encountered nearly twice as many females as males (all adults), perhaps because they were larger and more conspicuous in the crevices. Unlike pancake tortoises in our study, *H. signatus* was usually encountered in a state that suggested mild estivation and always as solitary individuals. Branch (1988) recorded this species as actively foraging among granite slabs in the early morning hours and grouping together under rock slabs for shelter. Perhaps these differing accounts reflect seasonal activity differences. The biology of two other crevice-dwelling South African tortoises, *Homopus boulengeri* and *H. bergeri*, is essentially unknown (Boycott and Bourquin, 1988; Branch, 1988).

Our investigation of pancake tortoises is ongoing. Marked and recaptured specimens, particularly in Tarangire National Park, continue to provide data on the growth, movements, and social behavior of this species. Based upon the observations we have reported here, mark-recapture studies may be a particularly fruitful source for further data.

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