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Status and distribution of the angonoka tortoise (*Geochelone yniphora*) of western Madagascar

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Abstract

From 1993 to 1995, field surveys were conducted in western Madagascar to assess the current status of the angonoka tortoise (*Geochelone yniphora*) in the wild. Tortoise presence was documented at 10 of 11 localities surveyed. These localities represent at least five populations, all within a 30-km radius of Baly Bay, near the town of Soalala. The populations occur on fragments of habitat ranging from < 50 to 4–6000 ha in size. One hundred and forty-five tortoises were marked in the five populations. Hatchling or juvenile tortoises were observed in all populations, indicating that reproduction was occurring. Most of the 145 tortoises (68%) were marked on Cape Sada, where monthly surveys were conducted. The tortoise density on the c. 150 ha peninsula was 0.66 tortoises/ha. The remains of 22 dead juveniles were found on Cape Sada over the 2-year period. This evidence, combined with the low number of juveniles in intermediate size classes in the Cape Sada population suggests that juvenile mortality may be high.

Keywords: Testudines; Testudinidae; *Geochelone yniphora*; Angonoka; Ploughshare tortoise; Madagascar

1. Introduction

The angonoka or ploughshare tortoise (*Geochelone yniphora*) is considered one of the rarest tortoises in the world (Angel, 1931; Juvik et al., 1981; Groombridge, 1982; Curl, 1986a; Durrell et al., 1989). This species has a distinctly domed carapace (Fig. 1) and received its English common name from its single elongate gular projection. The angonoka is endemic to Madagascar and occurs only in bamboo-scrub habitat in the Baly Bay region in the western part of the island (Blanc, 1974; Juvik, et al., 1981; Curl et al., 1985). All known localities of *G. yniphora* occur within a 30-km radius of Baly Bay. *Geochelone yniphora* was first described from specimens obtained from Arab sailors in the Comoro Islands in 1884 (Vaillant, 1889). The specimens were thought to have originated from an island north-northeast of Comoro, in the vicinity of Aldabra. A later specimen was thought to have come from Tulear in southwest Madagascar (Vaillant, 1889). The natural distribution of the species was not discovered until the early 20th Century when Voeltzkow (Siebenrock, 1903) collected a wild specimen at Cape Sada in northwestern Madagascar.

Although the natural range of the angonoka was discovered in the early 20th Century, little was known of the status of wild populations until the 1970s when a series of field surveys in the Baly Bay region were conducted (Juvik and Blanc, 1974; Juvik et al., 1981). They estimated that the population density of *G. yniphora* was unlikely to exceed five tortoises per km^2. They further estimated that with < 100-km^2 of habitat remaining, the total population size was likely to be no more than a few hundred tortoises. In 1983, Curl et al (1985) conducted field surveys and verbal interviews in the region and estimated that as few as 100–400 angonoka existed in the wild and that only 40–80-km^2 of bamboo-scrub habitat remained. Later surveys primarily were focused at Cape Sada, the most accessible tortoise population (Reid, 1991; Reid, 1993; Juvik et al., 1997). Results of these surveys suggested that the Cape Sada population was very small (< 30 individuals) and vulnerable.

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Fig. 1. Bourou Robert with an adult angonoka (*Geochelone yniphora*) from Cape Sada.

The reasons for the rarity of the angonoka are not fully understood. However, past commercial exploitation may have been a contributing factor. Historic records indicate that during the 17th Century, large numbers of *G. yniphora* were exported to the Comoro Islands where they were sold as food (Vaillant and Grandidier, 1910). Today, local people generally do not eat angonoka and because the species has become so rare, commercial trade is minimal. However, tortoises are sometimes kept as pets by local people (Durbin et al., 1996). Additional factors that may have contributed to the endangered status of the angonoka include habitat loss as a result of anthropogenic brush fires and predation of eggs and young tortoises by the non-native African bush pig (*Potamochoerus larvatus*) (Juvik et al., 1981; Groombridge, 1982; Curl et al., 1985; Durrell et al., 1989). Brush fires are set to promote growth of grasses for free ranging cattle and to drive cattle from the forest. Fires also are used to maintain a clearing around vegetable gardens to keep bush pigs away (Durbin et al., 1996). The African bush pig is widespread in the Baly Bay region (Juvik et al., 1997).

In 1986, Jersey Wildlife Preservation Trust (JWPT), in collaboration with the Malagasy Direction des Eaux et Forêts, began a captive breeding program for the angonoka in Madagascar (Curl, 1986b). The purpose of the program was to establish a secure breeding population of tortoises, with the intent of augmenting wild populations if necessary. In 1993, a 2-year ecological study of the Cape Sada angonoka population was initiated. In 1994 and 1995 JWPT field teams conducted regional surveys to assess the status of all wild populations of angonoka. This paper summarizes the results of these surveys.

2. Methods

2.1. Description of study area

The study area, hereafter referred to as the Baly Bay region, is located on the west coast of Madagascar c. 90-km south of the city of Mahajanga (lat. 16° 2' S, long. 45° 20' E). The climate in the Baly Bay region is tropical with a distinctly seasonal rainfall pattern. Nearly all rainfall occurs in the 6-month period from November to April (Donque, 1972). The mean annual temperature at the town of Soalala on Baly Bay is 26.5°C, with monthly means ranging from 26°C in July to 28°C in April.

Dry deciduous forest, savanna, and mangrove swamps are three distinct vegetation types in the Baly Bay region. The bamboo-scrub habitat of the angonoka may be a secondary stage of the dry deciduous forest (Curl et al., 1985). Bamboo-scrub habitat consists of a mosaic of shrubs, bamboo, savanna grasses, and open, unvegetated areas. The shrubs are generally <2-m in height, and the most common species are *Bauhinia* sp. and *Terminalia* spp. Bamboo (*Perrierbambos madagascariensis*) occurs in dense thickets within the habitat. A few shrubs and satrana palms (*Hyphaene shatan*) are interspersed in the bamboo thickets, but ground cover vegetation is largely absent. Small savanna-like patches and unvegetated rocky areas occur within the scrub-shrub habitat. Grasses in the savanna-like patches include *Aristida* sp., *Eragrostis* sp., and *Heteropogon contortus*.

2.2. Data collection

In 1993, a field research station was established at Cape Sada, on the eastern side of Baly Bay (Fig. 2). Detailed ecological data were collected on the Cape Sada angonoka population from October 1993 to June 1995 (Smith, 1995; Smith et al., in press). The research station also was used as a base from which regional tortoise surveys were conducted.

Regional field surveys were conducted from October 1994 through April 1995 at 11 localities. Areas surveyed were chosen based on both historic records and on interviews with local villagers. Surveys were concentrated in the wet season (from December to April),

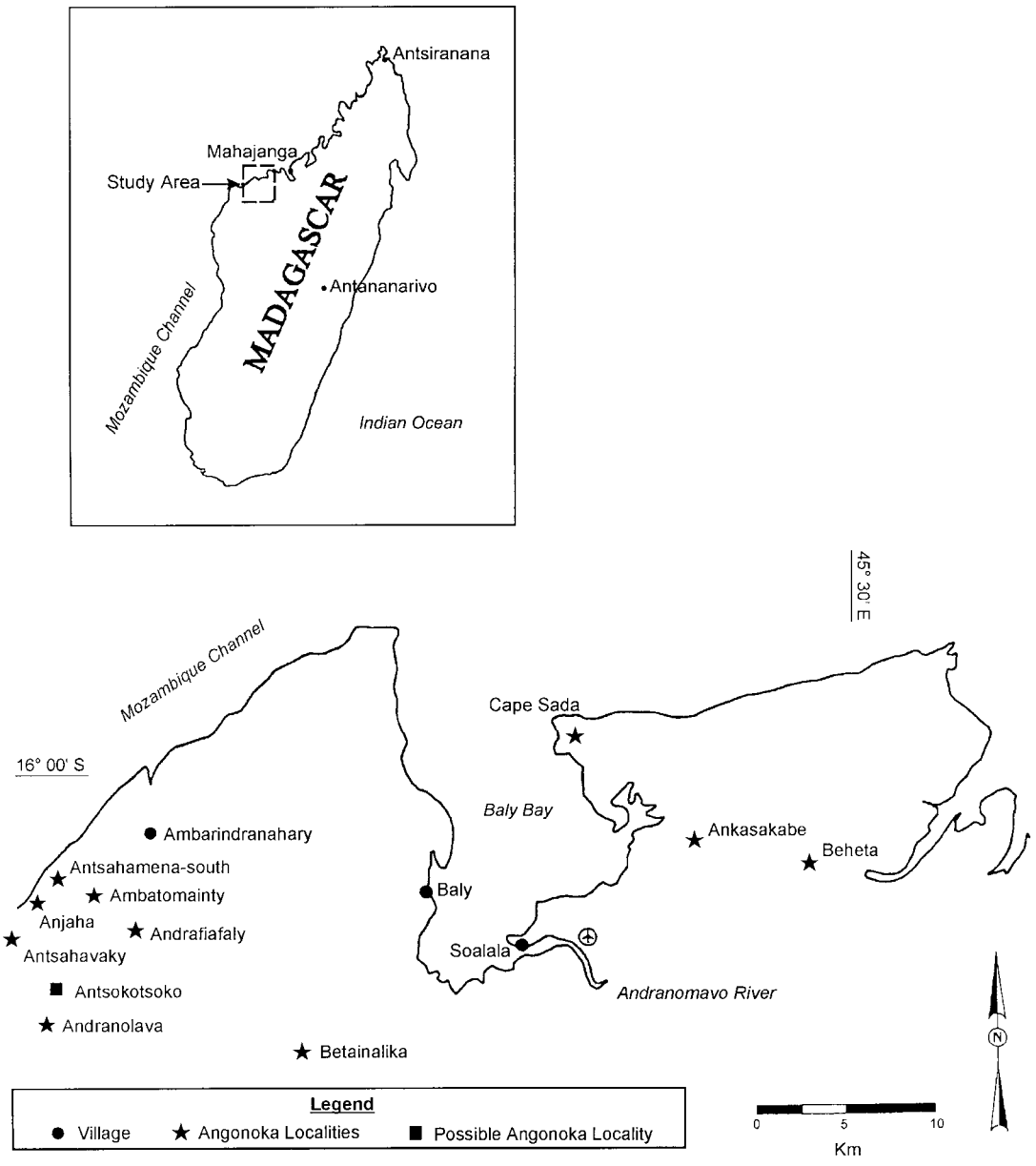

Fig. 2. Map of the study area depicting localities of the angonoka tortoise *Geochelone yniphora* in western Madagascar. All localities occur in a 30 km radius of Baly Bay.

when angonoka are most active. The localities surveyed and field trip dates are listed in Table 1. Surveys were conducted monthly at Cape Sada (from October 1993 to March 1995), in an attempt to mark all individuals in the population. All surveys generally were conducted between 0600–1100 h and 1500–1800 h.

The bamboo-scrub habitat contains impenetrable patches of shrubs and bamboo that precluded the use of formal transect surveys. Rather than clear transects through the habitat, surveys in this study consisted of timed searches for tortoises. During these searches, participants walked roughly parallel transects looking for tortoises, tracks, or feces. Transects were c. 10–20 m apart, depending upon the density of the vegetation. In heavily vegetated areas, where visibility was low, transects were as close as necessary to search each area thoroughly. The number of survey participants ranged from three to seven individuals including trained field biologists and local guides. To minimize observer variation, at least three highly experienced observers were used for all surveys. Local guides typically had no formal training but were familiar with the terrain and habits of angonoka. The observation rate for each area was calculated as the number of tortoises observed per survey-hour.

When a tortoise was encountered, the date, time, weather, microhabitat (i.e. scrub-shrub, bamboo, grass,

Table 1
Number of wild angonoka (*Geochelone yniphora*) observed during regional surveys around Baly Bay in western Madagascar from 1993 to 1995

Location	Survey dates	Males	Females	Juveniles	Total
East Baly Bay					
Cape Sada	6 October 1993–24 June 1995	14	27	58	99
Beheta	11–12 October 1994; 11–15 December 1994; 17–19 March 1995; 22 May 1995	9	6	3	18
Ankasakabe	20 March 1995; 8–9 April 1995	2	0	0	2
West Baly Bay					
Ambatomainty	3, 4 and 5 January 1995	2	2	0	4
Andrafiafaly	21, 22, and 27 December 1994	3	1	3	7
Andranolava[a]	26 December 1994	0	0	0	0
Anjaha	23 and 31 December, 1994; 2, 4, and 7, January 1995	4	2	6	12
Antsahavaky	24 December 1994	1	0	1	2
Antsokotsoko	26 and 28 December 1994; 21 April 1995	0	0	0	0
Antsahamena-South[a]	6 January 1995	0	0	0	0
Betainalika	17–21 April 1995	0	0	1	1

[a] Although no tortoises were seen, tracks and/or feces were observed.

or open), air and substrate temperature, relative humidity, and the tortoise's behavior was recorded, i.e. resting head-in, resting head-out, walking, feeding, combat (male–male interactions), courtship (male–female interactions), or nesting. Daily rainfall totals and minimum and maximum temperatures were recorded at Cape Sada. Tortoise localities were determined with an Ensign XL Global Positioning System (Trimble Navigation, Sunnyvale, CA), which was accurate to within 10–100 m. The extent of tortoise habitat in different regions was estimated using 1990 Landsat Thematic mapper digital data (Juvik et al., 1997).

Adult and subadult tortoises were marked by notching a series of marginal scutes (Cagle, 1939). Hatchling and small juvenile tortoises were marked with enamel paint on the marginal scutes. Straight-line carapace length (CL) was measured to the nearest 1 mm using Haglof Mantax aluminum calipers (Forestry Suppliers, Inc., Jackson, MS). A metric dial caliper (accurate to the nearest 0.01 mm) was used to measure gular length, anal notch, and anal fork of adult tortoises and CL of hatchling and juveniles <100 mm in length (McRae et al., 1981). Scute growth layers were counted using the first or second costal plate of all tortoises using methods outlined in Zug (1991). Layers were difficult to distinguish in very large tortoises; therefore a minimum number of layers was recorded in these individuals.

The sex of adult tortoises was determined based on differences in shell morphology. Adult male angonoka have an elongated gular and a concave plastron. Also, the width of the anal fork of adult males is nearly twice that of the anal notch. These characteristics generally could be distinguished in individuals >300 mm CL or with c. 13–16 scute growth layers.

3. Results

Tortoise presence was confirmed at 10 out of 11 areas surveyed (Fig. 2), and 145 tortoises were marked (Table 1). For comparative purposes, observation rates for the areas surveyed are presented in Table 2. Three populations east of Baly Bay were confirmed (Cape Sada, Ankasakabe, and Beheta), and at least two populations west of the Bay were identified (Betainalika and the region including Ambatomainty, Anjaha, Andrafiafaly, Antsahamena-South, Andranolava, and Antsahavaky). The distance between the closest east and west population is c. 24 km over land and extensive savanna and the

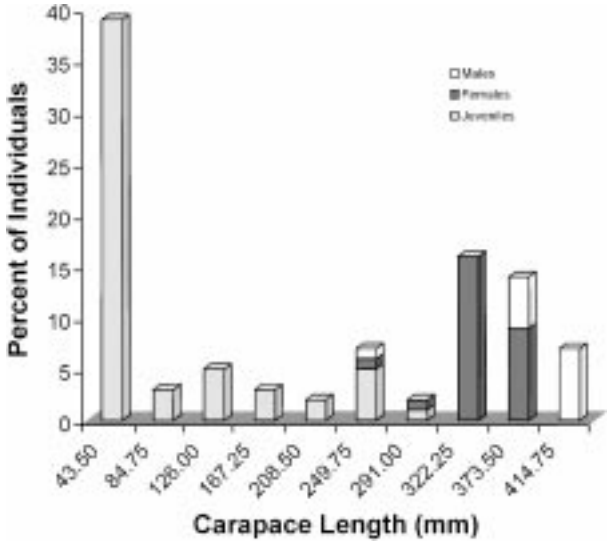

Fig. 3. Size class distribution of the Cape Sada angonoka (*Geochelone yniphora*) population ($n=98$). Secondary sexual characteristics could generally not be used to distinguish between the sexes in individuals <300 mm CL.

Table 2
Observation rates of angonoka (*Geochelone yniphora*) during 1994–1995 field surveys in western Madagascar[a]

Locality	Dates	Person hours	Number of tortoises observed	Observation rate
East Baly Bay				
Cape Sada[b]	December	32.0	4	0.13
	January	66.8	19	0.28
Beheta	October	31.5	3	0.10
	December	99.75	14	0.14
	March	32.5	2	0.06
Ankasakabe	April	32.5	2	0.06
West Baly Bay				
Ambatomainty	December–January	24.00	4	0.17
Anjaha	December–January	61.00	8	0.13
Andrafiafaly	December–January	63.00	7	0.11
Antsahavaky	December–January	28.00	1	0.04
Betainalika	April	49.00	1	0.02
Andranolava	December–January	8.75	0	[c]0.00
Antsokotsoko	December–January	22.20	0	0.00
Antsahamena-S	December–January	21.00	0	[c]0.00

[a] Rates were calculated as the number of tortoises observed per person/hour of survey.
[b] Only December and January survey results are presented here for comparative purposes.
[c] Tortoise tracks and/or feces observed.

Andranomavo River separate the two areas. Although most of the tortoises (68%) were found on Cape Sada, where monthly surveys were conducted, the most extensive tract of contiguous angonoka habitat occurs west of Baly Bay in the region including Ambatomainty, Anjaha, Andrafiafaly, Antsahamena-South, Andranolava, and Antsahavaky. This area extends more or less unbroken from Antsahamena in the north and Ambarindranahary in the east to Andranolava in the south. Survey results for the 11 localities are presented below.

3.1. East Baly Bay

3.1.1. Cape Sada

Ninety-six tortoises were encountered on Cape Sada between 1993 and 1995. This total includes 21 of 24 tortoises that were marked by JWPT field teams prior to 1993 (three tortoises that had been marked in previous surveys were not recaptured in our study). Of the 99 individuals marked on Cape Sada, 14 were male, 27 were female and 58 were juveniles with less than 300 mm CL. The sex ratio among adult tortoises was 1:1.93 and differed significantly from 1:1 ($\chi^2 = 4.05$, d.f. = 1, $p = 0.04$).

The mean CL of adult male tortoises on Cape Sada was 409.6-mm ($n = 14$, range = 282–456, SD = 45) as compared to 361.8-mm in adult females ($n = 26$, range = 285–405, SD = 29) (Table 3). Tortoises classified as juveniles ranged in size from 43.5-mm CL to 310-mm CL. Sixteen of the 58 juveniles were hatchlings that were measured as they emerged from nests. The mean CL of newly emerged hatchlings was 47.2-mm ($n = 16$, range = 43.5–52, SD = 3).

Nearly 40% of the tortoises captured on Cape Sada were juveniles with < 85mm CL (Fig. 3) indicating that successful reproduction is occurring in this population. However, only 22% of the tortoises were in intermediate size classes (84.8–322 mm CL). Although it is possible that intermediate sized tortoises were simply more difficult to find than adults or small juveniles, we suspect that these tortoises were under-represented in surveys because survivorship of hatchlings and juveniles is very low. The partial remains of 22 unmarked, dead juvenile angonoka were found during monthly surveys on Cape Sada. The remains of 15 of the 22 dead juvenile tortoises consisted of only a few scutes and the cause of mortality could not be determined. However, five of the dead juveniles with 2–3 scute growth layers appeared to have been killed by birds of prey or small mammals. Potential predators of small juvenile angonoka include the Madagascar buzzard (*Buteo brachypterus*), common tenrec (*Tenrec ecaudatus*), fosa (*Cryptoprocta ferox*), and introduced species such as civet cat (*Viverricula indica*), and black rat (*Rattus rattus*). Local people claim that boa (*Boa madagascariensis*) and yellow-billed kite (*Milvus migrans*) also are predators of young angonoka (Juvik et al., 1981). Two juveniles with five and seven scute growth layers (c. 70–100 mm CL) appeared to have been killed by a larger predator such as an African bush pig. The shells of these tortoises had been broken between bone sutures and large puncture wounds were present.

Tracks, feces, and digging of African bush pigs often were observed on Cape Sada, particularly during the wet season. Twelve angonoka nests were monitored for disturbance by predators during our study; however, no direct evidence of egg predation was observed. In a subsequent study at Cape Sada, a nest containing three eggs was destroyed by bush pigs (Pedrono, 1996).

During monthly surveys, tortoises were most frequently observed in January, when, on average, a tortoise was encountered every four survey-hours. High observation rates corresponded generally with months of high rainfall (Fig. 4). A comparatively high observation rate among adult tortoises in October probably reflected breeding activity (Smith, 1995). A large proportion of adult female tortoises was observed in May during peak nesting season. Many juvenile angonoka (with 1–3 scute growth rings) were observed in open areas in February and March. Very few tortoises were encountered during June, July, and August, the height of the dry season. A radio-telemetry study revealed that tortoises were inactive during these months, typically resting beneath vegetation (Smith et al., in press).

Although fire scars were evident on some of the large trees on Cape Sada, the area probably had not burned since the earliest JWPT field surveys in 1988 (Reid, 1989). However, a brush fire on Cape Sada after our

Table 3
Mean carapace length (mm) of wild caught angonoka (*Geochelone yniphora*) in western Madagascar

Location	Sex/life stage	*n*	Mean	Range	Standard deviation
East Baly Bay					
Cape Sada	Males	14	409.6	282–456	45.0
	Females	26	361.8	285–405	29.0
	Juveniles	42	120.9	44.9–310	79.6
	Hatchlings	16	47.2	43.5–52	3.0
Beheta	Males	9	360.2	298–410	41.5
	Females	6	342.2	282–378	39.7
	Juveniles	3	168.7	116–218	51.1
Ankasakabe	Males	2	414.0	396–432	25.5
West Baly Bay					
Western areas[a]	Males	10	405.0	262–481	61.1
	Females	5	375.2	353–395	16.3
	Juveniles	10	141.8	53.1–277	62.5
Betainalika	Juveniles	1	51.9	–	–

[a] Includes Ambatomainty, Anjaha, Andrafiafaly, and Antsahavaky.

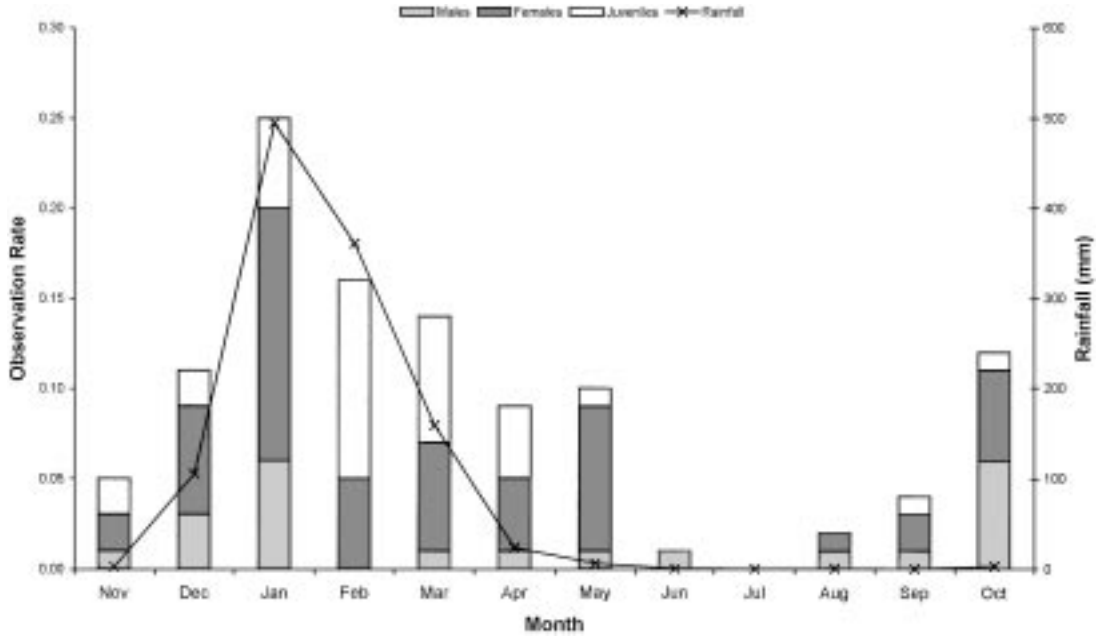

Fig. 4. Mean monthly observation rates of angonoka (*Geochelone yniphora*) at Cape Sada and monthly rainfall totals for the period from October 1993–June 1995. Observation rates were calculated as the number of tortoises observed per person-hour.

study resulted in the death of at least one adult tortoise (L. Durrell, pers. comm. October 1995).

Juvik et al. (1997) described three populations of angonoka at Cape Sada that inhabited "open scrub forest habitat" in the north, central and southern portion of the peninsula. However, during monthly surveys we found that tortoises often moved between the open scrub areas delineated by Juvik et al. (1997) and also used the dense bamboo thickets dividing them. Therefore, we feel that Cape Sada hosts a single population of angonoka. The ratio of marked to unmarked tortoises observed on Cape Sada declined steadily from February–June 1995 (Fig. 5) and no unmarked tortoises were found during the last three months of the study. It is likely that nearly all adult tortoises in the population have been marked, but some juvenile tortoises may have been missed. The Cape Sada peninsula is roughly 150-ha in size and the estimated tortoise density is 0.66 tortoises per ha.

3.1.2. Ankasakabe

Two adult male tortoises were observed at Ankasakabe in 32.5 survey hours in April 1995, yielding an observation rate of 0.06 tortoises per survey-hour (Table 2). This value is slightly less than that of Cape Sada during April surveys. Tracks of juvenile tortoises were seen on two occasions at Ankasakabe. The presence of juvenile tortoises indicates that a breeding population still exists at Ankasakabe. However, we suspect that the population is very small because the tortoise habitat is < 50 ha in size and contains only a few stands of bamboo and *Terminalia* sp. surrounded by extensive savanna. The area appears to burn frequently and is comparatively accessible to humans because an ox-cart path passes directly through the region.

Both male tortoises discovered at Ankasakabe had small holes in a rear marginal scute and the gular of one had been cut off. Local villagers had probably kept these tortoises as pets in the past. Our interviews with villagers revealed that captive tortoises often were kept tethered, and that the gular would be removed because it is believed to prevent the tortoise from eating.

3.1.3. Beheta

Beheta was the easternmost locality where tortoises were found and the habitat was c. 200 ha in size (Fig. 2). Eighteen tortoises, nine males (298–410 mm CL), six females (282–378 mm CL), and three juveniles (116–218 mm CL) were marked during nearly 164 survey-hours in October and December 1994, and March 1995. The highest observation rate at Beheta occurred during December (0.14 tortoises per survey-hour); this observation rate was similar to that recorded at Cape Sada (0.13 tortoises per survey-hour) over the same period. Although the observation rates at Beheta and Sada in this study were similar, further surveys are needed to determine if tortoise densities in the two populations are comparable.

Tortoise habitat at Beheta is similar to Cape Sada in that it contains bamboo, *Terminalia* spp. and *Bauhinia*

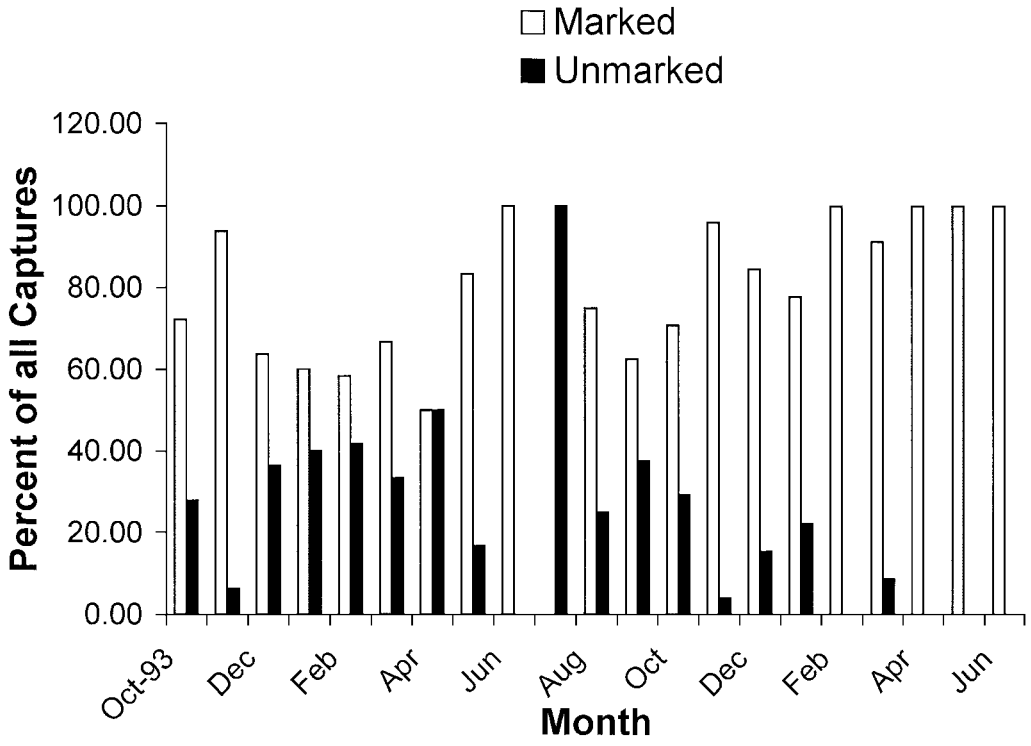

Fig. 5. The ratio of marked to unmarked tortoises observed on Cape Sada during field surveys from October 1993 to June 1995.

sp. However, unlike Sada, stands of shrubs and bamboo are comparatively sparse. Seasonal brush fires probably have had an impact on the tortoise habitat at Beheta. Villagers mentioned that dry season brush fires are widespread in the region. During the October 1994 visit, a brush fire swept through the area where we had recently seen an adult male tortoise. The area was searched during subsequent surveys and no evidence was found to suggest that the fire killed the tortoise. This animal must have relocated before or after the fire. An adult male fire-scarred tortoise and the partial remains of two other adult tortoises were observed in areas that had burned in the past. Although the cause of mortality in these tortoises could not be determined, due to their large size, adult angonoka probably have no natural predators suggesting that fire or natural causes were responsible for the death of these individuals.

One adult female tortoise discovered at Beheta had a hole in a rear marginal scute and had presumably been kept as a pet in the past. Like Ankasakabe, Beheta is comparatively accessible and villagers at Antanandava claim that tortoises are taken from the area on occasion. During a 1992 survey, Juvik et al. (1997) found considerable evidence of bush pig rooting at Beheta. Tracks, rooting, and feces of bush pigs were observed during this study, but no direct evidence of pig predation on eggs or young tortoises was documented.

3.2. West Baly Bay

3.2.1. Ambatomainty, Anjaha, Andrafiafaly, Antsahavaky, Antsahamena-south, Andranolava, and Antsokotsoko

Bamboo-scrub habitat in these seven areas appeared to be contiguous and probably supports the largest remaining angonoka population. Cloud cover present in the Thematic mapper images of this region did not allow an accurate estimate of the extent of bamboo-scrub habitat in this region. However, it appears to include an area between 4000 and 6000 ha in size. The region contains extensive tracts of bamboo and is relatively inaccessible to humans. The closest human settlements are the villages of Ankoro to the south and Ambarindranahary to the north. A seasonally occupied village exists on the coast at Antsahamena.

Twenty-five tortoises were observed in the December and January surveys; 10 were adult male (262–481 mm CL), five were adult female (353–395 mm CL), and 10 were juveniles (53.1-277 mm CL). The largest angonoka reported, a male with 481 mm CL, was found at Ambatomainty in the northern portion of the region. The highest observation rate also occurred at Ambatomainty (0.17 tortoises per survey-hour), but comparatively high observation rates were also recorded at Anjaha (0.14 tortoises per survey-hour) and Andrafiafaly (0.11 tortoises per survey-hour). These numbers are similar to those recorded at Cape Sada over the same period (0.11 and 0.24 tortoises per survey-hour in December and January, respectively).

The southern-most localities in this region occurred at Andranolava. Although no tortoises were observed here, tortoise feces were found in three separate locations in the area. Tortoise presence was not confirmed at Antsokotsoko, a large tract of bamboo-scrub habitat that lies between Andranolava and Andrafiafaly. The habitat at Antsokotsoko appears to be contiguous with Andranolava and Andrafiafaly and is similar to other sites in the region. Further surveys in this area are needed.

Evidence of brush fires was common throughout the West Baly Bay region. Angonoka were observed using recently burned bamboo-scrub habitat. Two of the 25 tortoises (juveniles with 80 and 140 mm CL, respectively) found during surveys had burn scars. The remains of an adult angonoka were discovered on the beach near the seasonal settlement at Antsahamena. Since local people apparently do not eat angonoka (Durbin, et al., 1996), this animal may have been killed and consumed by transient fishermen. Bush pig sign was observed throughout the region, but insufficient time was spent in the area to detect any direct impact of pigs on the tortoise population.

An undescribed species of tick (*Amblyomma sp*). was observed on five tortoises from Andrafiafaly, Ambatomainty, and Anjaha (L. Durden, pers. comm. October 1995). Two of the tortoises were adult female, two were adult males, and one was a juvenile with six scute growth rings. Each infected tortoise had from 2–5 ticks attached near the tail and hind legs. This observation represents the first record of an ectoparasite from free ranging *G. yniphora*.

3.2.2. Betainalika

Betainalika lies c. 6 km southeast of Andrafiafaly and is separated from the West Baly Bay tortoise habitat by dense deciduous forest and savanna. The bamboo-scrub at Betainalika encompasses c. 340 ha. The habitat contained only scattered bamboo stalks and appeared to burn frequently. Although the assessment of the habitat in this study was qualitative, Betainalika appeared to have the most extensive fire damage of all the areas visited.

Local villagers repeatedly mentioned that Betainalika had many angonoka, however, during 41 survey-hours in April 1995, only one tortoise was encountered (0.02 tortoise per survey-hour) and neither tracks nor feces were observed. The tortoise observed was a juvenile with 51.9 mm CL and probably was a 1995 hatchling. Despite the low observation rate in this study, the presence of a juvenile tortoise indicated that breeding adults were present in the area. Further surveys in this region are needed to accurately assess the status of this population.

4. Discussion

The tortoise localities identified in this study probably represent at least five separate populations, all of which occur within a 30-km radius of Baly Bay. The "east" and "west" populations are effectively isolated from one another by Baly Bay, the Andranomavo River, and extensive savanna. The most extensive tract of angonoka habitat occurs west of Baly Bay (including the regions of Ambatomainty, Anjaha, Andrafiafaly, Antsahavaky, Antsahamena-south, Andranolava, and Antsokotsoko). This area is c. 4000–6000 ha in size and probably contains the largest angonoka population. More intensive tortoise surveys are needed in this region to determine the population size, and the area should be evaluated to determine the precise extent and quality of the tortoise habitat. The Betainalika region also occurs west of Baly Bay and probably represents a separate population. Betainalika is much smaller than the west Baly Bay region and appeared to contain low tortoise densities. However, further surveys in this region also are warranted.

The three angonoka populations east of Baly Bay, Cape Sada, Beheta, and Ankasakabe, are small (<200 ha) and separated by extensive savanna. Cape Sada is only about 150 ha in size and hosts a population of c. 100 tortoises. Beheta is roughly the same size as Cape Sada and although the habitat appears somewhat degraded by fire, similar observation rates suggest that the populations may be similar in size. Tortoise habitat at Ankasakabe is extremely limited and this angonoka population is undoubtedly very small. However, the observation of tracks of a juvenile tortoise at Ankasakabe indicates that angonoka are able to reproduce successfully in small habitat fragments.

The tortoise density on Cape Sada (0.66 tortoises per ha) appears low when compared to other dry scrub-forest tortoises. For example, the density of Hermann's tortoise (*Testudo hermanni*) at a site in northeastern Spain was nearly 11 tortoises/ha (Mascort, 1997) and densities of 3–4 tortoises/ha have been reported for the Chaco tortoise (*Geochelone chilensis*) in Argentina (Waller and Micucci, 1997). Radiated tortoises (*Geochelone radiata*) in southern Madagascar inhabit a much drier climate than angonoka; however, estimates of 7–15 tortoises/ha have been reported for this species (R. Lewis unpubl. report, January 1995). It is not known whether the Cape Sada angonoka population is at, or near, carrying capacity. The low population density at Sada may reflect the effects of past harvest, poor habitat quality, or low survivorship. Comparative studies at other angonoka populations are needed to determine the carrying capacity of bamboo-scrub habitat.

Juvenile tortoises were found in all areas surveyed, indicating that successful reproduction is occurring throughout the range of the angonoka. Although African bush pigs are known to have destroyed one tortoise nest after this study (Pedrono, 1996), some nests are clearly surviving to produce hatchlings. However, at least two large juvenile tortoises on Cape Sada appeared to have been killed by a large mammal such as an African bush pig. Bush pig predation may have a significant effect on recruitment, particularly if they prey heavily on juvenile tortoises that are too large to be consumed by native predators. Additional dead juveniles observed on Cape Sada in this study, and an apparent lack of intermediate sized tortoises, may indicate low juvenile survivorship in this population.

Brush fires probably pose the most serious threat to remaining angonoka populations. The 1995 fire on Cape Sada confirmed that brush fires kill angonoka and it seems likely that frequent brush fires also affect the structure of the bamboo-scrub habitat. Although no quantitative data were collected, the bamboo-scrub at Beheta, Ankasakabe, and Betainalika appeared badly degraded by brush fires. Bamboo thickets at these sites were structurally quite different than at other areas. Bamboo was notably sparse and dense vines had encroached in some areas. Angonoka exhibit seasonal differences in microhabitat use (Smith et al., in press) and it may be extremely important to maintain the integrity of the bamboo-scrub ecosystem.

In order to assess the impact of anthropogenic fires on the bamboo-scrub ecosystem, the role of natural fire in the region must be determined. Paleoecological investigations have shown that brush fires occurred in western Madagascar prior to human settlement (Burney, 1997). However, the frequency of anthropogenic dry season fires is probably quite different from that of natural fires. Given the highly seasonal rainfall pattern in the region, it is unlikely that lightning fires would occur in the dry season (when most anthropogenic fires occur). Furthermore, lightning-induced wet season fires would probably be less catastrophic than dry season fires because the fuels would be moister. Research is needed to determine the direct effects of fire (both anthropogenic and natural) on the bamboo-scrub ecosystem.

To minimize the effects of anthropogenic brush fires it may be necessary to clear and maintain firebreaks around the remaining tortoise habitat. In 1995, villagers helped maintain a firebreak at the eastern edge of Cape Sada. However, a fire was deliberately set on Cape Sada in 1996, and in remote areas, it is likely that villagers will continue to burn the bamboo-scrub to drive their cattle from the forest. Local education efforts about the effects of brush fires should continue (Durbin et al., 1996).

In addition to evaluating the effects of brush fires on the angonoka, it will also be important to determine the effects of cattle and African bush pigs on the bamboo-scrub habitat. In the desert tortoise (*Gopherus agassizii*), tortoises are in direct competition with cattle for food (Avery and Neibergs, 1997), and in Argentina (Waller

and Micucci, 1997) cattle were responsible for degradation of Chaco tortoise habitat by grazing new shoots of shrubs following anthropogenic fires. Overlap in diet between feral pigs (*Sus scrofa*) and giant tortoises (*Geochelone elephantopus*) was documented on Isla Santiago in the Galapagos, although direct competition between the two species was not confirmed (Coblentz and Baber, 1987). Considerable pig rooting activity was observed in all regions surveyed in this study. Additional information is needed to evaluate the impacts of cattle and bush pigs on bamboo-scrub habitat. Fencing to exclude cattle and bush pigs from bamboo-scrub habitat is probably not economically feasible at this time, and could have a negative effect on relations with local people.

Most of the remaining angonoka populations are very remote and collection of tortoises does not appear to be a threat at this time. On a local level, tortoises may occasionally be kept as pets, but community education efforts have resulted in the donation of captive animals to the breeding program (Curl, 1986a; Reid et al., 1989), and others have apparently escaped or been released back into the wild (e.g. Beheta and Ankasakabe). However, the theft of 75 angonoka from the captive-breeding centre at Ampijoroa in 1996 demonstrates a demand for this rare species in the international pet trade. Declaration of the Baly Bay region as a National Park by the Malagasy government is imminent; however, wild populations still may be vulnerable to illegal collection in the future. The removal of adult tortoises from any of the wild populations could have catastrophic effects. The apparent low survivorship of juvenile angonoka coupled with a slow rate of development to sexual maturity could severely limit the capacity of a population to recover from the loss of adult tortoises (see Congdon et al., 1993). It may be necessary to use guards to protect the most accessible angonoka populations (e.g. Cape Sada and Beheta).

The angonoka is vulnerable to extinction in the wild primarily because of its extremely limited geographic distribution. The remaining populations are small, isolated, and all occur within only a 30 km radius of Baly Bay. A catastrophic event such as disease or severe weather could cause extinction of some or all populations.

Augmentation of the Cape Sada angonoka population with captive born juveniles is not warranted at this time. However, repatriation (release of individuals of a species into an area formerly occupied by that species) may be worthwhile in other areas. It is of critical importance to protect and manage all wild angonoka populations in order to preserve the species.

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References

Angel, M.F., 1931. Sur un examplaire de *Testudo hyniphora* de Madagascar. Bulletin de la Societé Zoologique de France 61, 383–385.

Avery, H.W., Neibergs, A.G., 1997. Effects of cattle grazing on the desert tortoise, *Gopherus agassizii*. In: Van Abbema, J. (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference. New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, pp. 13–20.

Blanc, C.P., 1974. Status survey of *Testudo yniphora*. World Wildlife Yearbook 1972–73, 93–94.

Burney, D.A., 1997. Theories and facts regarding Holocene environmental change before and after human colonization. In: Goodman, S.M., Patterson, B.D. (Eds.), Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, DC, pp. 75–89.

Cagle, F.R., 1939. A system of marking turtles for future identification. Copeia 1939 (3), 170–173.

Coblentz, B.E., Baber, D.W., 1987. Biology and control of feral pigs on Isla Santiago, Galapagos, Equador. Journal of Applied Ecology 24, 402–418.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7 (4), 826–833.

Curl, D.A., Scoones, I.C., Guy, M.K., Rakotoarisoa, G., 1985. The Madagascan tortoise *Geochelone yniphora*: current status and distribution. Biological Conservation 34, 35–54.

Curl, D.A., 1986a. A recovery programme for the Madagascan plowshare tortoise *Astrochelys (=Geochelone) yniphora*. Dodo, Journal of the Jersey Wildlife Preservation Trust 23, 68–79.

Curl, D.A., 1986b. The rarest tortoise on earth. Oryx 20 (1), 35–39.

Donque, G., 1972. The climatology of Madagascar. In: Battistini, R., Richard-Vindard, G. (Eds.), Biogeography and ecology in Madagascar. Dr. W. Junk B.V, The Hague, pp. 87–144.

Durbin, J., Rajafetra, V., Reid, D., Razandrizanakanirina, D., 1996. Local people and project angonoka—conservation of the ploughshare tortoise in north-western Madagascar. Oryx 30 (2), 113–120.

Durrell, L., Groombridge, B., Tonge, S., Bloxam, Q., 1989. *Geochelone yniphora* ploughshare tortoise, plowshare tortoise, angulated tortoise, angonoka. In: Swingland, I.R., Klemens, M.W. (Eds.), The Conservation Biology of Tortoises. Occasional Papers of the Species Survival Commission No. 5, IUCN, Gland, Switzerland, pp. 99–102.

Groombridge, B., 1982. The IUCN Amphibia-Reptilia Red Data Book, Part 1. IUCN, Gland, Switzerland.

Juvik, J.O., Blanc, C.P., 1974. The angonoka of Cape Sada. Animals 16, 148–153.

Juvik, J.O., Andrianarivo, A.J., Blanc, C.P., 1981. The ecology and status of Geochelone yniphora: a critically endangered tortoise in northwestern Madagascar. Biological Conservation 19, 297–316.

Juvik, J.O., Keister, A.R., Reid, D., Coblentz, B., Hoffman, J., 1997. The conservation biology of the angonoka, Geochelone yniphora, in northwestern Madagascar: Progress Report. In: Van Abbema, J. (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference. New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, pp. 345–350.

Mascort, R., 1997. Land tortoises in Spain: their status and conservation. In: Van Abbema, J. (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles — An International Conference. New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, pp. 307–312.

McRae, W.A., Landers, J.A., Cleveland, G.D., 1981. Sexual dimorphism in the gopher tortoise (*Gopherus polyphemus*). Herpetologica 37 (1), 46–52.

Pedrono, M., 1996. Rapport de terrain- Première partie: Octobre 1996–Décembre 1996. Unpublished report to Jersey Wildlife Preservation Trust. 11 pp.

Reid, D., 1989. Report of a field study at Baly Bay to observe behaviour of *Geochelone yniphora* in the wild. Unpublished report to Jersey Wildlife Preservation Trust. 11pp.

Reid, D., 1991. Report of a field study of wild *Geochelone yniphora* on Cap Sada, 7–27 January 1991. Unpublished report to Jersey Wildlife Preservation Trust. 9pp.

Reid, D., 1993. Report of a field study of wild *Geochelone yniphora* on Cap Sada in February 1993. Unpublished report to Jersey Wildlife Preservation Trust. 11pp.

Reid, D., Durrell, L., Rakotobearison, G., 1989. The captive breeding project for the angonoka (*Geochelone yniphora*) in Madagascar. Dodo. Journal of the Jersey Wildlife Preservation Trust 26, 34–48.

Siebenrock, R., 1903. Schildkröten von Madagaskar und Aldabra. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 27, 241–259.

Smith, L.L., 1995. Project angonoka field study—final report (August 1993–June 1995). Unpublished report to Jersey Wildlife Preservation Trust. 27pp.

Smith, L.L., Bourou, R., Joby, M., Sibo, C., in press. Home range and microhabitat use in the angonoka (*Geochelone yniphora*) in Madagascar. Chelonian Conservation and Biology.

Vaillant, L., 1889. Description d'une tortue terrestre d'espce nouvelle (*Testudo yniphora*). Nouvelle Archives Muséum d'Histoire Naturelle 3, 161–167.

Vaillant, L., Grandidier, G., 1910. Histoire naturelle des reptiles, 1re Part: Crocodiles et tortues. In: Grandidier, A., Grandidier, G. (Eds.), Histoire Physique, Naturelle et Politique de Madagascar. Paris, Hachette, pp. 1–86.

Waller, T., Micucci, P.A., 1997. Land use and grazing in relation to the genus *Geochelone* in Argentina. In: Van Abbema, J. (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles — An International Conference. New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, pp. 2–9.

Zug, G.R., 1991. Age determination in turtles. Society for the Study of Amphibians and Reptiles, Herpetological Circular No. 20. Lawrence, Kansas, 28 pp.