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Population study on *Astrochelys radiata* (Shaw, 1802) in the Tsimanampetsotsa National Park, southwest Madagascar

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Abstract. During three months of studying a population of *Astrochelys radiata* in the Tsimanampetsotsa National Park, data for 132 tortoises were recorded. On two parallel transects, carapace length and weight of each animal were carried out and the exact location of each animal discovered during surveys recorded. Population densities of 32 to 47 animals per km² were estimated. A four-day survey to the eastern boundary of the park was carried out to gain data from a less human influenced region. Even though the study took place during the dry season the tortoises were found in abundance. During this study a great number of large and therefore old tortoises were found on the transects. In contrast, the comparison study near the eastern edge of the Park exclusively yielded large tortoises. This fact could not be suitably analysed within this study due to time constraints but should be taken into consideration in future studies. Transect T2 showed greater population densities of *Astrochelys radiata* compared to transect T1. Even though low numbers of tortoises were recorded during the transect study a viable population of *A. radiata* at Tsimanampetsotsa can be inferred.

Keywords. Testudinidae, *Astrochelys radiata*, Madagascar, Tsimanampetsotsa, morphology, ecology, population structure.

Introduction

The island of Madagascar is well known for its species richness and high endemism, especially among its herpetofauna. Species diversity reaches an endemism rate of 99% in reptiles and 93% among amphibians (Nussbaum & Raxworthy 2000, Glaw & Vences 2007). The family Testudinidae is represented by five tortoise species in Madagascar, four of which are endemic to the Indian Ocean island (Leuteritz 2005, Glaw & Vences 2007). Whereas tortoise species in the north (*Kinixys belliana*), in the northwest (*Astrochelys yniphora*) and in the western part of Madagascar (*Pyxis planicauda*) each show a restricted distribution area, both southern tortoise species (*Astrochelys radiata*, *Pyxis arachnoides*) distribution ranges stretch along the south-western and southern coast of Madagascar. The latter species has been divided into three subspecies inhabiting adjacent regions (Glaw & Vences 2007). Subfossil remains of *A. radiata* have been found in the region of Morondava, about 300 km north of its current range area (Pedrono & Smith 2003). Today the distribution of the radiated tortoise is restricted to a narrow band of about 100 km along the south-western coast of the island of Madagascar (O'Brien 2002, Fig. 1). North of Toliara and to the east of Ambondro the species is almost extinct nowadays (Juvik 1975). Lewis (1995) reported a decline of the tortoises' range and population densities within the last ten years. The International Union for the Conservation of Nature and Natural Resources (IUCN) classified the radiated tortoise as a vulnerable species in 1982. Only after a recent tortoise specialist workshop hosted by the IUCN, Wildlife Conservation Society and Conservation International, the status of *A. radiata* was upgraded to critically endangered (IUCN 2008).

Typical habitat where *A. radiata* can be found comprises the dry deciduous forest in the Mahafaly Plateau south of Toliara (Nuss-

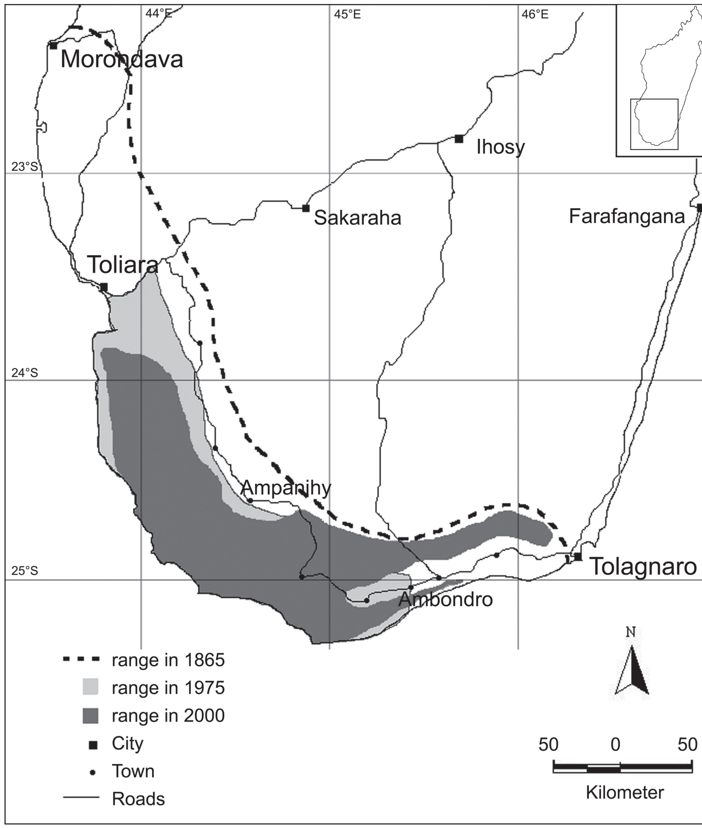

Fig. 1. Schematic map of southern Madagascar showing estimated ranges of *Astrochelys radiata* in the years 1865, 1975 and 2000 (data from O'Brien 2002).

baum & Raxworthy 2000, Seddon et al. 2000). Adult specimens may reach up to 38 cm carapace length and weigh up to 13 kilograms. Sexual dimorphism in adult tortoises is indicated by a concave plastron and a longer tail in male specimens (Pedrono & Smith 2003). Carapace colour varies from bright yellow to nearly black animals displaying a pattern of stripes radiating from the centre of each carapace scute. In old specimens the colouration may change to a more uniform colour.

Lying within the core distribution area of *A. radiata*, the Tsimanampetsotsa National Park draws scientific attention due to its unique deciduous dry forest. As this forest type belongs among the most endangered habitats, Du Puy & Moat (1998) strongly recommend putting additional areas of the Mahafaly Plateau under protection. The radiated tortoise is amongst the most common reptiles within the national park even though its population density was calculated to be only 27 animals per km^2 (Leuteritz 2002), whereas Lewis (1995) found densities of 262 animals per km^2 in Tsimanampetsotsa. Tsimanampetsotsa first received protected status in 1927 when a nature reserve was installed. In 1966 the protection status was converted to that of a national park embracing 43,200 ha of forest and wetland (Goodman et al. 2002). The residents of surrounding villages consider the park, and especially Lake Tsimanampetsotsa, sacred. Within its confines they both collect medicinal plants and bury their dead below the Mahafaly Plateau.

The flora of the national park is dominated by xerophytic plants, of the Didieraceae and Euphorbiaceae families, and contains a high percentage of endemic plant species (ANGAP et al. 1999). The management of the National Park is being carried out by Madagascar National Parks (formerly called Association Nationale pour la Gestion des Aires Protégées or ANGAP), which is represented by an office in the nearby village of Efoetse.

The removal of animals seems to remain the greatest threat to wild populations (Durrell et al. 1989, Behler 2002, Lewis 1995, O'Brien et al. 2003, Glaw & Vences 2007). ANGAP (2001) reports harvesting of *A. radiata* in the western part of Tsimanampetsotsa, both outside and inside the protected area. Within reach of the seashore tortoises can be easily shipped to Toliara. Collections seem to supply both national food markets and the international pet trade (O'Brien et al. 2003). Therefore, a decline of tortoise populations in the national park is at severe risk, and the protection of *A. radiata* is a specific declared aim of the programme of the Tsimanampetsotsa National Park (ANGAP 2001). Still, a national park can only help protect an existing population by preserving its natural habitat. Therefore this study aims to determine more information about the status of *A. radiata* within the National Park of Tsimanampetsotsa. Does a viable population of radiated tortoises exist in Tsimanampetsotsa? How can this population be characterised? Is this national park of importance for tortoise protection, and does it contain a viable reserve (or assurance) population of *A. radiata*? Which human activities within the national park influence tortoise habitat or behaviour? What preservation measures should be enacted to ensure the survival of *A. radiata* in Tsimanampetsotsa?

Material and methods

The main study area (which will be referred to as the western study area) lies in the northwestern part of Tsimanampetsotsa. Due to geological and floral structure three different types of habitat are discernible within the study area. On the northern banks of the Manampetse salt lake, a forest formation consists of a thick thornbush scrub and trees of up to seven meters in height. Mainly on sandy ground, the most common species within this forest formation are *Salvadora angustifolia*, *Euphorbia laro*, *Gyrocarpus americanus* and *Grewia grevei*. Aligning with the eastern shore of the salt lake a limestone cliff stretches in a northwestern to southeastern direction. On this limestone cliff and the adjacent plateau *Alluaudia comosa*, *Diospyros manampetse* and *Commiphora mahafalensis* are the most common plants. The thick thornbush reaches only four meters high and forms a dense, nearly impenetrable wall of vegetation. East of the calcite plateau a sink formation containing red sands predominates. Large trees are rarely found in this type of habitat which is dominated by *Didiera madagascariensis*. Other common plants are *Delonix andansonioïdes*, *Euphorbia plagiantha* and *Gyrocarpus americanus.*

Two former zebu-cart tracks were used as transects in the western study area and henceforth are referred to as transect 1 (T1) and transect 2 (T2). Running approximately parallel, both transects cross all three habitat types. They are of 2.9 (T1) and 2.4 (T2) kilometers in length, separated by an average distance of 1.5 kilometres (Fig. 2), which allows us to assume independent samples in tortoise data acquisition. Both transects were marked using flagging tape, and waypoints along the route were recorded using GPS-technology (geko 301, Garmin).

The survey was carried out during the dry season between 23 May and 19 August 2006. Transects were walked twice daily from 8:00 to 12:00 h and from 14:00 to 18:00 h in four-day periods starting on 29 May 2006, 15 June 2006, 24 June 2006, 10 July 2006, 24 July 2006 and 09 August 2006. Both transects were connected and could be walked in a circle. During the survey all four possibilities of starting positions on the transects were varied to allow equal daytime research during

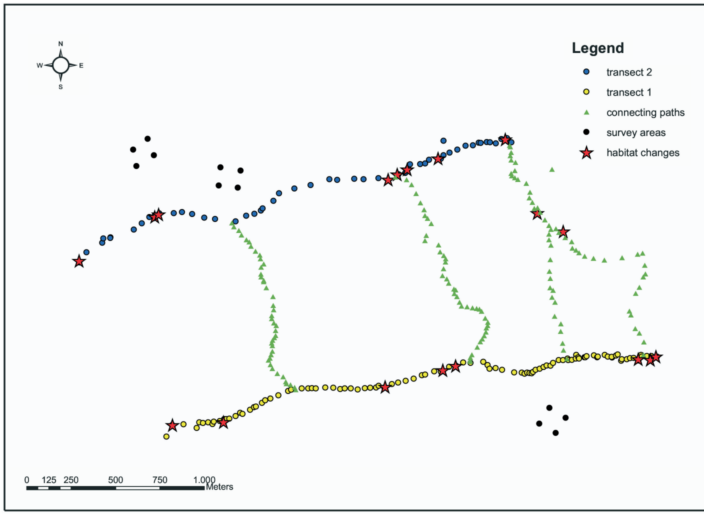

Fig. 2. Location of the permanent transects and survey squares within Tsimanampetsotsa National Park compiled from GPS data mapped in the study area.

the survey. With one exception these four-day-periods of transect walking were evenly distributed during the study period. Finding a tortoise the perpendicular distance of the animal to the transect was measured using a tape measure (30 m). The exact location of each tortoise was also recorded with a GPS. Measurements of carapace and plastron length, body height and width of each animal were carried out using a measuring tape (1.5 m) and a folding rule (2.0 m). Body mass was measured on a digital scale (My Weigh Ultra Ship 55). Where possible the animal's sex was determined based on plastron characteristics and tail length as explained. All animals whose gender could not be ascertained were recorded as juveniles. Age estimation of each tortoise was carried out. To quantify sexual dimorphism in *A. radiata* the anal fork width (in the following ASG) of each animal was measured as well as the posterior shell opening between carapace and plastron (LAP) (Fig. 3) using calipers (INOX Wisent, 15 cm). These measurements were carried out even if there was no unequivocal sexual classification. In order of their discovery all animals were marked with a number on the fifth central scute using a black felt pen. The same number was notched into the marginal scutes using a saw blade (Cagle 1939, Leuteritz 2002). Juveniles were marked only with the marker pen. To estimate the visual field on the transects the perpendicular distance to a tortoise dummy was measured using a tape measure (30 m) placing the dummy at greatest visibility. This measurement was carried out every 20 m along both transects. The

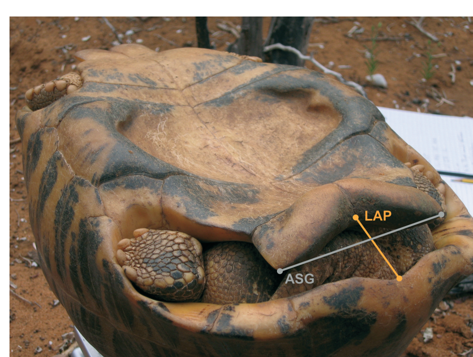

Fig. 3. Ventral view of plastron of a male radiated tortoise. The concave shape is clearly to be seen, as well as the thickened anal plastron scutes. The picture shows the parts of anal scutes measured in the study (LAP: posterior shell opening between plastron and carapace; ASG: anal fork width).

visual field calculated from the visibility and transect length served to estimate population densities of *A. radiata*. To record mean daily temperature in the survey area minimum and maximum temperature were measured twice daily at 7:00 and 19:00 h local time. Precipitation was recorded reading a pluviometer daily at 7:00 h local time.

Besides the transects, three squares of 100 × 100 m were marked, choosing one examination square in each habitat type (see Fig. 2). These squares were chosen at random to compare results to the transect data and searched four times during the study period between 8:00 to 11:00 h when tortoise activity was considered to be still quite low to ensure the tortoises would not move out of the study area before being detected. All data of tortoises found on both transects, the connections in between and on the three marked squares were used in the population study, including those animals that were found outside the six standardised transect surveys.

During a four day trip to the eastern boundary of the national park, short transects were installed along the route. Every two kilometres a transect of 200 m was carried out right-angled to the route, alternately to the right and the left side. Data on all tortoises found in these short transects was recorded. Additionally a transect of 2.5 km length was walked at the eastern part of the park to estimate tortoise density in this inland, less human influenced area. All data on tortoises found on the walk back was also recorded. All results from this trip are referred to as data from eastern study area. However tortoise data found on the four- day trip to the eastern boundary of the park is excluded in the population study and serves only for comparison purposes.

Tortoise population density estimations refer to the animals found in the standardised transect surveys. To estimate population density from transect surveys the following assumptions have to be taken into consideration (Krebs 1998): (1) animals on the transect line will never be missed; (2) animals are fixed at the initial sighting position; they don't move before being detected and they are not counted twice; (3) distances and angles from the transect line to the animal are measured exactly; (4) sightings of individual animals are independent events.

Calculation of population densities were carried out using the King formula (Brower et al. 1989):

$$D = \frac{10^4\, n^2}{2L \sum d_i}$$

D: the populations' density (number of individuals per hectare); *n*: number of animals sighted; *L*: transect length (in metres); d_i: distance of animals sighted to the transect (in metres); 104: factor for converting m² to ha.

This method assumes that there is a random distribution of animals over the area sampled and all animals are equally likely to be counted, the sighting of one animal does not influence sightings of other animals and no animal is counted more than once (Brower et al. 1989). Additionally, and for comparison purposes, population densities were calculated using the computer program DISTANCE. A hazard-rate key function was chosen, complemented by a cosine series expansion to ensure the best reproduction of tortoise dispersal data. In the programme, the integrated AIC term (Akaike Information Criterion) has been used to select the key function for best data representation. Additionally a right truncation of the data at 5% was carried out (Buckland et al. 2001). To perform statistical analysis of the data the following tests and calculations were used: To test the temporal and local dispersion of recaptures for sexual differences a Kruskal Wallis analysis was calculated. The Mann Whitney U-Test was performed to interpret different questions concerning tortoise data: Sexual differences in weight, age, carapace length, anal fork width (ASG) and the posterior shell opening (LAP) were analysed using the Mann-Whitney-U-Test. Mean carapace length and weight on the two transects were compared as well as the mean age dispersion of the tortoises in the western study area and that of animals found in the east of the National Park. A Spearman correlation was performed to implicate the carapace length of the tortoises from their weight, their age and the anal fork width of the animals (ASG). This test was also used to compare the number of tortoises found during the four-day-periods of transect walking. The age dispersion of male and female tortoises in the western study area as well as in the eastern and western part of the park were compared using a Chi^2-test. Furthermore this test was used to examine the activity and recapture data of the tortoises towards sexual influenced differences in tortoise dispersal. All statistical tests were performed using the computer program SPSS 13.0. For further descriptions of all tests see Bühl (2006). All GPS data mapped in the study area were edited using the computer program ArcMap.

Results

During the three-month survey in Tsimanampetsotsa National Park we made a total of 169 sightings of *A. radiata*, two of *Pyxis arachnoides* as well as finding two empty shells of *A. radiata* in Tsimanampetsotsa National Park (Tab. 1). The *A. radiata* observations in the western study area were represented by 103 initial sightings, 37 recaptures and a single empty shell. In the areas outside of the main study site, we observed three *A. radiata* near the village of Efoetse, 26 specimens in the eastern study area and another empty shell. Within the 103 first sightings of *A. radiata* in the western study area a total of 52 animals were found during transect survey days, whereas another 22 tortoises were detected outside the standardised catching periods. In the survey squares a total of 9 tortoises *A. radiata* were found and another 20 first sightings occurred on connecting paths between transect T1 and T2.

Behaviour

About 56% of the tortoises were active upon detection, which means they were walking or eating. The other 44% of animals were resting in the shade, sunbathing or sleeping. There was no gender based difference in activity at the time of detection ($p = 0.973$, Chi^2 test value = 0,055). Activity of tortoises is assumed to be restricted to daytime. During surveys before 9:00 a.m. and after 5:00 p.m. little tortoise movement was detected. Animal sightings occurred during all daytime hours.

Population structure

Out of 103 radiated tortoises found in the western study area, we confirmed the sex of 31 males and 27 females giving a sex ratio (male: female) of 1.15. The sex ratio in the eastern study area was calculated to 0.63 (10 males, 16 females).

Morphology

The mean carapace length and weight of male tortoises were significantly higher than females' (weight: $p = 0.022$, carapace length: $p = 0.007$; Mann-Whitney-U-Test; see Tab. 2). Furthermore the age difference between

Tab. 1. Tortoise sightings divided by study area, sort of sighting and tortoise species.

	western study area	eastern study area	village of Efoetse
first sightings *A. radiata*	103	26	3
recaptures *A. radiata*	37	–	–
empty shells *A. radiata*	1	1	–
first sightings *P. arachnoides*	2	–	–

Tab. 2. Mean value and standard deviation of different carapace measurements, as well as estimated age and weights of *A. radiata*, sorted by sex. Minimum and maximum values are given in parenthesis. Animals that could not be classified by their sex where recorded as juveniles. ASG: anal fork width, LAP: posterior shell opening between carapace and plastron.

	weight [g]	carapace length [cm]	ASG [cm]	LAP [cm]	age [years]
all tortoises	3424 ± 2229 (24 - 7680)	23.1 ± 7.0 (4.5 - 34.5)	5.6 ± 2.0 (1 - 10.5)	2.7 ± 1.0 (0.5 - 4.9)	21.3 ± 11.6 (2 - 50)
male	5520 ± 1218 (3210 - 7680)	29.6 ± 2.7 (24.5 - 34.5)	7.8 ± 1.3 (5.9 - 10.5)	3.3 ± 0.7 (2.1 - 4.7)	31.8 ± 10.6 (13 - 50)
female	4578 ± 1482 (2080 - 7180)	26.9 ± 3.7 (20.5 - 32.5)	5.8 ± 0.8 (4.2 - 7.4)	3.6 ± 0.8 (2.2 - 4.9)	26.0 ± 7.5 (15 - 40)
juvenile	1264 ± 708 (24 - 2680)	16.5 ± 4.1 (4.5 - 22.5)	3.9 ± 1.0 (1 - 5.9)	1.8 ± 0.1 (0.5 - 2.9)	11.3 ± 3.3 (2 - 16)

male and female tortoises was significant ($p = 0.034$) with a greater number of older male tortoises found, while the anal fork width differs highly significantly in male and female animals ($p < 0.001$). No differences could be observed between the LAP-data of male and female radiated tortoises ($p = 0.140$). Both groups differ clearly from the data of juvenile tortoises. Body mass of the tortoises within the western study area was bimodal, showing peaks between 1-2 kg and 5-6.5 kg (Fig. 4). The weight and carapace length of the tortoises are significantly correlated; with juvenile and adult animals treated separately in data examination (juvenile: r = 0.937, adult: r = 0.851 with $p < 0.001$ in both cases). The dispersion of carapace length also shows a bimodal distribution. Observed lower numbers of individuals are between 22.6 cm and 25 cm of carapace length. A linear correlation between the anal fork width and the carapace length could be observed (r = 0.882; $p < 0.001$; Spearman-Correlation).

Compared to transect T2 tortoise data of males and females collected on transect T1 shows greater mean carapace length and weight measures (Tab. 3). In contrast the juvenile tortoise data shows greater means on the second transect. A significant difference between weight and carapace length of the adult animals could only be detected in the data of male carapace lengths (Mann-Whitney-U-Test: $p = 0.03$). The data of the females (weight: $p = 0.058$; carapace length: $p = 0.111$) and the weights of the males ($p = 0.238$) did not show significant differences between the

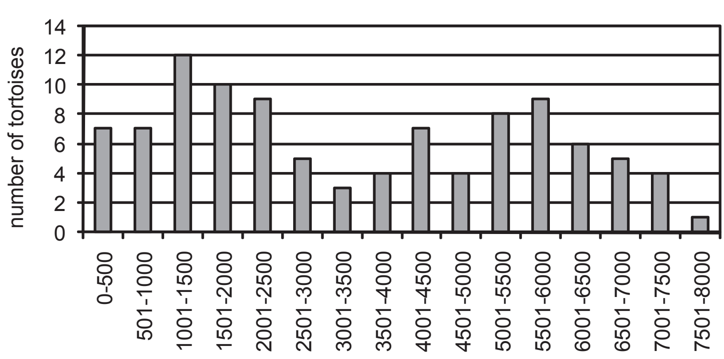

Fig. 4. Distribution of weights of *Astrochelys radiata* from Tsimanampetsotsa National Park, subdivided into classes of 500 g.

Tab. 3. Mean values of weights and carapace length of *Astrochelys radiata* including their standard deviation, divided into the two transects and the animals' sex.

	T1	T2				
	weight [g] (std.-dev.)	carapace length [cm] (std.-dev.)	number	weigth [g] (std.-dev.)	carapace length [cm] (std.-dev.)	number
male	5817 ± 1051	30.8 ± 2.1	13	5135 ± 1367	28.5 ± 2.9	13
female	5044 ± 982	28.1 ± 2.9	9	3673 ± 1686	24.8 ± 4.5	9
juvenile	857 ± 544	15.0 ± 3.2	14	1737 ± 629	18.6 ± 2.3	16
total			36			38

two transects. In contrast the data of juvenile tortoises shows a significant difference between the two transects (weight: $p = 0.002$; carapace length: $p = 0.006$).

Looking at the tortoises with an estimated age of over 30 years a greater number of males were detected during the study period. A total of 16 males were found with an estimated age of 30 years or older whereas only 7 females of this age class were detected in the study area. This discrepancy emerges even more clearly by looking at the tortoises with an estimated age of over 40 years. Four males were thus classified, but no female older than 40 years was found. In the statistical comparison of the age distribution of males and females in the western study area no significant difference could be detected using the Chi²-test ($p = 0.118$). Figure 5 shows the age distribution of *A. radiata* in both western and eastern study areas. While over 50% of tortoises found in the western study area were estimated to be between ten and twenty years old, about 65% of the tortoises in the east were estimated to be over 40 years old. In comparing these data it must be emphasized that the trip to the east of the Park lasted only four days. The total of 26 animals found on this excursion provide a database too small for a detailed comparison. However, the findings suggest regional differences of tortoise populations in the national park and highlight further questions for future studies.

Considering the mean estimated age of the tortoises in both study areas ($p < 0.001$, Mann-Whitney-U-Test) as well as for the age distribution ($p < 0.001$, Chi²-homogeneity-test) there are significant differences between the two regions. The correlation of age and carapace length can be described as a curve with a steep gradient that flattens with the age of the animals (Fig. 6). In this analysis the curve has been cut into two sections with an age limit of 23 years as pivot point.

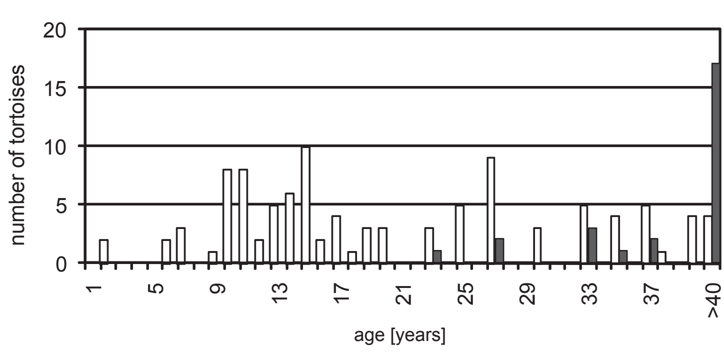

Fig. 5. Age distribution of radiated tortoises found in the main study area and during the trip to the east of the Park.

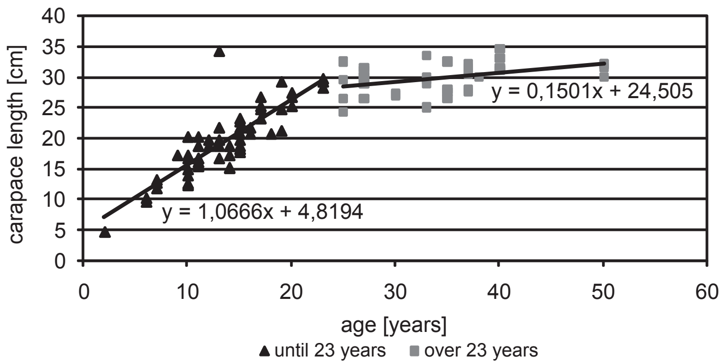

Fig. 6. Carapace lengths (in cm) and age distribution of *Astrochelys radiata*. The data is divided in animals up to the age of 23 and those older than 23 years. The formulas for the lines of best fit are given in the diagram.

The group of animals up to 23 years shows a strong linear correlation between the two variables (r = 0.826, $p < 0.001$), whereas the group of animals older than 23 years shows only a weak correlation (r = 0.494, $p = 0.001$; Spearman-Correlation). The carapace length measurement of animals over 23 years ranges from 24 to 35 cm.

Out of those 103 tortoises found in the western study area, a total of 25 animals were recaptured. As nine animals were recaptured more than once the total number of recaptures adds up to 37. A well-balanced ratio of males, females and juveniles was detected in the recaptures, and no sex-based component could be examined within recapture data (Kruskal-Wallis-ANOVA: $p = 0.513$; Chi^2-test: $p = 0.358$). About 90% of all recaptures were within 200 m of the original capture spot.

During the four-day periods of transect survey each transect was walked twice daily. With a total length of 2853 m on transect T1 and 2349 m on transect T2; a total distance of 251.9 km has been walked during the study period. With a total of 52 first captures of radiated tortoises a theoretical distribution of one tortoise every 4843.4 m or 0.21 tortoises per walked km can be calculated. Figure 7 clearly shows a constant increase of cumulative first catches of *A. radiata* during the study period. This curve reaches no plateau. A coefficient of correlation of r = 1 has been calculated for the interrelation of the number

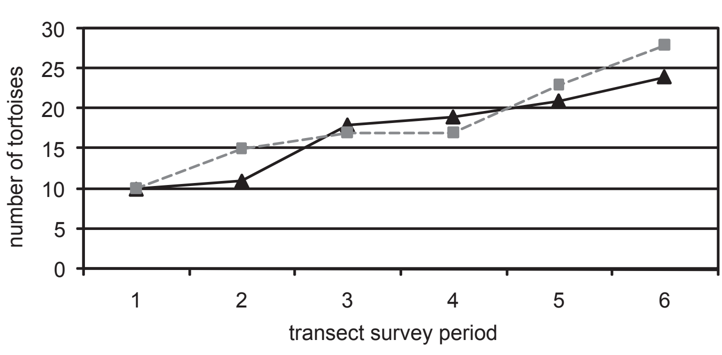

Fig. 7. Cumulative tortoise catches during transect surveys. The diagram displays the number of first sightings.

Tab. 4. Population densities of *Astrochelys radiata* in animals per km², calculated using the King formula, with the computer program DISTANCE and estimated via the visual field of each transect, calculated from the sighting distance and transect length. The program DISTANCE gives a limit of confidence with it's calculations. In the category 'sightings up to 12 m' those tortoises with a transect distance of over 12 m were not included in the calculation. This corresponds to the truncation of 5% of all tortoise counts in the computer program DISTANCE.

	King	DISTANCE	visual field
all tortoises	39.0	37.9 (22.2 - 64.8)	34.3
sightings up to 12 m	47.0	41.9 (22.8 - 76.9)	32.1
T1	34.0	23.1 (16.2 - 32.8)	23.2
T2	50.0	64.7 (23.0 - 182.2)	50.2

of capture periods and the number of tortoises found on transect T1 ($p = 0.01$; Spearman-Correlation). The coefficient of correlation between the capture periods and the number of tortoises on transect T2 reaches $r = 0.986$ ($p = 0.01$). The tortoise data from the standardised transect surveys was used to calculate tortoise population densities (Tab 4). The results of the three methods of calculation show little differences in result values. In comparing the two transects all calculation methods display a greater tortoise population density on transect T2.

Discussion

During a three-month survey in the Tsimanampetsotsa National Park a total of 103 radiated tortoises were detected in the main study area. As the diagram of cumulative tortoise captures shows, only a part of the tortoise population has been recorded (Fig. 7). The great number of tortoise finds during the first transect period could have been a function of it being the end of rainy season. The increase of tortoise captures on transect T2 during fifth and sixth transect period suggests increasing tortoise activity at the end of dry season. Possibly the animals had been unable to store up enough fat during rainy season to outlast a long winter break, and thus had to leave their wintering grounds. *Astrochelys radiata* could be seen on transects during all daytime hours and no specific daytime activity could be observed. In contrast Leuteritz et al. (2005) and O'Brien (2002) both state to have observed increased tortoise activity during morning and afternoon hours. These two surveys were carried out during the rainy season which leads to the assumption of a seasonally changing activity scheme of *A. radiata*. Nussbaum & Raxworthy (2000) observed *A. radiata* throughout the year without perceiving a distinct hibernation period of the tortoises. A seasonal comparison of tortoise activity is still lacking. Several authors mention having observed greater tortoise activity after rainfall (Nussbaum & Raxworthy 2000, Pedrono & Smith 2003), which this study also indicates.

When comparing the two transects, only the carapace length of male radiated tortoises shows significant differences between animals detected on T1 and T2. The female tortoise data and the weights of the male tortoises do not differ. Among adult tortoises no significant population differences attributable to the transects could be observed. Therefore all animals detected during the transect survey apparently belong to the same tortoise population.

During a survey in seven different study areas Leuteritz (2002) provides mean carapace lengths for *A. radiata* between 18.5 and 30.9 cm. Compared to Leuteritz' (2002) data the mean carapace length detected in this study is quite low (23.1 ± 7.0 cm). This could be interpreted as a function of greater juvenile tortoise activity during the dry season, or could indicate the paucity of large tortoises in the study area. Maximum carapace lengths of *A. radiata* are stated to lie between 38 cm (Pedrono & Smith 2003) and 40 cm (Lewis 1995, Nussbaum & Raxworthy 2000), whereas Lewis (1995) derives this figure from only one specific study area and gives a maximum carapace length of 38 cm for other regions, too. This study's maximum carapace length of 34.5 cm is clearly lower than those observed in other studies.

Correlation of carapace length and weight permit an estimation of the age at which the tortoises reach maturity. Beyond an estimated age of 23 years, the carapace length of radiated tortoises increases very little. Adults examined in this study had carapace lengths between 24 and 35 cm. Therefore, the carapace length of mature tortoises varies by up to 10 cm; given the maximum carapace length of 40 cm the variation in carapace length in fully grown tortoises may be 16 cm. Lower numbers of individuals detected in the weight classes of 2501 to 4000 g and 4501 to 5000 g could be related to lower activity of these animals during the dry season, but could also reflect the loss of tortoises during a long, severe dry period a few years ago whose impact can now be observed in lower counts of specific weight and therefore age classes.

In this study, male tortoises appear to have a greater mean carapace length and weight than females in the study area. This conclusion mirrors that of O'Brien (2002) who tabulates mean carapace lengths observed in eight different study areas in southwestern Madagascar. However, O'Brien does not clarify whether a significant difference exists in carapace length between males and females, as this data had originated from other analyses and statistical testing has not been carried out. Within this actual study a significant difference in the age distribution of male and female tortoises was observed with more old males than females, probably caused by selective collection through poachers. As older tortoises usually attain a greater carapace length the differences in tortoise size considering their sex could also be related to the fact of a male domination in old animals and therefore be misinterpreted in this study as a sign of sexual dimorphism in radiated tortoises.

The characteristic shape of the anal scutes and plastron best exemplify sexual dimorphism in *A. radiata*. A significant difference between male and female tortoises concerning the distance of the LAP was not found. However the data show significant differences between anal fork width (ASG) in male and female tortoises. The narow but tapering anal fork of the females probably offers advantages in egg deposition. A tendency towards a narrow versus wide anal fork is observable in subadult animals and therefore the animals' sex may possibly be detected thus before other sexual characteristics in plastron shape and tail length become distinct (see Fig. 3).

In the course of the study period, an even ratio of male and female tortoises could be ascertained. However, a remarkable proportion of male tortoises having an estimated age in excess of 30 years was detected in this study. The age distribution of tortoises in the east of the National Park seems unbalanced, though a relatively brief period (only four days) was devoted to focused study there. In the less anthropogenically influenced inland area, exclusively animals with an estimated age of over 30 years and carapace lengths over 30 cm were found. Both areas surveyed by Goodman et al. (2002) are close to the survey area of this study. Four years ago these areas showed an uneven distribution in sex ratio of *A. radiata* which differs from the one detected in this study. Goodman et al. (2002) stated a dominance of male tortoises in the west of the Park (Mitoho) and an even sex ratio in the east (Bemananteza). Among 13 adult tortoises found in Mitoho there was only one female *A. radiata*. Furthermore no tortoise with an estimated age of over 40 years was found (Goodman et al. 2002). The lack of old tortoises in the west of the National Park was confirmed in this study.

Comparing the actual study to that of Goodman et al. (2002), the varying domination of male and female tortoises in the study areas with uneven sex-ratio is striking. The area of Bemananteza in the east of the Park shows an evenly distributed sex ratio with an index of 1.17 (Goodman et al. 2002) whereas in the actual study a dominance of female animals was detected calculating a sex-index of 0.63 in the east of the National Park. Goodman et al. (2002) attributed the observed sex ratio in the stronger human-influenced area of Mitoho to the removal of *A. radiata*. Female tortoises are more often collected as large females sometimes contain eggs (Leuteritz et al. 2005). The continuous collection of large tortoises could select for small animals, resulting in the reduced carapace lengths detected in the actual study. Likewise the female-biased sex ratio found in the east of the park suggests lower collection pressures beyond the Mahafaly Plateau.

Because the survey of Goodman et al. (2002) took place during rainy season, a comparison to the actual study must be framed against the background of an annual cycle of varying tortoise activity (Leuteritz et al. 2005, O'Brien 2002). Leuteritz (2002) provides population densities of 28 to 5744 animals per km^2 from seven survey areas in the southwestern Madagascar. This was also the biggest range in radiated tortoise densities observed in last year's studies. Lewis (1995) calculated densities between 262 and 1077 tortoises per km^2 in five survey areas. Both studies stated the lowest tortoise densities in Tsimanampetsotsa National Park which leads tortoise densities ranging from 28 to 262 animals per km^2 in this area. Surveying three study areas O'Brien (2002) calculated tortoise densities between 314 and 1535 animals per km^2. In comparison to these studies population densities determined in the actual survey are considerably lower, consisting of 32 to 47 radiated tortoises per km^2. Only the population density of 27 tortoises per km^2 stated by Leuteritz (2002) in Tsimanampetsotsa National Park of is lower still, whereas Leuteritz found only one radiated tortoise during a three-day-trip to the National Park. Again it must be emphasized that the actual study took place during the dry period and should not be hastily compared to other studies. Low population densities could be attributed to lower tortoise activity during the dry season. Considering that both Lewis (1995) and Leuteritz (2002) detected their lowest tortoise densities in Tsimanampetsotsa, a low abundance of radiated tortoises in the National Park may be inferred. Given the balanced proportion of male and female tortoises and the still impressive number of tortoises found in this dry season study, Tsimanampetsotsa still seems to have a viable population of *A. radiata*. Goodman et al. (2002) also conclude that a viable population exists in Tsimanampetsotsa and emphasise that the National Park provides an important conservation opportunity for *A. radiata*. On the other hand, ANGAP (2001) warns of a highly fragmented tortoise population due to collection of animals from shoreline areas outside the national park.

So far, a detailed comparison of tortoise activity correlated to seasonal differences to explain apparent variations in population structure of *Astrochelys radiata* is needed. A detailed study might also shed light on whether the eastern tortoise population contains only old specimens which no longer reproduce. This would explain the absence of juvenile tortoises there in the course of our study. However, the lack of juveniles in the eastern survey area could also be explained by a better food supply in this region allowing juveniles to build up enough reserves for sustained hibernation throughout the dry season. Moreover, a comparative survey during the rainy season could show clearly whether there are differences in male and female tortoise activity which could thereby explain an annual variation in the sex ratio.

Until now, *A. radiata* has been protected by a 'fady,' a taboo which forbids local people to eat or even to touch the tortoises. This 'fady' is only respected by some local tribes in southwestern Madagascar while others seem not to be constrained by this taboo. As people from other parts of the island migrate to the south the 'fady' weakens and tortoise populations become increasingly exploited by poachers. Killing tortoises for crop protection seems to occur, however tribes who respect the local 'fady' do not seem to cooperate with poachers.

Tortoises are still considered sacred and believed to contain the ancestors' spirit when found close to a grave (Nussbaum & Raxworthy 2000, Juvik 1975). Several graves can be found along the transect T2. During the study period a new grave was constructed below the limestone cliff of the Mahafaly Plateau. Therefore local people still bury their dead within the National Park, which may possibly explain why there is a greater number of tortoises on the second transect. A reduced collection of tortoises due to reluctance to disturb ancestors could be a factor here. During the construction of a new grave a considerable amount of natural vegetation was cut down which probably has negative impacts on tortoise populations. A broad and sensible conservation of *A. radiata* therefore must take into consideration the impact of human land use.

Whereas there are current plans to extend the National Park, adequate accessibility by park rangers must be given priority in order to exercise control so as to prevent poaching of the tortoises, for despite their protection by national and international law (UNEP-WCMC 2009, Lewis 1995), they are still collected and sold for food and as pets. ANGAP (2001) reports poachers operating even within the National Park. Moreover they suspect some local farmers of collaborating with the poachers as they consider the tortoises pests that destroy their crops (Lewis 1995). Left out of the ANGAP scenario is the fact that tortoises are wild animals that can choose their whereabouts. By concentrating protection activities within the National Park it might be forgotten that the animals may leave the sanctuary and then be removed by a farmer or a poacher. Therefore, the difficult challenge remains to raise awareness of the local people and to educate them in favour of nature conservation, essential to assure the protection of *A. radiata* in its natural habitat.

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