ARTICLES

Chelonian Conservation and Biology, 1999, 3(3):393–400

Home Range and Microhabitat Use in the Angonoka (*Geochelone yniphora*) in Madagascar

Lora L. Smith[1,2,4], Bourou Robert[2,3], Mahatoly Joby[2,3], and Sibo Clément[2,3]

[1]*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA [E-mail: angonoka@grove.ufl.edu];*
[2]*Jersey Wildlife Preservation Trust, Les Augrés Manor, Trinity, Jersey JE3 5BP Channel Islands, United Kingdom;*
[3]*Université de Mahajanga, BP 652, Mahajanga, Madagascar;*
[4]*Present Address: Department of Natural Sciences, University of North Florida, Jacksonville, FL 32224 USA*

Abstract. – Thirteen wild angonoka (*Geochelone yniphora*) were radio-tagged and tracked for up to two years to define and quantify the home range and document microhabitat use of this endangered tortoise. Wet season home ranges were larger than dry season ranges ($t = 2.88$; $df = 12$; $p = 0.02$); however, considerable individual variation was observed. Mean wet season home range for male tortoises was 21.1 ha ($n = 3$; SD = 6.4) as compared to only 6.6 ha (SD = 4.5) in the dry season. For females, the mean wet season home range size was 12.2 ha ($n = 5$; SD = 9.4), whereas mean dry season home range was only 3.6 ha (SD = 5.0). Mean wet season home range in juveniles was 1.8 ha ($n = 5$; SD = 1.8) as compared to 0.6 ha (SD = 0.5) in the dry season. In general, angonoka used microhabitats according to their availability; however, seasonal effects on habitat selection were detected. Tortoises were encountered more often in open unvegetated areas during the wet season than during the dry season, when open grassy areas were more commonly used. The shifts in microhabitat use observed in this study may relate to seasonal differences in temperature and moisture. These shifts underscore the importance of maintaining vegetative diversity in angonoka habitat.

Key Words. – Reptilia; Testudines; Testudinidae; *Geochelone yniphora*; tortoise; home range; microhabitat use; brush fires; ecology; conservation; Madagascar

The angonoka or ploughshare tortoise (*Geochelone yniphora*) is listed as Endangered in the IUCN Red List of Threatened Animals (IUCN, 1996) (Fig. 1). The angonoka is endemic to Madagascar and found in only a few small patches of bamboo-scrub forest around Baly Bay (Fig. 2) (Juvik et al., 1981; Curl et al., 1985). All remaining angonoka populations are small and isolated, and our preliminary data indicate that fewer than 1000 tortoises remain in the wild.

The endangered status of *G. yniphora* is in part a reflection of the historic trade in tortoises from the Baly Bay region. From the 17th through the 19th century Arab traders collected large numbers of tortoises from the area for export to the nearby Comoro Islands (Vaillant and Grandidier, 1910), and indeed, for many years this was considered to be the possible type locality for this species (Vaillant, 1885). Generally, angonoka are not eaten locally, and the species has become so rare and difficult to find that commercial exploitation of wild tortoises is negligible.

Currently, brush fires are thought to be the most serious threat to the angonoka (Durrell et al., 1989). Fires are set by local people to stimulate new growth of grasses for cattle, to drive cattle from the forest, and to create clearings to keep bush pigs (*Potamochoerus larvatus*) away from cultivated lands (Durbin et al., 1996). The annual burning destroys bamboo-scrub which is the only known habitat of the angonoka (Curl, 1986). It is estimated that only 40–80 km^2 (4000–8000 ha) of bamboo-scrub habitat exists today within the range of this tortoise (Curl et al., 1985), and this figure would thus represent the maximum estimate for the overall range of the species.

Angonoka have been bred in captivity since 1982 within the USA and in Madagascar (McKeown et al., 1982; Reid et al., 1989); however, little is known about the ecology of this tortoise, which makes development and implementation of a conservation plan for the species difficult. The objectives of this study were to determine home range size and microhabitat use patterns in adult and juvenile angonoka. We examined (1) variation in home range size among males, females, and juveniles; (2) differences in home range size across seasons; (3) differences in microhabitat use between male, female, and immature tortoises; and (4) seasonal differences in microhabitat use.

MATERIALS AND METHODS

Study Site. — Cape Sada is a 150 ha peninsula located at the mouth of Baly Bay in Mahajanga Province of western Madagascar (16°02'S, 45°20'E) (Fig. 2). The maximum elevation on the Cape is 50 m above mean sea level. There are no human settlements within the Cape itself, but the beaches and coastline are used seasonally by local fishermen.

Cape Sada has a mosaic of vegetation types that are collectively referred to as bamboo-scrub, except for the

Figure 1. An adult angonoka (*Geochelone yniphora*).

northern part, which contains a dense komanga (*Erythrophleum couminga*) forest. The primary microhabitat types within the bamboo-scrub are scrub-shrub, bamboo thickets, grassy areas, and open unvegetated patches (Figs. 3a-d). The scrub-shrub microhabitat contains shrubs less than 2 m in height with scattered grasses and sedges in the ground cover. The most common shrub species are *Bauhinia* sp. and *Terminalia* sp. Bamboo (*Perrierbambos madagascariensis*) occurs in dense thickets within the bamboo-scrub ecosystem. These thickets contain a few shrubs and satrana palms (*Hyphaene shatan*), but ground cover vegetation is rarely present. Small grassy areas (generally less than 5 m^2 in area) occur within the scrub-shrub community. These areas contain savanna grasses including *Aristida* sp., *Eragrostis* sp., and *Heteropogon contortus* and a variety of sedges. For the purposes of this study, the grassy areas are referred to as savanna microhabitat although they do not fit the typical definition of savanna (Koechlin, 1982). Small open areas (typically < 3 m^2 in area) with an igneous rock substrate occur within the scrub-shrub and savanna microhabitats.

Northwest Madagascar is characterized by a tropical climate with distinct annual wet and dry seasons (Donque, 1972). Nearly all precipitation occurs in the six month period from November through April and mean annual temperature in the Baly Bay region exceeds 25°C (Fig. 4).

Data Collection. — Thirteen tortoises (three males, five females, and five juveniles with 8–10 scute growth rings) were radio-instrumented and tracked for periods ranging from 121 to 630 days (Table 1). Adult tortoises were fitted with SB-2 module transmitters and juveniles with smaller SM-1H modules that weighed 30 and 7 g, respectively (AVM Instrument Co., Livermore, CA). Transmitters (including batteries) weighed less than 1% of body weight and were attached to the posterior costal scutes of the tortoise with PC-11 Epoxy Paste (Protective Coating Co., Allentown, PA) (Fig. 5).

The tortoises were located by direct observation using an LA-12 receiver (AVM Instrument Co., Livermore, CA). Each animal was located seven mornings (between 0600–1030 hrs) and seven afternoons (between 1430–1800 hrs) per month, weather permitting. At each location, the time, weather, air and substrate temperature, relative humidity, and microhabitat type (scrub-shrub, bamboo, savanna, or open) were recorded.

A 50 m^2 grid was created across most of Cape Sada. Tortoise locations were marked with colored flagging, numbered consecutively, and the distance and compass bearing to the nearest grid point taken. If no transect or grid point was available, localities were determined with an Ensign XL Global Positioning System (Trimble Navigation, Sunnyvale, CA).

Data Analysis. — Minimum convex polygon (MCP) (Mohr, 1947) and kernel area (KA) (Worton, 1989) methods were used to estimate home range size. MCP is a widely used method of estimating home range size, and is simply the smallest possible convex polygon containing all observation

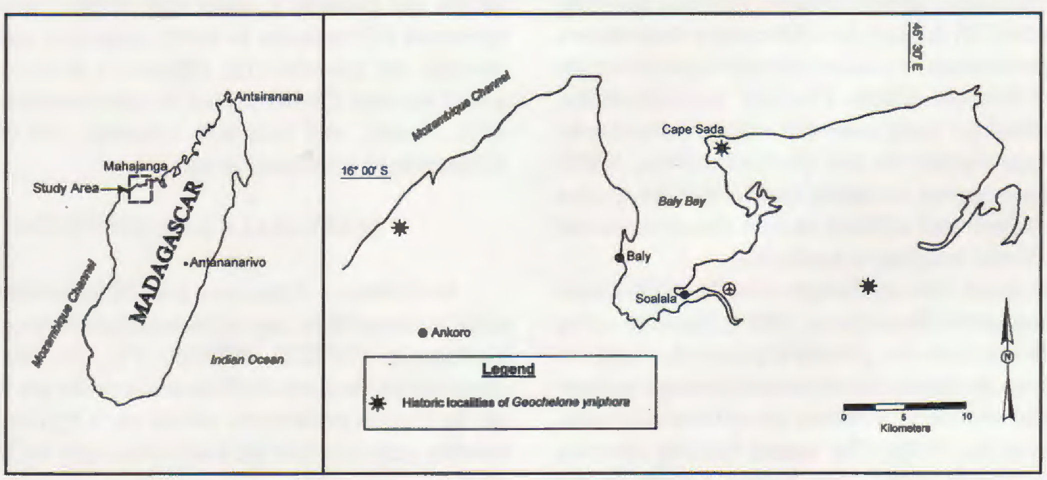

Figure 2. Historic localities of the endangered angonoka tortoise (*Geochelone yniphora*) in western Madagascar. The study was conducted on the Cape Sada peninsula, northeast of Baly Bay.

Figure 3. Vegetation types within the bamboo-scrub habitat on Cape Sada, Madagascar. (**a, top left**): *Bauhinia* sp. and *Terminalia* sp. dominate the scrub-shrub vegetation type. (**b, top right**): The savanna contains a mixture of grasses, including *Aristida* sp., *Eragrostis* sp., and *Heteropogon contortrix*, and occurs only as small patches, generally less than 5 m^2. (**c, bottom left**): Bamboo thickets contain bamboo (*Perrierbambos madagascariensis*), a few shrubs, and satrana palms (*Hyphaene shatan*). (**d, bottom right**): Small open areas occur within the scrub-shrub and savanna habitat.

points. MCP method is sensitive to movements on the periphery of the animal's range and may include areas of central land not visited by the animal. KA is a utilization distribution method and reflects intensity of use, presented graphically as contour lines, each of which is a set of points where the probability of occurrence is constant. Both analyses were carried out using the computer program Ranges V (Kenward and Hodder, 1996). MCPs were based on 100% of the fixes and KAs calculated using 95% contours. Least-squares cross-validation was carried out to choose the optimum smoothing factors in KA analysis (Silverman, 1986; Kenward and Hodder, 1996).

Sampling periods were grouped into two seasons for analysis (November – April = wet season; May – October = dry season). A Wilcoxon paired-difference test was used to examine wet and dry season effects on home range size and a Kruskal-Wallis test was used to test for differences in home range size between males, females, and juveniles in both wet and dry season.

A 1990 thematic mapper satellite image (Juvik et al., 1997) was used to quantify the extent of the various microhabitat types on Cape Sada. Areas were estimated using a polar planimeter. A Chi-squared goodness-of-fit test was used to determine whether there was a difference between observed and expected microhabitat use, based on habitat availability.

Analysis of categorical data (percent of observations by sex, season, and microhabitat) was carried out using analysis

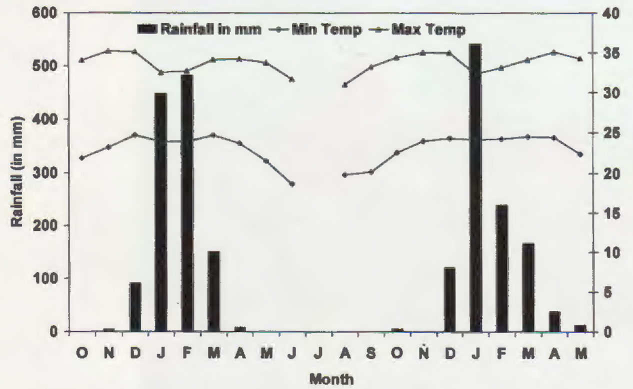

Figure 4. Monthly rainfall and minimum and maximum temperatures at Cape Sada, Madagascar. Data were collected from October 1993 through May 1995.

of covariance (PROC GLM) (SAS Institute, 1992). If significant treatment effects were detected, Tukey's studentized range (HSD) test was used to determine where the differences occurred (Kushner and De Maio, 1980). Scrub-shrub was excluded from the microhabitat analysis because it accounted for most of the available habitat and interactions would be difficult to distinguish.

RESULTS

Home Range. — There was considerable variation in home range size among individual tortoises, however, several general patterns were evident. MCP values were greater than KA values in both wet and dry seasons, but patterns across seasons and sex/life stages were the same (Table 2). Because both methods yielded similar results, and KA estimates probably best reflect actual home range size, only comparisons among KA values are discussed here. Wet and dry season home range sizes were significantly different ($t = 2.88$; df = 12; $p = 0.02$). Mean wet season home range size for adult male tortoises was 21.1 ha (SD = 6.4) as compared to only 6.6 ha (SD = 4.5) in the dry season (Table 2). Mean wet season home range size for adult females was 12.2 ha (SD = 9.4), whereas the mean dry season home range size was only 3.6 ha (SD = 5.0). Juvenile mean wet season home range size was 1.8 ha (SD = 1.8) as compared to 0.6 ha (SD = 0.5) in the dry season.

Wet season home range areas were significantly different between the sex/life stages ($H = 9.33$; $p < 0.01$). The average size of juveniles tracked in this study was 167 mm CL as compared to 427 and 362 mm CL in adult males and females, respectively. In general, body size is related to home range size, because larger animals often need to forage farther to meet their energy requirements than do small animals (McNab, 1963), although other factors such as metabolism and feeding strategy also influence home range size. This phenomenon may explain the difference in home range size between adult and juvenile angonoka. Immature tortoises of other species occasionally use larger home ranges than adults because they conduct long distance dispersal movements (Auffenberg and Iverson, 1979; Aguirre et al., 1984; Diemer, 1992). The juveniles followed in this study did not exhibit this behavior. In adult angonoka, behavior rather than body size probably best explains the

Table 1. Radiotracking information for 13 angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. Data were collected from October 1993 through June 1995.

Tortoise No.	Carapace Length (mm)	Tracking Interval	Number of Records
Juveniles:			
42	173	2/95 – 6/95	63
44	168	11/93 – 6/95	256
51	156	10/93 – 6/95	282
83	167	10/94 – 6/95	130
88	172	10/94 – 6/95	121
Mean:	167		
Males:			
7	430	10/93 – 6/95	278
13	398	10/93 – 6/95	288
54	454	12/93 – 6/95	229
Mean:	427		
Females:			
1	376	10/93 – 6/95	303
3	329	10/93 – 6/95	301
9	344	10/93 – 6/95	285
12	361	10/93 – 6/95	292
19	399	11/93 – 6/95	264
Mean:	362		

Table 2. Mean home range size (in hectares) of 13 radio-instrumented angonoka (*Geochelone yniphora*) on Cape Sada, Madagascar. Home range size was estimated using minimum convex polygon method (MCP) (Mohr, 1947) and kernel area (KA) (Worton, 1989). Data were grouped into two seasons for analysis (May – October = dry season; November – April = wet season). For each category the mean is followed by ± 1 SD and the range.

Sex/ Life Stage	Dry Season		Wet Season	
	MCP	KA	MCP	KA
Juveniles ($n = 5$)	1.4 ± 1.1 (0.1–2.5)	0.6 ± 0.5 (0.0–1.3)	2.2 ± 1.5 (1.0–4.8)	1.8 ± 1.8 (0.6–5.0)
Males ($n = 3$)	9.2 ± 4.6 (4.6–13.9)	6.6 ± 4.5 (1.4–9.8)	38.5 ± 7.0 (31.6–45.5)	21.1 ± 6.4 (6.4–28.4)
Females ($n = 5$)	8.7 ± 9.8 (1.0–25.6)	3.6 ± 5.0 (0.5–12.5)	17.7 ± 18.2 (10.6–42.0)	12.2 ± 9.4 (4.7–28.5)

Figure 5. A juvenile angonoka (*Geochelone yniphora*) with a radio transmitter attached to the posterior costal scutes.

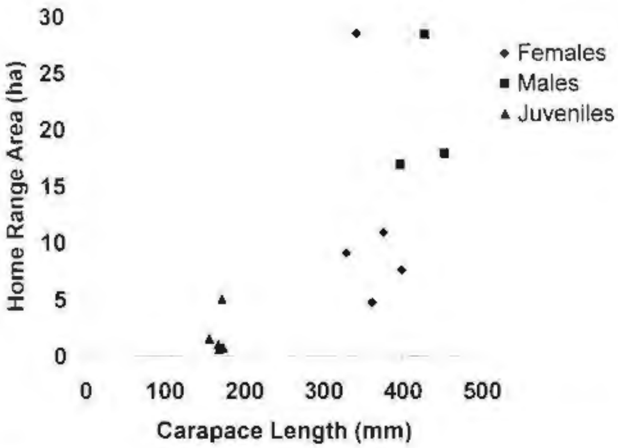

Figure 6. Wet season (November – April) home range size as related to carapace length in 13 angonoka (*Geochelone yniphora*) at Cape Sada, Madagascar. Home range was calculated using kernal area (KA) method (Worton, 1989).

variation in home range size between the sexes (Fig. 6). Males in this study were more nomadic than females and traveled over large areas, possibly in search of mates.

No statistically significant difference in dry season home ranges between the sex/life stages was detected (H = 0.54; $p > 0.10$). These results may be an artifact of the small sample size in this study because the mean juvenile home range size (0.6 ha) was much smaller than that of adult males (6.6 ha) and females (3.6 ha).

Microhabitat Use. — Scrub-shrub is the predominant microhabitat type on Cape Sada and occupies approximately 59% of the peninsula. The bamboo microhabitat occurs primarily on the highest elevations of the Cape and covers approximately 28% of the study area. Patches of savanna occupy approximately 4%. Open microhabitat was difficult to distinguish on the satellite image because it typically occurs in patches only a few square meters in size within the scrub-shrub or savanna. However, open areas probably occupy about 4% of the site. Komanga forest covers approximately 5% of the peninsula.

Tortoises were most often observed in scrub-shrub, (2070 of 3149 observations; 65.7%) followed by bamboo (819; 26.0%), savanna (164; 5.2%), and open habitat (96; 3.1%). Radio-instrumented angonoka were never encountered in the komanga forest. In general, angonoka on Cape Sada used microhabitats relative to their availability (χ^2 = 6.26; df = 4; $p = 0.20$); however, season appeared to have an

Table 3. Analysis of covariance of the effects of season and habitat where a tortoise was observed, and sex/life stage (males, females, and juveniles) on percent of observations of angonoka tortoises on Cape Sada, Madagascar. $*p < 0.05$ indicates values that were not uniformly distributed.

Comparison	df	F	*p*
Habitat	2	38.42	0.0001*
Season	1	0.03	0.8684
Sex	2	0.82	0.4436
Habitat*Season	2	3.21	0.0447*
Habitat*Sex	4	1.78	0.1390

Table 4. Results of Tukey's studentized range (HSD) test comparing mean percent of observations of angonoka tortoises by season and habitat type ($n = 18$) on Cape Sada, Madagascar. Habitat types included bamboo (BA), open (OP) and savanna (SA). MSD = minimum significant difference, * = significantly different ($p < 0.05$).

Habitat	Season	Mean	SD	Difference	MSD
BA	Dry	21.77	19.20	6.08	11.773
BA	Wet	27.86	15.34		11.773
OP*	Dry	1.55	2.63	2.24	1.864
OP	Wet	3.79	2.87		1.864
SA*	Dry	10.04	13.71	7.23	6.630
SA	Wet	2.81	1.89		6.630

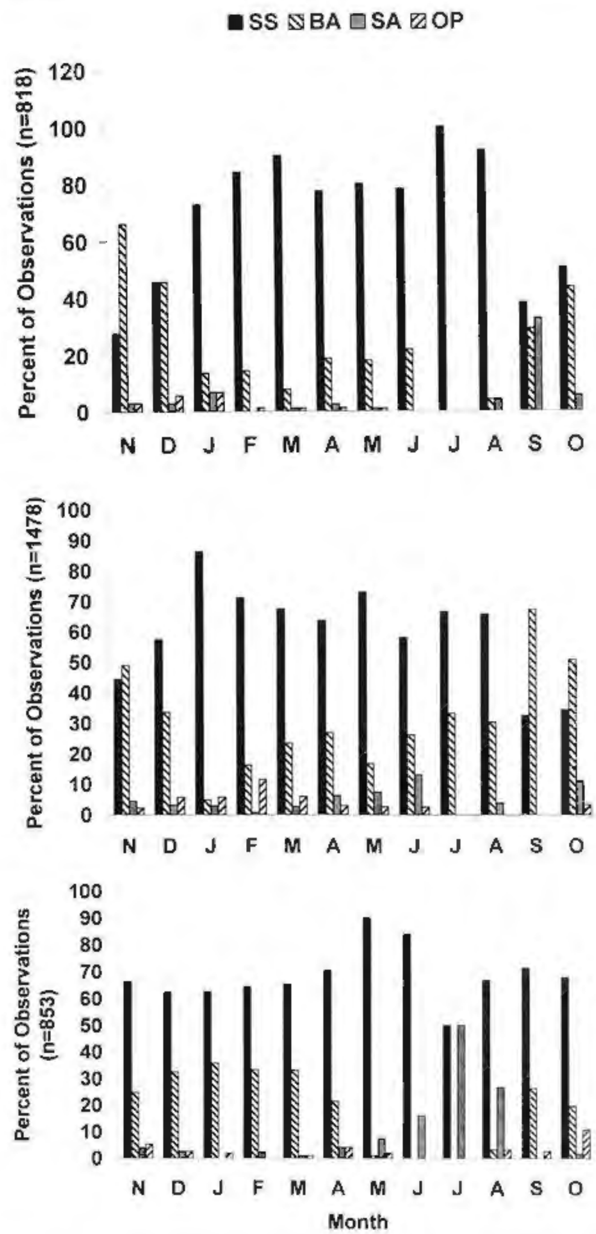

Figure 7. Habitat use in three male (**a, top**), five female (**b, middle**), and five juvenile (**c, bottom**) angonoka tortoises (*Geochelone yniphora*) at Cape Sada, Madagascar. Numbers represent percent of observations of radio-instrumented tortoises in scrub-shrub (SS), bamboo (BA), savanna (SA), and open (OP) habitat from October 1993 through June 1995.

effect on microhabitat selection ($F = 3.21$, $df = 2$, $p = 0.0447$) (Table 3). All angonoka used the open microhabitat significantly more often in wet season than in dry season (Table 4). Angonoka were observed significantly more often in savanna in dry season than in wet season (Table 4).

Although no significant difference in microhabitat use between male, female, and juvenile tortoises was detected ($F = 0.82$; $df = 4$; $p = 0.1390$), when the data were examined by month (Figs. 7a-c), it appeared that adults of both sexes used bamboo more often in the late dry season (September and October) and early wet season (November). Juvenile tortoises appeared to use the bamboo microhabitat more frequently during wet season months than during the dry season months (Fig. 7c).

DISCUSSION

Despite a great deal of individual variability, seasonal differences in adult home range size were observed in this study. Home range areas were larger in wet season, when food and water were plentiful, than in dry season, when these resources were limited. Tortoises were most often observed in scrub-shrub and bamboo, the most common microhabitat types on Cape Sada. However, use of other microhabitats differed among seasons. For example, angonoka were encountered more frequently in the open microhabitat during the wet season, because in general tortoises were more vagrant in wet season when environmental temperatures were high and moisture was not limited. Tortoises were observed feeding on the few herbs and grasses available in open areas during the wet season, and females often were observed passing through open areas as they searched for nest sites (Smith et al., 1995). In the dry season, angonoka used savanna more often than in wet season. This difference may relate to the tortoise's ability to maintain an optimal body temperature by sheltering under savanna grasses during the cool, but sunny, dry season. Giant tortoises (*Aldabrachelys elephantina* [= *Dipsochelys dussumieri*]) and box turtles (*Terrapene carolina*) also exhibit seasonal shifts in habitat use to thermoregulate (Stickel, 1950; Reagan, 1974; Swingland and Lessells, 1978; Dodd et al., 1994).

Although no difference in microhabitat use was detected between adult male, adult female, and juvenile angonoka in this study, adults appeared to use bamboo more often in October and November (late dry season). This coincides with breeding activity (Smith et al., 1995) and may indicate that bamboo habitat is important as a staging area for courtship. Differences in habitat use may exist between different angonoka populations. For example, female angonoka in a population west of Baly Bay used savanna more often in wet season than in dry season because females often chose nest sites in this habitat (M. Pedrono, *pers. comm.*). The savanna habitat used by female angonoka in the western population was more similar to true savanna. Female tortoises on Cape Sada tended to nest in the scrub-shrub or bamboo microhabitat, and only rarely in open, unvegetated areas (Smith et al., 1995).

The findings of this study regarding seasonal shifts in microhabitat use by the angonoka underscore the importance of maintaining the diversity of vegetation types within the bamboo-scrub ecosystem. Furthermore, grasses and vines in frequently burned angonoka habitat replace bamboo and shrubs, the two primary components of this ecosystem. The loss or reduction of these components of the ecosystem may severely reduce the suitability of the habitat for tortoises.

The role, if any, of natural brush fires in the maintenance of the bamboo-scrub habitat of the angonoka is not completely understood. Only a few studies have documented the effects of fire on tortoise species and their habitat. Natural fires ignited by lightning promote species diversity in the sandhill habitat of the gopher tortoise (*Gopherus polyphemus*) in the southeastern USA (Laessle, 1958). Gopher tortoises have adapted to a fire-maintained ecosystem by using subterranean burrows for refuge. The evergreen shrub/grassland (renosterveld) habitat of the South African geometric tortoise (*Psammobates geometricus*) also is fire-maintained (Baard, 1995). However, frequent wildfires degrade the renosterveld ecosystem and unseasonable fires can kill adult and juvenile tortoises (Baard, 1993). Catastrophic effects of anthropogenic fires have also been documented in Hermann's tortoise (*Testudo hermanni*) in Greece (Hailey and Goutner, 1991).

In western Madagascar, natural fires would be expected to take place in the wet season, when lightning storms occur. However, anthropogenic fires typically are set in the dry season and probably function quite differently than natural fires. Natural fires occur sporadically and undoubtedly with much lower frequency than man-made brush fires. Furthermore, dry season fires are probably more intense than wet season fires because fuel loads are greater. Therefore, intense dry season fires could be expected to have a greater impact on tortoises. It seems likely that man-made fires, by altering the bamboo-scrub habitat or killing tortoises outright, are a major threat to remaining angonoka populations.

As of June 1995, the angonoka population on Cape Sada consisted of at least 99 tortoises (14 adult males, 27 adult females, 42 juveniles, and 16 hatchlings) (Smith, et al., 1995). Mark and recapture data suggested that nearly all of the tortoises in this population had been found (Smith et. al., 1995). Using the wet season KA estimates from this study, the 14 adult males would be expected to use at total of approximately 295.4 ha, as compared to 329.4 ha for the 27 adult females. There are only about 150 ha of bamboo-scrub habitat on Cape Sada, therefore, it is apparent that home ranges of adults of both sexes overlap a great deal. The mean carapace length of the 42 juveniles on Cape Sada was 120.0 mm ($SD = 79.6$) which is similar to that of the 5 juveniles followed in this study (Table 1). Again, using the mean wet season KA estimate obtained in this study, the 42 juveniles on Cape Sada would be expected to use roughly 75.6 ha of habitat. Although the home range size of hatchling angonoka is not known, they probably use areas no greater than those of larger juveniles. Assuming the mean home range of hatchlings is the same as that of larger juveniles, the 16 hatchlings in this population would be expected to use 28.8 ha of habitat. As a rough estimate, the total area used by juveniles and hatchlings on Cape Sada would be 104.4 ha. There is probably some overlap in the home ranges of young angonoka; but conservatively, Cape Sada might be able to support at least 30% more juveniles than currently occur there. We found no significant difference in microhabitat use between adults and juveniles, and all tortoises used microhabitats relative to their availability. Therefore, juveniles probably are not restricted to only certain microhabitats and Cape Sada may indeed be below carrying capacity for juveniles and hatchlings. The presence of hatchlings on Cape Sada indicates that angonoka are reproducing successfully; however, the population structure is skewed toward adults and hatchlings, suggesting that juvenile mortality may be high (Smith et al., 1995). Long term monitoring of the population is needed to determine whether the population is increasing (despite high juvenile mortality), decreasing, or stable (at or below carrying capacity). Questions concerning carrying capacity are particularly important with only 4000–6000 ha of bamboo-scrub habitat remaining.

As mentioned previously, the angonoka is being bred in captivity with the intent of augmenting wild populations. We believe that habitat protection and restoration, rather than repatriation, should be a conservation priority for this species at this time, though with populations at currently depleted levels, repatriation may also be necessary, particularly to avoid inbreeding or bottleneck problems. Studies are currently underway to determine the amount of bamboo-scrub habitat remaining. Future research should focus on identifying components of the bamboo-scrub ecosystem that are most important to angonoka, and in determining the carrying capacity of this habitat.

ACKNOWLEDGMENTS

This project would not have been possible without the support of the Malagasy Government, particularly the Direction des Eaux et Forêts. Funding was provided by the Jersey Wildlife Preservation Trust. We wish to thank Lee Durrell, the Honorary Director of JWPT, for her support of the project. We are also grateful to the rest of the JWPT team, including Don Reid, Joanna Durbin, Lala Jean Rakotoniana, Hasina Randriamanampisoa, and Daurette Razandrizanakanirina, for their assistance with project logistics. Adany Lolo and Mossimo provided help in the field. Djamaldine Said Aly and family, Ali Hassanaly and family, Njaribe, Felix, Njarikely, and the people of Soalala, Antsira, Marotia, Antranolava, Antanandava, and Anjiamaloto graciously provided food, lodging, and friendship throughout the study. We are also most grateful to C.K. Dodd, Jr. and Richard Franz for their support and encouragement throughout the field study. Robert Smith assisted with computer analyses and Water & Air Research, Inc. provided use of a computer. We also thank the reviewers for their constructive comments on this manuscript.

LITERATURE CITED

AGUIRRE, G., ADEST, G.A., AND MORAFKA, D.J. 1984. Home range and movement patterns of the Bolson tortoise *Gopherus flavomarginatus*. Acta Zoolog. Mexicana (N.S.) 1:1-28.

AUFFENBERG, W., AND IVERSON, J.B. 1979. Demography of terrestrial turtles. In: Harless, M., and Morlock, H. (Eds.). Turtles: Perspectives and Research. New York: John Wiley and Sons, pp. 541-569.

BAARD, E.H.W. 1993. Distribution and status of the geometric tortoise, *Psammobates geometricus*, in South Africa. Biol. Conserv. 63:235-239.

BAARD, E.H.W. 1995. A preliminary analysis of the habitat of the geometric tortoise, *Psammobates geometricus*. S. Afric. J. Wildl. Res. 25(1):8-13.

CURL, D.A. 1986. The rarest tortoise on earth. Oryx 20(1):35-39.

CURL, D.A., SCOONES, I.C., GUY, M.K., AND RAKOTOARISOA, G. 1985. The Madagascar tortoise (*Geochelone yniphora*): current status and distribution. Biol. Conserv. 34(1):35-54.

DIEMER, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. J. Herpetol. 26(2):158-165.

DODD, C.K., JR., FRANZ, R., AND SMITH, L.L. 1994. Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. Chel. Conserv. Biol. 1(2):97-106.

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

DURBIN, J., RAJAFETRA, V., REID, D., AND RAZANDRIZANAKANIRINA, D. 1996. Local people and Project Angonoka - conservation of the ploughshare tortoise in north-western Madagascar. Oryx 30:113-120.

DURRELL, L., GROOMBRIDGE, B., TONGE, S., AND BLOXAM, Q. 1989. *Geochelone yniphora*, ploughshare tortoise, plowshare tortoise, angulated tortoise, angonoka. In: Swingland, I.R., and Klemens, M. (Eds.). The Conservation Biology of Tortoises. Occasional Papers of the IUCN Species Survival Commission. No. 5. Gland, Switzerland, pp. 99-102.

HAILEY, A., AND GOUTNER, V. 1991. Villas, villagers and tortoises in Greece - a sequel. Oryx 25(3):169-171.

IUCN. 1996. 1996 IUCN Red List of Threatened Animals. Gland, Switzerland: IUCN, 368 pp.

JUVIK, J.O., ANDRIANARIVO, A.J., AND BLANC, C.P. 1981. The ecology and status of *Geochelone yniphora*: a critically endangered tortoise in northwestern Madagascar. Biol. Conserv. 19:297-316.

JUVIK, J.O., KIESTER, A.R., REID, D., COBLENTZ, B., AND 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. N.Y. Turtle and Tortoise Society, pp. 345-350.

KENWARD, R.E., AND HODDER, K.H. 1996. RANGES V. An analysis system for biological location data. Dorset, UK: Institute of Terrestrial Ecology, Furzebrook Research Station.

KOECHLIN, J. 1972. Flora and vegetation of Madagascar. In: Battistini, R., and Richard-Vindard, G. (Eds.). Biogeography and Ecology in Madagascar. The Hague: Dr. W. Junk B.V., pp. 145-190.

KUSHNER, H.W., AND DE MAIO, G. 1980. Understanding Basic Statistics. San Francisco, CA: Holden-Day, Inc., 381 pp.

LAESSLE, A.M. 1958. The origin and successional relationship of sandhill vegetation and sand pine scrub. Ecol. Monogr. 28:361-387.

McKEOWN, S., JUVIK, J.O., AND MEIER, D.E. 1982. Observations on the reproductive biology of the land tortoises *Geochelone emys* and *Geochelone yniphora* in the Honolulu Zoo. Zoo Biology 1:223-235.

McNAB, B.K. 1963. Bioenergetics and the determination of home range size. Amer. Naturalist 97:133-140.

MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Nat. 37:223-249.

REAGAN, D.P. 1974. Habitat selection in the three-toed box turtle, *Terrapene carolina triunguis*. Copeia 1974:512-527.

REID, D., DURRELL, L., AND RAKOTOBEARISON, G. 1989. The captive breeding project for the angonoka *Geochelone yniphora* in Madagascar. Dodo, J. Jersey Wildl. Preserv. Trust 26:34-48.

SAS INSTITUTE. 1992. Categorical data analysis course notes. Cary, NC: SAS Institute, Inc.

SILVERMAN, B.W. 1986. Density estimates for statistics and data analysis. London: Chapman and Hall, 312 pp.

SMITH, L.L., JOBY, M., BOUROU, R., AND SIBO, C. 1995. Project Angonoka field study - final field report. Unpublished Report to Jersey Wildlife Preservation Trust, 27 pp.

STICKEL, L.F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecol. Monogr. 20:351-378.

SWINGLAND, I.R., AND LESSELLS, C.M. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll: movement polymorphism, reproductive success, and mortality. J. Anim. Ecol. 48:639-654.

VAILLANT, L. 1885. Sur une tortue terrestre d'espèce nouvelle, rapportée par M. Humblot au Muséum d'Histoire naturelle. Compt. Rend. Acad. Sci. Paris 101(6):440-441.

VAILLANT, L., AND GRANDIDIER, G. 1910. Histoire naturelle des reptiles. Première partie: crocodiles et tortues. In: Grandidier, A., and Grandidier, G. (Eds.). Histoire Physique, Naturelle et Politique de Madagascar. Vol.17. Paris: Hachette, 86 pp.

WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1):164-168.

Received: 20 August 1997
Reviewed: 6 August 1998
Revised and Accepted: 10 October 1998