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Habitat Use and Diet of *Astrochelys radiata* in the Subarid Zone of Southern Madagascar

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Abstract. – *Astrochelys radiata* is one of the threatened tortoise species of Madagascar. We studied their home range size, use of shelters, and diet in Tsimanampetsotsa National Park. The goal was to identify suitable habitats and food chemistry. These data could serve as bases for future evaluations of the suitability of habitats under altered environmental conditions, such as degradation and climate change. The study was performed with the help of radio-tracking in two different types of vegetation: dry deciduous forest on sand and spiny bush on limestone between November 2007 and October 2008. Monthly range sizes were 2.3 ha in the littoral forest and 1.4 ha on the limestone massif when calculated with the kernel method. Based on the minimum convex polygon, the values were 1.0 and 0.5 ha, respectively. Monthly range size did not vary significantly between sexes, but range sizes were larger in the littoral forest than on limestone. *A. radiata* chose shelters under trees with large trunk diameters (> 15-cm DBH) and lower heights than trees in representative samples in the habitats. Plant items eaten and not eaten by this species were analyzed for primary and secondary plant chemicals. *A. radiata* consumed a wide variety of plants. Its diet was composed of leaves (91%), flowers (5%), and fruits (4%) from 109 plant species. During the dry season, high energy content was the most important factor for food selection by *A. radiata*.

Key Words. – Reptilia; Testudines; tortoise; home range; shelter; nutrition; food chemistry; life history; seasonality

Madagascar has a unique herpetofauna with some 400 species, of which more than 90% are endemic (Glaw and Vences 2007). This includes four threatened species of endemic terrestrial tortoises, all listed on the International Union for Conservation of Nature (IUCN) Red List for Endangered Species. In the past, the Radiated tortoise, *A. radiata,* has been abundant and was often found along roads in the southwestern and southern parts of Madagascar. As such, it has served as a symbol of Madagascar's south. Habitat destruction, illicit exploitation for food, for supposed medicinal purposes, and for the pet trade led to a reduction in its distribution by about 20% during the past 25 yrs (Nussbaum and Raxworthy 2000; O'Brien et al. 2003; Irwin et al. 2010). Tortoises are killed and consumed by the Vezo and Antanosy, who occupy the northeastern and southeastern limits of the species' range. In contrast, tortoises are taboo (fady) for the Mahafaly and Antandroy. This taboo seems to be largely responsible for the survival of the species on the Mahafaly and Karimbola plateaus (Nussbaum and Raxworthy 2000; Lingard et al. 2003). Apart from local consumption, the international pet trade also contributes substantially to the decline of the species in its natural habitats (Ganzhorn 2011). These activities resulted in the classification of *A. radiata* as ''Critically Endangered'' according to the IUCN Red List criteria (Leuteritz and Rioux Paquette 2008). Today, the tortoise's natural distribution is limited to xeric spiny forests from south of the Onilahy River to the Cap Saint Marie with isolated populations as far east as Andohahela National Park (O'Brien et al. 2003; Sage 2003; Leuteritz et al. 2005; Pedrono 2008).

Despite its status as ''Critically Endangered'' and flagship for southern Madagascar, more information is needed to arrive at sustainable management plans for *A. radiata.* Recent studies have focused on the distribution, harvest, reproductive ecology, population genetics, and phylogeny of this species (Durrell et al. 1989; Van der Kuyl et al. 2002; O'Brien et al. 2003; Leuteritz et al. 2005; Rioux Paquette et al. 2005; Le et al. 2006; Seui 2006; Fritz and Bininda-Emonds 2007; Rioux Paquette and Lapointe 2007; Paquette et al. 2007, 2010; Rakotondrainy 2008; Hammer and Ramilijaona 2009; Paquette and Lapointe 2009; Rasoma et al. 2010; Hammer 2013). Despite the large number of studies, little is known about the natural history of *A. radiata,* such as home range size, habitat, and food requirements in different types of habitats. Although possibly unsuitable habitat structures can be envisaged, chemical properties of food and their changes are not obvious; but food chemistry, as measured in the field, can provide hints of the nutritional requirements of the animals for proper ontogenetic development and successful reproduction (Nagy et al. 1998; Hazard et al. 2010). Foraging theory has stimulated research on the diets and foraging behaviors of a variety of animals. The basic assumption of foraging theory is the optimization of the energy budget (Schoener 1971; Pyke et al. 1977). However, food and consumers do not consist only of energy. Nutritional values, nutrient balancing, and water contents could explain the choice for food (Raubenheimer and Simpson 2004). In addition, many plants contain toxic compounds that render them impossible or very expensive to process (Karban and Myers 1989).

Terrestrial tortoises are classified as herbivores or omnivores that can persist on low-quality diets (Woodbury and Hardy 1948; Zug 1993; Joshua et al. 2010). Nevertheless, some studies indicate unexpected specializations and feeding on a very limited subset of plants available to the animals (El Mouden et al. 2006), indicating some kind of preferences or limitations due to energy, mineral, or specific nutrient concentrations (Oftedal and Allen 1996; Nagy et al. 1998; Leuteritz 2003; Hazard et al. 2010).

The current anthropogenic pressures limit habitat availability. Grazing by livestock leads to habitat degradation (Ratovonamana et al., in press). Anticipated temperature increases threaten to reduce the suitable habitats for the species even further (Ratovonamana et al. 2011). These changes will result in changes in floristic, structural, and chemical vegetation characteristics. Thus, it is important to determine the species' present habitat and food requirements in habitats within the center of its distribution. These areas are assumed to represent suitable habitats for the species with population densities ranging from 27 to 5700 individuals/km^2 (Leuteritz et al. 2005). Data from these habitats (such as compiled by Leuteritz 2003) could then be used in the future to investigate whether or not marginalized habitats would satisfy the requirements of this species in terms of habitat and food characteristics.

Therefore, the aims of this study were the following: first, to describe sources of variation in individual range size and the use of shelters in two different habitats; and second, we wanted to describe the floristic and chemical composition of the tortoise food in relatively undisturbed habitats. These data can be used as a baseline for comparisons of the habitat suitability in degraded areas or habitats modified otherwise. The results should identify the suitability of different habitats under scenarios of future habitat change.

METHODS

Study Site. — The study was carried out in the Parc National de Tsimanampetsotsa, located in southwestern Madagascar (24°03′–24°12′S, 43°46′–43°50′E), 85 km south of Toliara at the western escarpment of the limestone Mahafaly Plateau. The study area is situated between the camp ''Andranovao'' (24°01.578′S and 43°44.238′E) and the Grotte de Mitoho (24°02.973′S and 43°45.095′E), 38 to 114 m above sea level (asl).

The vegetation of the study region is xerophytic and can be divided into three principal formations starting at the coastal plain and moving inland (Mamokatra 1999; Ratovonamana et al. 2011): 1) a formation resting on sand and thin reddish clays and occupied by *Didierea madagascariensis* (Didiereaceae) and a variety of Euphorbiaceae and Burseraceae, 2) an area at approximately 50 m asl and near the foot of the Mahafaly Plateau, dominated by sparse vegetation, with the exception of *Salvadora angustifola* (Salvadoraceae) in close vicinity to the soda lake (Lac Tsimanampetsotsa), and 3) an area on the limestone Mahafaly Plateau. Rising to 200 m asl, there is an abrupt shift to a spiny bush formation and the families Didiereaceae, Euphorbiaceae, and Burseraceae dominate. Trees on limestone are distinctly smaller in height and occur in much lower density, resulting in much reduced vegetation cover and biomass production than in the littoral forest. More details of the study site are provided by Hammer and Ramilijaona (2009), Andriatsimietry et al. (2009), Rakotondranary et al. (2010), Rasoma et al. (2010), Bohr et al. (2011), and Ratovonamana et al. (2011). The study was performed in the littoral forest formations on sand close to the lake (littoral forest) and in spiny bush on limestone (Fig. 1).

Rainfall was measured with rain gauges. Rainfall in the region is highly seasonal and rarely exceeds 400 mm/yr, with most rains falling between December and February (Donque 1975). As a general classification, the year is divided into a wet season from December to April and a dry season from May to November, even though several years can pass without any measurable or significant rainfall. The region experiences considerable variation in daily mean temperatures, ranging between 17° and 34°C (Ratovonamana et al., unpubl. data, 2011). Temperature was measured with temperature loggers (Hydrochron IButton; Dallas Semiconducter, Dallas, TX), placed at 1.5 m on the southern (shady) side of a tree.

Radio-tracking and Study Period. — For the estimation of range sizes, tortoises were fitted with radio-transmitters (Biotrack). Transmitters were fixed to the back of adult tortoises as described by Boarman et al. (1998). Between 4 and 9 animals of each sex were tracked simultaneously in the littoral forest on sand at the western base of the limestone massif, and on the limestone plateau itself. Animals were followed during the wet and in the dry seasons. The locations of the animals were recorded by triangulation every hour for 8 hrs/d. Global Positioning System (GPS) coordinates were taken for each record. Tortoises were tracked for 4 d/mo (dry season: October–November 2007 and October 2008; wet season: March–April 2008) (Fig. 2). The GPS locations within each of

Figure 1. Study sites for *Astrochelys radiata* in different types of habitat: littoral forest on sand (upper pictures); and spiny bush on limestone (lower pictures; photos by J. Rasoma).

the two habitat types (littoral and limestone) were analyzed using the Home Range Extension in ArcView 3.3 (Rodgers and Carr 1998).

Estimation of Monthly Range Size. — Monthly range sizes were estimated by the Adaptive Kernel Method (AKM) based on the 95% confidence interval and by the Minimum Convex Polygon (MCP) method. The AKM yields comparable results to the conventional MCP method but is more robust with respect to the biological independence of observations and tracking errors (Worton 1995; Kernohan et al. 1998; Boyle et al. 2009). The AKM gives an indication where the animal spends most of its time, while the MCP represents the conventional methods for range estimates. Some of the animals could be tracked over the whole study period. Others lost their tags and different animals had to be used to continue the study.

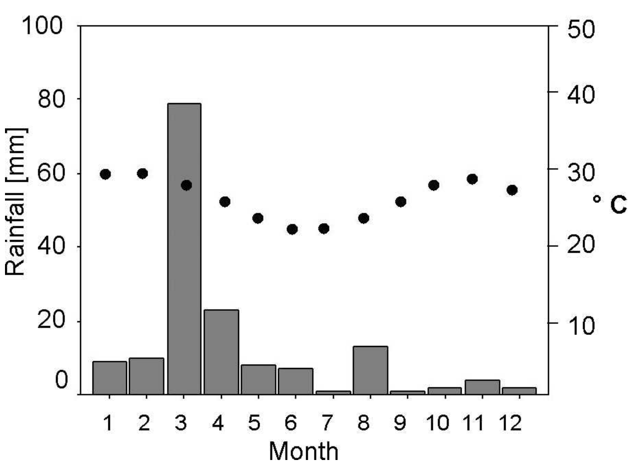

Figure 2. Monthly mean temperature (right axis; black dots) and mean rainfall per month (left axis; bars) between 2006 and 2009; modified from Ratovonamana et al. (2011).

Cumulative range estimates were calculated for 10 to 150 all-day follows using the AKM to determine at how many fixes the range estimates reached an asymptote. Due to the application of the 95% confidence interval in the AKM, the size estimation of ranges fluctuates widely at smaller sample size but stabilizes quickly with increasing sample size. In the littoral forest, range size kept increasing with increasing number of fixes (Fig. 3). In the limestone area, range size remained more stable (Fig. 4).

In order to account for the different number of fixes per individual, we used only animals for which 30 fixes were completed per mo. We defined the monthly range of an individual by 30 fixes. This area does not represent the actual monthly home range but rather relative home range size that can be used for standardized comparisons. For animals followed for more than 1 mo/season, the monthly values were averaged. Thus, each individual entered the analysis only once per season.

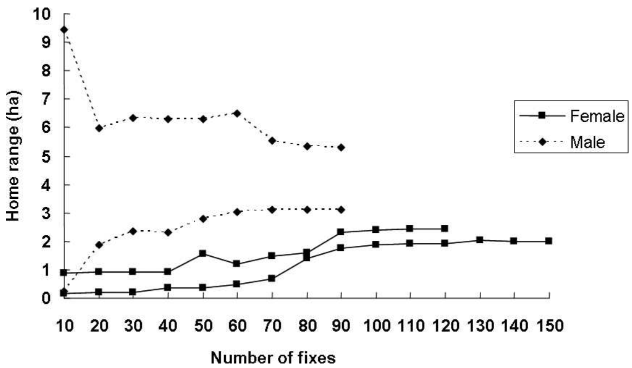

Figure 3. Change of home range size with increasing number of radio-telemetry fixes of four individual tortoises (*Astrochelys radiata*) in the littoral habitat based on the Adaptive Kernel Method.

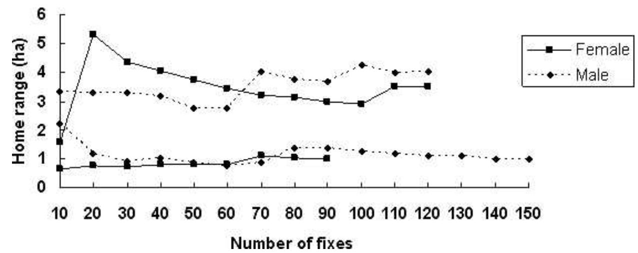

Figure 4. Change of home range size with increasing number of radio-telemetry fixes of four individual tortoises (*Astrochelys radiata*) in the limestone habitat based on the Adaptive Kernel Method.

Shelter. — Radiated tortoises were less active during the cool and dry season and seemed to aestivate under conditions that are not well-defined yet. In case an animal was considered to be inactive and remained at a given spot for extended periods of time (up to 4 d during this study), we considered this spot to represent some kind of shelter. Most of these sites were located underneath trees. Occasionally animals were found in crevices. These were not considered any further. Each tree, where an individual was found sleeping, was identified and its diameter and height were measured. For comparisons, the same measurements were recorded in standardized vegetation plots established in the two types of habitat (Ratovonamana et al., unpubl. data).

Diet. — The composition of the diet of *A. radiata* was recorded opportunistically by direct observation during the radio-tracking activities. When a tortoise was seen feeding, the observer identified food items with binoculars without disturbing the tortoise. Foraging was observed for about 15 min or until the tortoise stopped feeding. Thus, the feeding data are composed of varying numbers of observations from different individual tortoises.

Plant Samples. — We collected plants at the time when tortoises were found feeding on any given item. We collected parts of the plant that were identical to the part consumed. These could be the stems, leaves, flowers, and fruits. For comparisons, we collected plant items that were available to the animals but that we never saw to be consumed by *A. radiata.* During the wet season, we collected only 2 species that we did not see to be consumed by the tortoises. Due to rapid changes in phenology during the end of the wet season, we were unable to assign items as ''nonfood'' and collect them at the end of the wet season because they were gone by then, and plants had changed their properties in such a way that it seemed impossible to use these items for comparisons between ''food'' and ''nonfood'' during the wet season. Each plant species was collected at the time when it was seen to be eaten. Each sample was used only once and only for the analysis of samples either during the wet or during the dry season. Plants were identified within an associated botanical PhD Thesis (Ratovonamana et al., unpubl. data). One hundred fifty-five samples were collected and analyzed. From each sample, 5 g of dry material was collected. Plant species were identified in the field at least to family level. Further determinations were made in the herbarium of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, and the herbarium of the Direction des Resources Forestières et Piscicoles (= FO.FI.FA), Antananarivo.

Chemical Plant Analyses. — We analyzed samples from plants eaten and plant not eaten by the tortoise for the following dietary components: water, neutral detergent fiber (NDF), acid detergent fiber (ADF), ash, nitrogen, soluble protein, sugar, total phenolics condensed tannins and the presence of alkaloids. Plant samples were dried in the sun or in a drying oven, ground to pass a 2-mm sieve, and dried again overnight at 50°–60°C prior to analyses. The water content was measured in the field as the difference between fresh weight and dry weight of the sample. Samples were analyzed for NDF and ADF (Goering and Van Soest 1970; Van Soest 1994) as modified according to the instructions for use in an ANKOM FIBER ANALYZER. Hemicellulose was calculated as the difference between NDF and ADF. After analyses of fiber components the residue was combusted at 600°C for 4 hr to measure the ash content. Total nitrogen was determined using the Kjeldahl procedure. Multiplying N by 6.25 can convert total nitrogen to crude protein. Concentrations of soluble sugar were determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. This measurement correlates well with concentrations obtained with enzymatic analyses of glucose, fructose, and galactose (Ganzhorn and Tomaschewski, unpubl. data). The digestible energy content was based on the conversion factors for protein and carbohydrates to energy as follows: 1 g crude protein = 1 g carbohydrates = 4.1 kcal = 17.15 KJ (Schmidt-Nielsen 1979). Total energy content of 1 g of a plant sample was calculated as (% crude protein + % soluble sugar + % hemicellulose) × 17.15 KJ/100. Analyses of total phenolics (Folin and Ciocalteau 1927) and condensed tannins (measured as equivalents of quebracho tannin with the butanol method; Oates et al. 1977) were

Table 1. Monthly home range size (ha) of *Astrochelys radiata* in two different habitat types during the humid and the dry season respectively, based on the Adaptive Kernel Method. Mean ± standard deviation; n = number of individual tortoises; values in italics represent the minimum, the median, and the maximum value.

	Littoral forest		Limestone		
Sex	Humid	Dry	Humid	Dry	Total
Female	2.02 ± 1.22 $n = 6$ *0.91, 1.55, 3.54*	1.19 ± 0.67 $n = 7$ *0.31, 0.60, 2.76*	1.21 ± 1.23 $n = 4$ *0.21, 0.82, 3.00*	1.60 ± 1.01 $n = 9$ *0.22, 1.68, 3.07*	1.53 ± 1.07 $n = 26$ *0.21, 1.25, 3.54*
Male	2.20 ± 1.13 $n = 7$ *0.17, 2.24, 3.40*	3.52 ± 3.72 $n = 7$ *0.25, 14.79, 10.73*	1.93 ± 1.31 $n = 6$ *0.61, 1.53, 3.59*	0.70 ± 1.05 $n = 9$ *0.0, 0.76, 3.28*	2.02 ± 2.22 $n = 29$ *0.0, 1.38, 10.73*
All animals	2.25 ± 2.18 $n = 27$ *0.17, 1.48, 10.73*		1.35 ± 1.12 $n = 28$ *0.00, 1.00, 3.59*		

based on water extracts (Bollen et al. 2004; Stolter et al. 2009). We performed three different qualitative tests for alkaloids (Dragendorff, Wagner, Mayer; Cromwell 1955). Alkaloids were assumed to be present in a sample if two or three of the tests showed a positive reaction. If only one reagent indicated the presence of alkaloids, we assumed that this represented a false positive reaction. Biochemical analyses were carried out at the Institute of Zoology, Department of Ecology and Conservation at Hamburg University.

Statistical Analyses. — Data were tested for normality with the help of Kolmogorov-Smirnov 1-sample test. Square-root transformation was applied to the range data prior to analyses of variance (ANOVA) or *t*-tests to improve normality. If residuals deviated from normality we applied nonparametric tests. Tests were performed with the help of SPSS (1999). When the same data set was used for multiple pairwise comparisons, *p*-values were adjusted through Bonferroni correction.

RESULTS

Monthly Ranges. — Based on the AKM, monthly home-range sizes varied between 0 ha (animals remaining stationary over ≥ 4 d) and 11 ha (Table 1). Range estimates based on minimum convex polygons (MCP) were smaller than estimates based on the adaptive kernel method and varied between 0 and 5.25 ha (Table 2). The range sizes estimated by the two methods are very closely correlated and the relationship can be expressed by the following regression: Size (in ha, as measured by MCP) = 0.44 × size (in ha, as measured by AKM) − 0.04 ($R^2 = 0.91$, $p < 0.001$, $n = 55$).

Two animals remained almost stationary during the dry season and moved only within a few square meters within the month. Both did not remain at the same spot but changed positions. These low values occurred during the dry season. However, the largest monthly ranges were also recorded during the dry season, with 2 animals moving between 5 and 11 ha (Tables 1 and 2).

According to ANOVA, the interaction between the independent variables ''sex'', ''season'', and ''habitat'' was significantly related to monthly range size ($F = 4.96$, $p = 0.03$). Further analyses were hampered by low sample size. In pairwise comparisons of the pooled data, monthly ranges were larger in the littoral than in the limestone habitat (Tables 1 and 2; $t = 2.08$, $p = 0.04$ and $t = 2.33$, $p = 0.02$ for the AKM and MCP, respectively). Individuals differed substantially in their ranging activities in the wet as well as in the dry season. Some males had very large monthly ranges and larger ranges than females (Fig. 5), but monthly ranges did not differ significantly between female and male *A. radiata* and did not differ between the two seasons even though individuals differed substantially in

Table 2. Monthly home range size (ha) of *Astrochelys radiata* in 2 different habitat types during the humid and the dry season respectively, based on the Mean Convex Polygon method. Mean ± standard deviation; n = number of individual tortoises; values in italics represent the minimum, the median, and the maximum value.

	Littoral forest		Limestone		
Sex	Humid	Dry	Humid	Dry	Total
Female	0.87 ± 0.58 $n = 6$ *0.32, 0.75, 1.89*	0.67 ± 0.66 $n = 7$ *0.11, 0.38, 1.98*	0.39 ± 0.30 $n = 4$ *0.09, 0.30, 0.84*	0.66 ± 0.56 $n = 9$ *0.00, 0.47, 1.55*	0.67 ± 0.56 $n = 26$ *0.0, 0.45, 1.98*
Male	0.74 ± 0.43 $n = 7$ *0.0, 0.72, 1.48*	1.61 ± 1.75 $n = 7$ *0.0, 1.09, 5.25*	0.78 ± 0.53 $n = 6$ *0.17, 0.74, 1.50*	0.28 ± 0.25 $n = 9$ *0.0, 0.23, 0.81*	0.81 ± 1.0 $n = 29$ *0.0, 0.55; 5.25*
All animals	0.98 ± 1.03 $n = 27$ *0.03, 0.72, 5.25*		0.52 ± 0.47 $n = 28$ *0.00, 0.37, 4.70*		

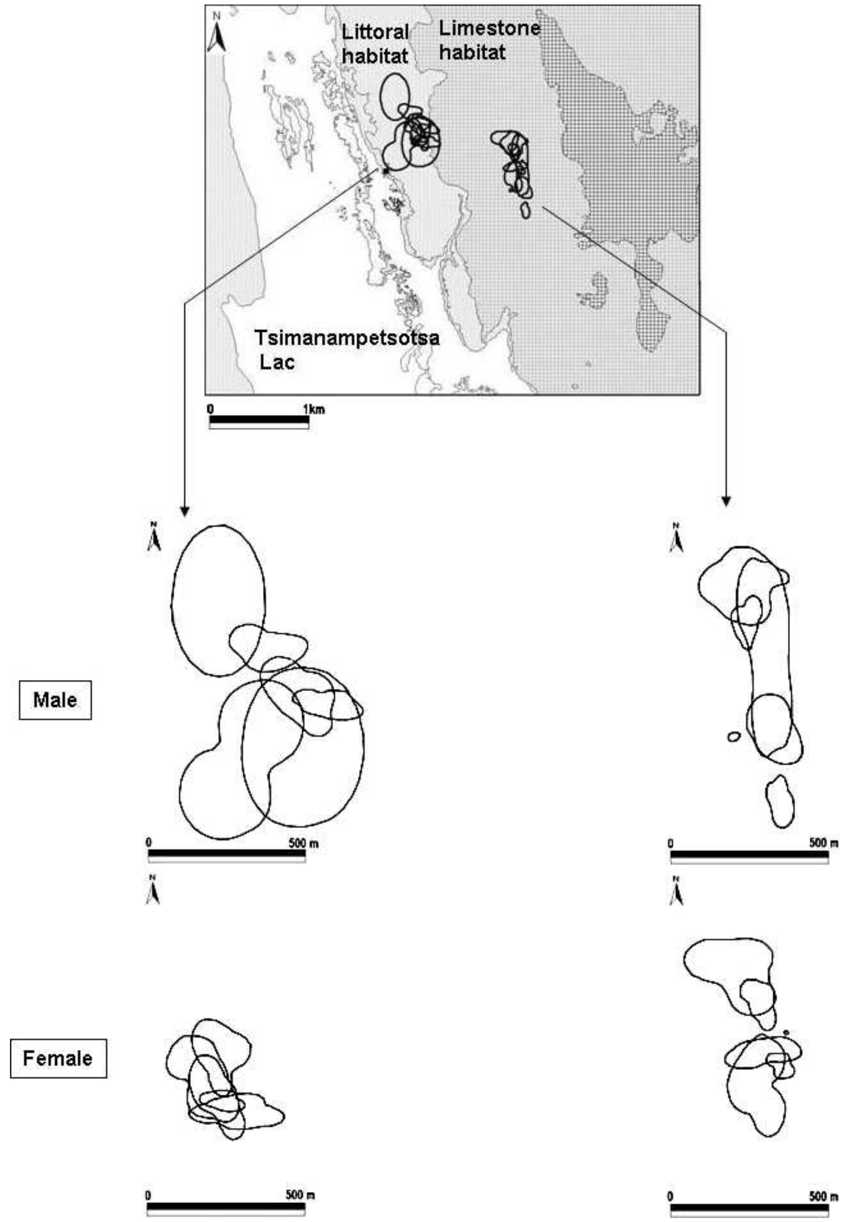

Figure 5. Monthly male and female *Astrochelys radiata* home-range size in the littoral zone (left) and in the limestone habitat (right).

their ranging activities in the wet as well as in the dry season ($t < 1.2$, not significant for all comparisons). Range overlap was not calculated because we could not track all animals that used the area.

Shelter. — Twenty-seven tree species were recorded as shelters used by tortoises at Tsimanampetsotsa NP (Table 3). Nineteen species occurred in the littoral and 11 species in the limestone habitat. Five species of tree were used as shelter at both type of habitat (*Alluaudia comosa, Commiphora mahafaliensis, Euphorbia stenoclada, Operculicarya decaryi,* and *Tamarindus indica*). Sheltering trees in the littoral habitat were taller than in the limestone habitat (Table 4).

In the littoral forest, trees used for shelter had larger diameters at breast height (DBH) but were lower in height than trees found in the vegetation plots (DBH: $t = 19.30$, df $= 254$, $p < 0.01$; height: $t = 8.81$, df $= 250$, $p < 0.01$; Table 4). In the limestone area, the DBH also differed between used trees and trees in the vegetation plot ($t = 7.22$, df $= 178$, $p < 0.01$) but height differences did not show a significant difference between trees providing shelters and trees in the vegetation plot ($t = 1.74$, df $= 178$, $p = 0.08$).

Food Composition. — Of the 155 samples collected, 70.3% were eaten and 29.7% had not been seen to be eaten by *A. radiata.* The food samples consisted of bark (0.9%), fruits (3.7%), flowers (4.6%), and leaves (90.8%), with 35.8% of the samples coming from herbaceous species, 30.3% trees, 24.7% shrubs, and 9.2% liana (Appendix 1).

The number of animals seen feeding varied systematically with time of day and season (Fig. 6). During the rainy season, most tortoises were feeding in the early morning. Fewer animals fed after 1000 hrs. Between

Table 3. Characteristics of trees used for shelter by *Astrochelys radiata*.[a]

Shelter			Littoral forest		Limestone	
Family	Scientific name	Local name	N.O.	R.A.	N.O.	R.A.
Fabaceae	*Acacia bellula*	Roindrano	1	10.1		
Fabaceae	*Albizia atakatake*	Atakatake	1			1.8
Fabaceae	*Albizia tulearensis*	Mendoravy	2	4.7		
Didieraceae	*Alluaudia comosa*	Somondratake	2		26	7.3
Salvadoraceae	*Azima tetracantha*	Tsingilo	3	0.4		
Burseraceae	*Commiphora mahafaliensis*	Maroampotoe	13	0.4	2	2.7
Burseraceae	*Commiphora orbicularis*	Tarabivave		5.4	3	1.8
Boraginaceae	*Cordia caffra*	Varo	1	0.1		
Euphorbiaceae	*Croton geayi*	Pisopiso pc			2	24.5
Euphorbiaceae	*Croton* sp.	Zalazala	1	6.5		
Didieraceae	*Didierea madagascariensis*	Sono	4	19.6		
Boraginaceae	*Erhetia grevei*	Lampana	4	1.1		
Euphorbiaceae	*Euphorbia stenoclada*	Samata	1	1.1	3	15.5
Hernandiaceae	*Gyrocarpus americanus*	Kapaipoty	9	27.9		
Malvaceae	*Humbertiella quararibeoides*	Seta			1	7.3
Fabaceae	*Lemuropisum edule*	Tara			1	2.7
Olacaceae	*Olax adronensis*	Bareraka	1	3.6		
Anacardiaceae	*Operculicarya decaryi*	Jabihy	2	0.4	6	1.8
Cactaceae	*Opuntia stricta*	Raketamena	7			
Salvadoraceae	*Salvadora angustifolia*	Sasavy		12		0.9
Euphorbiaceae	*Securinega seyrigyi*	Hazomena			7	2.7
Fabaceae	*Senna meridionalis*	Maronono			1	8.2
Fabaceae	*Tamarindus indica*	Kile	1	1.4	3	
Combretaceae	*Terminalia disjuncta*	Taly	1	0.7		16.4
Fabaceae	*Tetraperocarpon geayi*	Vaovy	1	4.6		6.4
		Roots	1			
		Association of vegetation	1			

[a] N.O. = number of observation of tortoises using the tree as burrow; R.A. = relative abundance (%) of the tree species in vegetation plots (%).

1200 and 1300 hrs, nearly all animals were resting in the shade. Feeding started again in the afternoon until 1800 hrs. Feeding observations also varied seasonally, with fewer animals seen feeding during the dry season.

Comparisons of the chemical composition between food items and nonfood items were only possible for the dry season. During the wet season, the phenological characteristics of food items changed quickly. During this time of the year, it was difficult to define items not eaten and to compare them with items that were eaten; therefore, we did not collect a sufficient number of items classified as ''not eaten'' during the wet season to allow comparisons of the chemical composition of food and nonfood items. During the dry season, items consumed by the tortoises contained more digestible energy than items not seen to be eaten (Mann-Whitney U-test: $Z = 2.89$, $p = 0.004$; Table 5). The content of hemicellulose was also higher in food than in nonfood items, though this difference was not significant statistically ($Z = 1.65$, $p = 0.10$). No other chemical component differed significantly between these 2 types of plant items.

During the wet season, food items had lower concentrations of phenolics than during the dry season ($Z = 3.71$, $p < 0.001$). The chemical composition of food items did not differ for any other component between the wet and the dry season.

DISCUSSION

Documentation of habitat use patterns may help to understand the habitat requirements of a species and thus may contribute to land management decisions for conservation purposes. To this aim, we investigated the monthly range sizes of the Radiated tortoise as a function of dry and humid season, vegetation formation, and sex. Ranges were larger in the littoral forest than on the limestone plateau. There were no significant differences in the size of monthly ranges, neither between seasons nor

Table 4. Diameter at breast height and height of trees used as shelter and comparative samples of trees in the 2 types of *Astrochelys radiata* habitat. Significant differences between used trees and trees in the representative sample are indicated by asterisks: *** $p \leq 0.001$. Mean ± standard deviation; n = sample size.

	Littoral forest		Limestone	
	Trees used	Representative sample	Trees used	Representative sample
Diameter (cm)	20 ± 17 *** (n = 37)	15 ± 7 (n = 226)	16 ± 13 *** (n = 49)	9 ± 3 (n = 132)
Height (cm)	346 ± 198 *** (n = 37)	438 ± 105 (n = 226)	158 ± 62 (n = 49)	177 ± 51 (n = 132)

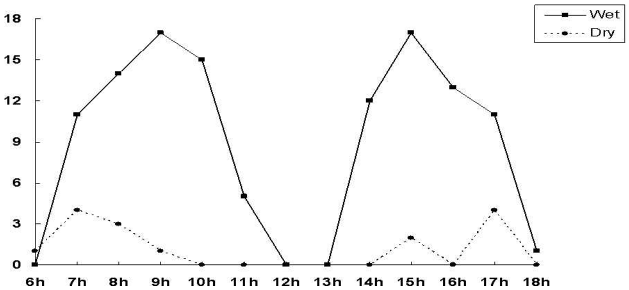

Figure 6. Diurnal variation in feeding records of *Astrochelys radiata* during in the wet and the dry season.

between males and females in this study, even though the ranges of male *A. radiata* were slightly larger than those for females during both seasons. The lack of seasonal differences is unexpected because Radiated tortoises are less active during the dry than during the wet season (Hammer and Ramilijaona 2009; Rasoma et al. 2010), as are *Pyxis a. arachnoids,* a sympatric species (Walker et al. 2007). Ranges overlapped extensively between males and females. According to the conventional interpretation of mating systems as derived from ranging data, this suggests a promiscuous mating system (Ostfeld 1990). In this system it is to be expected that males have larger home ranges than females, in order to look for mating opportunities (e.g., McRae et al. 1981; Barrett 1990). This should be true at least during the mating season (November and December).

It was also unexpected that ranges were larger in the dry deciduous forest on sand than in the less productive limestone area. Density estimates of Radiated tortoises indicated higher densities in the dry deciduous forest on sand than on limestone (Hammer and Ramilijaona 2009; Rasoma et al. 2010). Also, herbaceous food availability is higher in the dry deciduous forest on sand than on limestone (Ratovonamana et al., in press). These differences in densities should be reflected in smaller ranges on sand (where the densities are higher) than on limestone. Yet, this was not the case.

The high variation of monthly range sizes within and between individuals seems to be common in tortoises (McMaster and Downs 2009). This might reflect mixed strategies of time and energy optimization (Schoener 1971). Animals could either maximize food intake by searching food over large surfaces or they could simply remain inactive or aestivate and save energy. Based on the very variable ranges of the different tortoises, we assume that these different strategies are not specific for certain habitats, sex, or a certain season. We did not quantify food availability in the littoral forest as compared with the vegetation of the limestone plateau. But vegetation cover, especially in the herb layer, is much lower on limestone than on sand. The smaller monthly ranges of *A. radiata* on limestone indicate that the animals have to be considered time minimizers that do not invest energy in searching for food over large areas when food is scarce.

Shelters used by *A. radiata* were between rocks, most often at the base of large trees. In areas where the tortoises' ranges overlapped, the same shelter could be used by several tortoises. The most important factor for choosing a shelter seemed to be related to the shadow provided by overarching trees. In both habitats (limestone and littoral), *A. radiata* chose the base of trees with large DBH but low heights. Plant species associated with shelters most frequently were *Commiphora mahafaliensis, Gyrocarpus americanus,* and *Opuntia stricta.* All of them were well-represented in the littoral habitat. Tortoises were found associated with the first species mainly during the dry season. It grows as a bundle of stalks and provided

Table 5. Chemical composition of plant items preferred and nonpreferred as food by *Astrochelys radiata* during the dry and the wet season. For consistency, 25% quartiles, medians (in bold), and 75% quartiles are listed for all components. For the dry season, items eaten were compared with the items not eaten with the Mann-Whitney U-test or with the χ^2 test in case of alkaloids; significance levels are indicated with asterisks: ** $p \leq 0.01$.

	Dry season		Wet season
	Eaten $N = 63$	Not eaten $N = 44$	Eaten $N = 46$
Water (%)[a]	10.0, **12.5**, 19.0	6.6, **11.3**, 17.9	10.0, **15.0**, 32.1
NDF (%)[b]	31.5, **39.8**, 52.3	30.6, **42.1**, 53.5	33.1, **41.6**, 53.3
ADF (%)[c]	16.3, **24.0**, 31.9	17.6, **27.9**, 37.5	15.9, **24.5**, 33.5
Hemicellulose (%)	11.2, **15.1**, 25.5	11.3, **13.5**, 16.6	12.4, **17.5**, 22.9
Sugars (%)	5.0, **7.3**, 12.6	4.1, **7.9**, 10.8	4.7, **6.2**, 9.6
Nitrogen (%)	1.6, **2.1**, 2.5	1.3, **1.9**, 2.6	1.8, **2.3**, 3.4
Soluble protein (%)	2.5, **3.3**, 4.8	2.0, **3.5**, 4.8	2.6, **3.7**, 5.3
Ash (%)	7.2, **9.3**, 13.1	6.8, **10.6**, 13.7	8.3, **10.8**, 15.2
Digestible energy (kJ/g)[d]	557, **667**, 857**	519, **593**, 664	578, **707**, 853
Total phenolics (%)	1.4, **2.4**, 5.5**	1.6, **2.4**, 5.5	0.6, **1.4**, 2.4
Condensed tannins (%)	0.0, **0.0**, 0.4	0.0, **0.0**, 0.5	0.0, **0.0**, 0.0
% items with alkaloids[e]	25.4%	20.5%	30.4%

[a] % water refers to fresh weight.
[b] Neutral detergent fiber.
[c] Acid detergent fiber.
[d] The calculation for digestible energy is based on the concentrations of crude protein, sugars, and hemicellulose.
[e] % items with alkaloids refers to the number of items analyzed.

protection against the heat while all other trees lost their leaves. The second species was used during the humid season. It is also an important food species, and thus tortoises might combine the need for shelter with a nearby food resource. *O. stricta* was used for food and shelter in both seasons. Roots and stumps may decrease the ability of predators (e.g., dogs) to dig tortoises out of their shelter. Shelters may also protect the animals against the sun and high temperatures and thus reduce the loss of water (McGinnis and Voigt 1971; Bulova 2001). Conservation of water and energy are important for tortoises (Henen et al. 1998). Tortoises used several different shelters, occupying them from several minutes to several weeks (Riedle et al. 2008). Daily and seasonal movements among shelters may be influenced by variation in shelter microclimate because tortoise may chance shelters if they are not suitable for thermoregulation (Bulova 2001). The variability observed in activity, the ranging pattern, and the impression that shelters are important for thermoregulation suggest a strategy to optimize energy expenditure through behavioral variation (Huey and Tewksbury 2009).

Foraging theory has stimulated research on the diets and foraging behaviors of a variety of animals. The basic assumption of foraging theory is the optimization of the energy budget (Schoener 1971; Pyke et al. 1977). However, food and consumers do not consist only of energy. Nutritional values, nutrient balancing, and water contents could explain the choice for food (Raubenheimer and Simpson 2004). In addition, many plants contain toxic compounds that render them impossible or very energetically expensive to process (Karban and Myers 1989).

Terrestrial tortoises are classified as herbivores or omnivores that can persist on low-quality diets (Woodbury and Hardy 1948; Zug 1993; Joshua et al. 2010). Nevertheless, some studies indicate unexpected specializations and feeding on a very limited subset of plants available to the animals (El Mouden et al. 2006), indicating some kind of preferences or limitations due to energy, mineral, or specific nutrient concentrations (Nagy et al. 1998; Hazard et al. 2010). In particular, desert tortoises in North America (*Gopherus agussizii*) avoid food rich in potassium (Oftedal and Allen 1996). The need to excrete surplus minerals may be relevant in southwestern Madagascar because the groundwater tastes bitter, suggesting high mineral concentrations in the system. These high concentrations should be reflected in the chemical plant composition. Unfortunately we do not yet have any information on the mineral content of plants of this region.

In our study, *A. radiata* fed on a large number of different plant species and food types. The protein concentration of food items is of prime importance for animals (White 1993), but we did not find any indication for food selection on the basis of nitrogen or protein concentrations. The average nitrogen concentrations of the food and nonfood items were within the range of protein concentrations of food items found to be consumed by other tortoises; therefore, we assume that *A. radiata* did not need to discriminate based on nitrogen concentrations (Nagy et al. 1998; Hazard et al. 2009, 2010). In contrast to nitrogen concentrations, the caloric value of food items of the tortoises was higher in food than in nonfood items. We could not control for food availability or assess food digestibility, so our interpretations must be limited. Nevertheless, the results are consistent with the current thinking in studies on wildlife feeding and nutrition (Robbins 1993) and optimal foraging theory, which assume that animals optimize energy intake (Pyke et al. 1977). The impact of secondary substances is more difficult to interpret because effects of these components can be complex (Foley and Moore 2005; Wallis et al. 2012). Condensed tannins have been identified as one of the most important groups of secondary substances that prohibit nutrient extraction from food stuff in a quantitative way (Robbins et al. 1987; Cork and Catling 1996; DeGabriel et al. 2009). But neither phenolics, nor condensed tannins or alkaloids, differed between food and nonfood items during the dry season. The concentrations of these substances could have been below the threshold above which they become effective feeding deterrents, or phenolics and tannins can also be used to counteract gut parasites (Glander 1982; Huffman 2001).

In conclusion, the data from the ranging pattern and the chemical food composition indicate that *A. radiata* optimizes its energy budget. We were unable to arrive at a comprehensive answer about the factors that limit the animals with our approach to analyzing the two energy components (ranging and food) as separate questions, but an optimal foraging approach would be most promising for future studies.

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LITERATURE CITED

Andriatsimietry, R., Goodman, S.M., Razafimahatratra, E., Jeglinski, J.W.E., Marquard, M., and Ganzhorn, J.U. 2009.

Seasonal variation in the diet of *Galidictis grandidieri* Wozencraft, 1986 (Carnivora: Eupleridae) in a sub-arid zone of extreme southwestern Madagascar. Journal of Zoology 279:410–415.

Barrett, S.L. 1990. Home range and habitat of the desert tortoise (*Xerobates agassisi*) in the Picacho Mountains of Arizona. Herpetologia 46:2–206.

Boarman, W., Goodlett, T., Goodlett, G., and Hamilton, P. 1998. Review of radio transmitter attachment techniques for turtle research and recommendations for improvement. Herpetological Review 29:26–33.

Bohr, Y.E.M.B., Giertz, P., Ratovonamana, Y.R., and Ganzhorn, J.U. 2011. Gray-brown mouse lemurs (*Microcebus griseorufus*) as an example of distributional constraints through increasing desertification. International Journal of Primatology 32:901–913.

Bollen, A., Van Elsacker, L., and Ganzhorn, J.U. 2004. Tree dispersal strategies in the littoral forest of Sainte Luce SE-Madagascar. Oecologia 139:604–616.

Boyle, S.A., Lourenço, W.C., Da Silva, L.R., and Smith, A.T. 2009. A home range estimates vary with sample size and methods. Folia Primatologica 80:33–42.

Bulova, S.J. 2001. How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. Journal of Thermal Biology 27:175–189.

Cork, S.J. and Catling, P.C. 1996. Modelling distributions of arboreal and ground-dwelling mammals in relation to climate, nutrients, plant chemical defences and vegetation structure in eucalypt forests of southeastern Australia. Forest Ecology and Management 85:163–175.

Cromwell, B.T. 1955. The alkaloids. In: Paech, K. and Tracy, M.V. (Eds.). Modern Methods of Plant Analysis. Volume 4. Heidelberg: Springer, pp. 367–374.

DeGabriel, J.L., Moore, B.D., Foley, W.J., and Johnson, C.N. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. Ecology 90:711–719.

Donque, G. 1975. Contribution Géographique à l'Étude du Climat de Madagascar. Antananarivo: Nouvelle Imprimerie des Arts Graphiques, 478 pp.

Durrell, L., Goombridge, B., Tonge, S., and Bloxam, Q. 1989. *Geochelone radiata,* Radiated tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Gland: IUCN Species Survival Commission, Occasional Papers, pp. 96–98.

El Mouden, E.H., Slimani, T., Ben Kaddour, K., Lagarde, F., Ouhammou, A., and Bonnet, X. 2006. *Testudo graeca graeca* feeding ecology in an arid and overgrazed zone in Morocco. Journal of Arid Environments 64:422–435.

Foley, W.J. and Moore, B.D. 2005. Plant secondary metabolites and vertebrate herbivores—from physiological regulation to ecosystem function. Current Opinion in Plant Biology 8:430–435.

Folin, O. and Ciocalteau, V. 1927. On tyrosine and tryptophane determination in proteins. The Journal of Biological Chemistry 73:627–650.

Fritz, U. and Bininda-Emonds, O.R.P. 2007. When genes meet nomenclature: tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*. Zoology 110:298–307.

Ganzhorn, J.U. 2011. Conservation through payments for an ecosystem service? Madagascar Conservation & Development 6:55–56.

Glander, K.E. 1982. The impact of plant secondary compounds on primate feeding behavior. Yearbook of Physical Anthropology 25:1–18.

Glaw, F. and Vences, M. 2007. A Field Guide to the Amphibians and Reptiles of Madagascar. Verlags GbR, Köln: Vences & Glaw, 480 pp.

Goering, H.K. and Van Soest, P.J. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agriculture Handbook No. 379. U.S. Department of Agriculture, 20 pp.

Hammer, J. M. 2013. Do big females produce bigger eggs? The influence of female body mass on egg mass in *Astrochelys radiata*. In: Castellano, C.M., Randriamahazo, H., Lewis, R.E., Mittermeier, R.A., Hudson, R., and Rhodin, A.G.J. (Eds.). Turtles on the Brink in Madagascar. Proceedings of Two Workshops on Status and Conservation of Malagasy Tortoises and Freshwater Turtles. Lunenburg: Chelonian Research Monographs.

Hammer, J.M. and Ramilijaona, O. 2009. Population study on *Astrochelys radiata* (Shaw, 1802) in the Tsimanampetsotsa National Park, southwest Madagascar. Salamandra 45:219–232.

Hazard, L.C., Shemanski, D.R., and Nagy, K.A. 2009. Nutritional quality of natural foods of juvenile Desert tortoises (*Gopherus agassizii*): energy, nitrogen, and fiber digestibility. Journal of Herpetology 43:38–48.

Hazard, L.C., Shemanski, D.R., and Nagy, K.A. 2010. Nutritional quality of natural foods of juvenile and adult Desert tortoises (*Gopherus agassizii*): calcium, phosphorus, and magnesium digestibility. Journal of Herpetology 44:135–147.

Henen, B.T., Peterson, C.C., Wallis, I.R., Berry, K.H., and Nagy, K.A. 1998. Effects of climatic variation on field metabolism and water relations of desert tortoises. Oecologia 117:365–373.

Huey, R.B. and Tewksbury, J.J. 2009. Can behaviour douse the fire of climate warming? Proceedings of the National Academy of Sciences 106:3647–3648.

Huffman, M.A. 2001. Self-medicative behavior in the Great Apes—an evolutionary perspective into the origins of human traditional medicine. BioScience 51:551–561.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M.J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J., Wilmé, L., and Ganzhorn, J.U. 2010. Patterns of species change in anthropogenically disturbed habitats of Madagascar. Biological Conservation 143:2351–2362.

Joshua, Q.I., Hofmeyr, M.D., and Henen, B.T. 2010. Seasonal and site variation in Angulate tortoise diet and activity. Journal of Herpetology 44:124–134.

Karban, R. and Myers, J.H. 1989. Induced plant responses to herbivory. Annual Review of Ecological and Systematics 20: 331–48.

Kernohan, B.J., Millspaugh, J.J., Jenks, J.A., and Naugle, D.E. 1998. Use of an adaptive kernel home-range estimator in a GIS environment to calculate habitat use. Journal of Environmental Management 53:83–89.

Le, M., Raxworthy, C.J., McCord, W.P., and Mertz, L. 2006. A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 40:517–531.

Leuteritz, T.E.J. 2003. Observations on the diet and drinking behaviour of radiated tortoises (*Geochelone radiata*) in southwest Madagascar. African Journal of Herpetology 52: 127–130.

Leuteritz, T. and Rioux Paquette, S. 2008. *Astrochelys radiata*. In: IUCN 2009. IUCN Red List of Threatened

Species. Version 2009.2. www.iucnredlist.org (25 November 2009).

Leuteritz, T.E.J., Lamb, T., and Limberaza, J.C. 2005. Distribution, status, and conservation of Radiated tortoise (*Geochelone radiata*) in Madagascar. Biological Conservation 124:451–461.

Lingard, M., Raharison, N., Rabakonandrianina, E., Rakotoarisoa, J.-A., and Elmqvist, T. 2003. The role of local taboos in conservation and management of species: the Radiated Tortoise in southern Madagascar. Conservation and Society 2:223–246.

Mamokatra. 1999. Etude pour l'élaboration d'un plan d'aménagement et de gestion au niveau de la Réserve Naturelle Intégrale de Tsimanampetsotsa. Diagnostic physico-bio-écologique. Antananarivo: Deutsche Forstservice GmbH, Feldkirchen et Entreprise d'Etudes de Développement rural « Mamokatra », 176 pp.

McGinnis, S.M. and Voigt, W.G. 1971. Thermoregulation in the desert tortoise, *Gopherus agassizii*. Comparative Biochemistry and Physiology A 40:119–126.

McMaster, M.K. and Downs, C.T. 2009. Home range and daily movement of Leopard Tortoises (*Stigmochelys pardalis*) in the Nama-Karoo, South Africa. Journal of Herpetology 43: 561–569.

McRae, W.A., Landers, J.L., and Garner, J.A. 1981. Movement patterns and home range of the Gopher tortoise. American Midland Naturalist 106:165–179.

Nagy, K.A., Hennen, B.T., and Vyas, D.B. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32:260–267.

Nussbaum, R.A. and Raxworthy, C.J. 2000. Commentary on conservation of ''Sokatra'', the Radiated tortoise of Madagascar. Amphibian and Reptile Conservation 2:6–14.

O'Brien, S., Emahalala, E.R., Beard, V., Rakotondrainy, R.M., Reid, A., Raharisoa, V., and Coulson, T. 2003. Decline of the Madagascar Radiated tortoise *Geochelone radiata* due to overexploitation. Oryx 37:338–343.

Oates, J.F., Swain, T., and Zantovska, J. 1977. Secondary compounds and food selection by colobus monkeys. Biochemical Systematics and Ecology 5:317–321.

Oftedal, O.T. and Allen, M.E. 1996. Nutrition as a major facet of reptile conservation. Zoo Biology 15:491–497.

Ostfeld, R.S. 1990. The ecology of territoriality in small mammals. Trends in Ecology and Evolution 5:411–415.

Paquette, S.R., Behncke, S.M., O'Brien, S.H., Brenneman, R.A., Louis, E.E., Jr., and Lapointe, F.J. 2007. Riverbeds demarcate distinct conservation units of the Radiated tortoise (*Geochelone radiata*) in southern Madagascar. Conservation Genetics 8:797–807.

Paquette, S.R. and Lapointe, F.J. 2009. A statistical procedure to assess the significance level of barriers to gene flow. Journal of Genetics and Genomics 36:685–693.

Paquette, S.R., Louis, E.E., Jr., and Lapointe, F.J. 2010. Microsatellite analyses provide evidence of male-biased dispersal in the Radiated Tortoise *Astrochelys radiata* (Chelonia: Testudinidae). Journal of Heredity 101:403–412.

Pedrono, M. 2008. The tortoises and turtles of Madagascar. Kota Kinabalu: Natural History Publications, 147 pp.

Pyke, G.H., Pulliam, H.R., and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

Rakotondrainy, R.M. 2008. Contribution à l'étude de la population de tortues radiée Astrochelys radiata (Shaw, 1802) dans la région d'Itampolo, Sud-ouest de Madagascar. Diplôme d'Etudes Approfondies. Antananarivo: Université d'Antananarivo, 61 pp.

Rakotondranary, J.S., Ratovonamana, Y.R., and Ganzhorn, J.U. 2010. Distributions et caractéristiques des microhabitats de *Microcebus griseorufus* (Cheirogaleidae) dans le Parc National de Tsimanampetsotsa (Sud-ouest de Madagascar). Malagasy Nature 4:55–64.

Rasoma, R.V.J., Ranivoarivelo, S., Marquard, M., Ramilijaona, O.R., Rakotomalala, D., Raselimanana, A.P., and Ganzhorn, J.U. 2010. Estimation de la densité des populations d'une espèce menacée de tortue terrestre (*Astrochelys radiata*) dans le Parc National Tsimanampetsotsa au Sud de Madagascar. Malagasy Nature 4:33–48.

Ratovonamana, Y.R., Rajeriarison, C., Edmond, R., and Ganzhorn, J.U. 2011. Phenology of different vegetation types in Tsimanampetsotsa National Park, south-western Madagascar. Malagasy Nature 5:14–38.

Ratovonamana, Y.R., Rajeriarison, C., Edmond, R., Kiefer, I., and Ganzhorn, J.U. Impact of livestock grazing on forest structure, plant species composition and biomass in south-western Madagascar. Scripta Botanica Belgica. (In Press).

Raubenheimer, D. and Simpson, S.J. 2004. Organismal stoichiometry: quantifying non-independence among food components. Ecology 85:1203–1216.

Riedle, J.D., Averill-Murray, C., Lutz, C.L., and Bolen, D.K. 2008. Habitat use by Desert Tortoises (*Gopherus agassizii*) on alluvial fans in the Sonoran Desert, South-central Arizona. Copeia 2008:414–420.

Rioux Paquette, S.R. and Lapointe, F.J. 2007. The use of shell morphometrics for the management of the endangered Malagasy radiated tortoise (*Geochelone radiata*). Biological Conservation 134:31–39.

Rioux Paquette, S., Shore G.D., Behncke, S.M., Lapointe, F.-J., and Louis, E.E. 2005. Characterization of polymorphic microsatellite markers for the endangered Malagasy Radiated tortoise (*Geochelone radiata*). Molecular Ecology Notes 5: 527–530.

Robbins, C.T. 1993. Wildlife Feeding and Nutrition. New York: Academic Press, 352 pp.

Robbins, C.T., Mole, S., Hagerman, A.E., and Hanley, T.A. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68:1606–1615.

Rodgers, A.R. and Carr, A.P. 1998. HRE: The Home Range Extension for ArcView, User's Manual. Thunder Bay, Ontario: Ministry of Natural Resources, 22 pp.

Sage. 2003. Plan Communal de Développement: Commune Rurale Beheloke. Toliara: Unité Technique Régionale Sage, 89 pp.

Schmidt-Nielsen, K. 1979. Animal physiology: adaptation and environment. Cambridge: Cambridge University Press, 560 pp.

Schoener, T.W. 1971. Theory of feeding strategies. Annual Review of Ecological and Systematics 2:369–404.

Seui, M. 2006. Etude de la dynamique et de la structure des populations de tortues radiées (*Geochelone radiata*) dans le Sud-ouest de Madagascar. Master II en Biologie, Evolution et Contrôle des Populations. Tours: Université François-Rabelais, 34 pp.

SPSS. 1999. SPSS Base 9.0 User's Guide. Chicago: SPSS Inc.

Stolter, C., Niemela, P., Ball, J.P., Julkunen-Tiito, R., Vanhatalo, A., Danell, K., Varvikko, T., and Ganzhorn, J.U. 2009. Comparison of plant secondary metabolites and digestibility of three different boreal coniferous trees. Basic Applied Ecology 10:19–26.

Van der Kuyl, A.C., Ballasina, D.L.P., Dekker, J.T., Maas, J., Willemsen, R.E., and Willemsen, R.E. 2002. Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12S rRNA gene sequences. Molecular Phylogenetics and Evolution 22:174–183.

Van Soest, P.J. 1994. Nutritional Ecology of the Ruminant. Second edition. Ithaca: Cornell University Press, 476 pp.

Walker, R.C.J., Woods-Ballard, A.J., and Rix, C.E. 2007. Population density and seasonal activity of the threatened Madagascar spider tortoise (*Pyxis arachnoides arachnoides*) of the southern dry forests; South West Madagascar. African Journal Ecology 46:67–73.

Wallis, I.R., Edwards, M.J., Windley, H., Krockenberger, A.K., Felton, A., Quenzer, M., Ganzhorn, J.U., and Foley, W.J. 2012. Food for folivores: nutritional explanations linking diets to population density. Oecologia (Berlin) 169:281–291.

White, T.C.R. 1993. The inadequate environment: nitrogen and the abundance of animals. Berlin: Springer-Verlag, 425 pp.

Woodbury, A.M. and Hardy, R. 1948. Studies of the desert tortoise, *Gopherus agassizzii*. Ecological Monographs 18:45–200.

Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

Zug, G.R. 1993. Herpetology. New York: Academic Press, 527 pp.

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Appendix 1. Plant species consumed by *Astrochelys radiata;* superscripts indicate the part of the plant considered in the analyses.[a]

Families	Species	Local name	Growth type	Season consumed
Acanthaceae	*Ruellia* sp.	Laindramotro fleur violacée	Herb[l]	wet
Acanthaceae	*Crossandra humilis*	Herbacée fleur blanche	Herb[l]	wet
Acanthaceae	*Ruellia albopurpurea*	Folatataom-bohitsa	Herb[l]	wet, dry
Acanthaceae	*Crossandra poissonii*	Sangan'akoho	Tree[l]	wet, dry
Acanthaceae	*Verbena* sp.	Hanandela	Herb[l]	wet
Acanthaceae	*Hypoestes phyllostachya*	indeter.	Shrubby tree[l]	wet
Aizoaceae	*Mollugo decandra*	Andriamani-ndry	Herb[l]	wet, dry
Amaranthaceae	Indeter.	Indeter.	Herb[l]	wet
Amaranthaceae	Indeter.	Ahintsoky	Herb[l]	wet
Amaranthaceae	*Aerva madagassica*	Vonimbato	Arborescent shrub[l]	wet
Anacardiaceae	*Operculicarya decaryi*	Jabihy	Tree[l]	wet, dry
Apocynaceae	*Cynanchum nodosum*	Ranga	Liana[l]	wet
Apocynaceae	*Secamone teunifolia*	Langolora	Liana[l]	wet
Bignoniaceae	*Stereospermum nematocarpum*	Mahafangalitse	Tree[l,fl]	wet, dry
Bignoniaceae	*Rhigozum madagascariens*	Hazonta vahy	Tree[l]	dry
Boraginaceae	*Cordia mairea*	Mera	Tree[l]	wet
Brassicaceae	*Boscia longifolia*	Paky	Tree[l]	dry
Brassicaceae	*Boscia tenifolia*	Lalangy	Tree[l]	dry
Burseraceae	*Commiphora orbicaulis*	Taraby vavy	Tree[l]	wet, dry
Burseraceae	*Commiphora humbertii*	Taraby manitra	Arborescent shrub[l]	wet, dry
Cactaceae	*Opuntia monocantha*	Viro mena	Bush[l]	wet, dry
Celastraceae	*Gymnosporia linearis*	Roimpataka	Bush[l]	wet, dry
Celastraceae	*Cassinodea* sp.	indeter.	Tree[l]	dry
Combretaceae	*Terminalia disjuncta*	Lokotaly, Taly	Tree[l]	wet, dry
Combretaceae	*Terminalia disjuncta*	Fatra	Tree[l]	dry
Commelinaceae	*Commelina madagascariensis*	Kisanandolo	Herb[l]	wet
Convolvulaceae	*Ipomea* sp.	Rafomoky, Moky lahy	Liana[l]	wet
Convolvulaceae	*Convolvulus* sp. 1	indeter.	Liana[l]	wet
Convolvulaceae	*Convolvulus* sp. 2	indeter.	Liana[l]	wet
Convolvulaceae	*Ipomea alba*	Moky vahy	Liana[l]	wet
Convolvulaceae	*Convolvulus* sp. 3	Mandady ambany	Herb[l]	wet
Cyperaceae	*Cyperus* sp. 1	Moita	Herb[l]	wet
Cyperaceae	*Cyperus* sp. 2	Cyperus 2	Herb[l]	wet
Didieraceae	*Alluaudopsis fiherenensis*	Marotaho	Arborescent shrub[l]	wet
Euphorbiaceae	*Acalypha decaryana*	Fandrivotse	Arborescent shrub[l]	wet
Euphorbiaceae	*Euphorbia stenoclada*	Samata	Tree[l]	wet
Euphorbiaceae	*Securinega seyrigyi*	Hazo mena	Tree[l]	wet, dry
Fabaceae	*Indigofera* sp. 2	Laindramotro lava ravy	Bush[l]	wet
Fabaceae	*Chadsia grevei*	Sangan'akoho lahy 1	Arborescent shrub[l]	wet, dry
Fabaceae	*Tribulis terrestris*	Hisambazaha	Herb[l]	wet
Fabaceae	*Indigofera* sp. 1	Laindramotro 2	Bush[l]	wet
Fabaceae	*Indigofera mouroundavensis*	Anjavily	Bush[l]	wet
Fabaceae	*Senna meridionalis*	Maronono	Tree[l]	wet
Fabaceae	*Chadsia grevei*	Sangan'akoho lahy 2	Arborescent shrub[l,fl]	wet, dry
Fabaceae	*Lemuropisum edule*	Tara	Arborescent shrub[fl]	wet, dry

Appendix 1. Continued.

Families	Species	Local name	Growth type	Season consumed
Fabaceae	*Albizia tulieariens*	Mendoravy	Tree[l]	dry
Fabaceae	*Tamarindus indica*	Kily	Tree[l]	wet, dry
Fabaceae	*Acacia rovumae*	Roin'osy	Tree[l]	dry
Fabaceae	*Tephrosia alba*	Sofasofam-bohitsy	Arborescent shrub[l]	wet, dry
Fabaceae	*Indigofera diversifolia*	Laindramotro	Herb[l]	wet
Fabaceae	*Indigifera moroundavensis*	Sabobohotse	Herb[l]	wet
Fabaceae	*Mundulea* sp. 2	Taivosotse	Tree[l]	dry
Fabaceae	*Indigofera* sp. 1	Engetse	Arborescent shrub[l]	dry
Fabaceae	*Albizia mahalao*	Balabake	Tree[l]	dry
Fabaceae	*Mundulea* sp.	Sofasofa	Arborescent shrub[l]	wet, dry
Hernandiaceae	*Gyrocarpus americanus*	Kapaipoty	Tree[l,f]	wet
indeter.	indeter.	Herbaceous fleur graine	Herb[l]	wet
indeter.	indeter.	Lychen	Herb[l]	dry
indeter.	indeter.	Monkitsa	Herb[l]	wet
indeter.	indeter.	Fandriandambo	Arborescent shrub[l]	wet
indeter.	indeter.	Tirinkitroky	Herb[l]	wet
Lamiaceae	*Verbena* sp. 2	Hanadela fleur violacee	Herb[l]	wet
Lamiaceae	*Karomia microphylla*	Forombitiky	Tree[l]	dry
Lamiaceae	indeter.	indeter.	Tree[l]	dry
Lythraceae	*Capuronianthus mahafaliensis*	Ringitse	Arborescent shrub[l]	wet
Malvaceae	indeter.	Kotaky	Bush[l]	wet
Malvaceae	*Grewia grevei*	Tombokam-paha	Arborescent shrub[l]	wet
Malvaceae	*Grewia humblotii*	Selimpasy	Arborescent shrub[l]	dry
Malvaceae	*Grewia mahafaliensis*	Selin'ala	Arborescent shrub[l]	dry
Malvaceae	*Grewia* sp. 1	Hazo foty (be)	Arborescent shrub[l]	dry
Malvaceae	*Hibuscus* sp.	indeter.	Herb[l]	wet
Meliaceae	*Neobeguea mahafaliensis*	Handy	Tree[l]	wet, dry
Nychtiginiacea	*Boheravia rapens*	Bea	Tree[l]	wet
Pedialiaceae	*Uncarina stellulifera*	Farehita	Tree[fl]	wet
Poaceae	*Panichum mahafalense*	Ahimanara	Herb[l]	wet
Poaceae	*Dactyloctenum capitatum*	Ahitrala	Herb[l]	wet
Poaceae	*Panichum pseudoveoltzkowi*	Ahikototo	Herb[l]	wet
Poaceae	*Chlorys* sp.	Ex cynodon	Herb[l]	wet
Poaceae	*Panicum* sp.	Ahitrandraka	Herb[l]	wet
Poaceae	indeter.	Ahitrala epi cassant	Herb[l]	wet
Poaceae	*Panicum subalbidum*	Ahipisaky	Herb[l]	wet
Poaceae	*Cynodon dactylon*	Kindresy	Herb[l]	wet
Poaceae	*Sporobolus coromandelianus*	Dremotse	Herb[l]	wet
Poaceae	*Panicum maximum*	Ahotrombilahy	Herb[l]	wet
Poaceae	*Setaria pumila*	Ahitronga	Herb[l]	wet
Polygalaceae	*Polygala greveana*	Vongo	Bush[l]	wet
Polygalaceae	*Polygala* sp. 3	Laindramotro sp. 3	Herb[l]	wet
Polygalaceae	*Polygala* sp. 4	Laindramotro Petite fleur	Herb[l]	wet
Portulacaceae	*Portulca* sp.	Sabasaba	Herb[l]	wet
Portulacaceae	*Tallinela microphylla*	Tsirora, Tarakitoke	Arborescent shrub[l]	wet
Rhamnaceae	*Bathiorhamus cryptophorus*	Losy	Tree[l]	dry
Rhamnaceae	*Colubrina perrieri*	Tsinefon'ala	Arborescent shrub[l]	dry
Rubiaceae	*Paederia grandidieri**	Tamboro 2	Liana[l,f]	wet
Rutaceae	*Cedrelopsis gracilis*	Katrafaidobo	Tree[l]	dry
Rutaceae	*Cedrelopsis grevei*	Katrafaifilo	Tree[l]	dry
Salvadoraceae	*Salvadora anguistifoia*	Sasavy	Tree[l,f]	wet
Sapindaceae	*Erythrophysa aesculina*	Handimbohitse	Tree[l]	dry
Sapotaceae	*Zanthoxyllum* sp.	Nato	Tree[l]	dry
Scrophulariaceae	*Radamea montana*	-	Herb[l,f,s]	wet
Scrophulariaceae	*Leucosalpa poissonii*	-	Liana[l,fl]	wet
Tribulaceae	*Tribulus cistoides*	Hisamena	Herb[l]	wet
Velloziaceae	*Xerophyta tuleariensis*	Osa	Herb[l]	wet
Acanthaceae	*Justica spicata*	Fitsetsendrano	Herb[l]	not eaten
Acanthaceae	*Blepharis calcitrapa*	Sitsitsy	Herb[l]	not eaten
Amaranthaceae	*Aerva javanica*	Volofoty	Herb[l]	not eaten
Apocynaceae	*Folotsia madagascariensis*	Folotsy	Liana[l]	not eaten
Apocynaceae	*Secamone geayi*	Kililo	Liana[l]	not eaten
Asteraceae	*Polycline plateoformis*	Zira	Herb[l]	not eaten
Asteraceae	*Pluchea grevei*	Samonty	Arborescent shrub[l]	not eaten
Boraginaceae	*Cordia caffra*	Varo	Tree[l]	not eaten
Boraginaceae	*Erhetia grevei*	Lampana	Tree[l]	not eaten
Brassicaceae	*Maerua* sp.	Somangy	Tree[l]	not eaten
Brassicaceae	*Maerua nuda*	Somangy lahy	Tree[l]	not eaten
Brassicaceae	*Maerua filiformis*	Somangy vavy	Tree[l]	not eaten

Appendix 1. Continued.

Families	Species	Local name	Growth type	Season consumed
Brassicaceae	*Cadaba virgata*	Tsiariarin'-aliotse	Arborescent shrub[l]	not eaten
Buddlejaceae	*Androya decaryi*	Manateza	Tree[l]	not eaten
Burseraceae	*Commiphora lamii*	Holidaro	Tree[l]	not eaten
Burseraceae	*Commiphora marchandii*	Vingovingo	Tree[l]	not eaten
Combretaceae	*Combretum grandidieri*	Vahy mena felany	Liana[l]	not eaten
Cucurbitaceae	*Cucurbitum* sp.	Vontangodolo	Liana[l]	not eaten
Didieraceae	*Alluaudia comosa*	Somondratraka	Tree[l]	not eaten
Didieraceae	*Didierea madagascariensis*	Sono	Tree[l]	not eaten
Ebenaceae	*Diopsyros manampetsae*	Fivikakanga	Bush[l]	not eaten
Euphorbiaceae	*Givotia madagascariensis*	Farafatra	Tree[l]	not eaten
Euphorbiaceae	*Euphorbia tirucalli*	Laro	Tree[l]	not eaten
Euphorbiaceae	*Croton* sp.	Pisopiso	Bush[l]	not eaten
Fabaceae	*Alantsilodendron alluaudianum*	Avoha mainty	Arborescent shrub[l]	not eaten
Fabaceae	*Crotalaria androyensis*	Kantsakantsa	Herb[l]	not eaten
Fabaceae	*Henonia scoparia*	Fofotse	Arborescent shrub[l]	not eaten
Fabaceae	*Indigofera* sp.	Laindramotro x	Bush[l]	not eaten
Fabaceae	*Albizia atakataka*	Atakatake	Arborescent shrub[l]	not eaten
Lamiaceae	*Commoranthus minor*	Vavaloza	Tree[l]	not eaten
Loranthaceae	*Bakerella* sp.	Manalo 1	Parasite	not eaten
Loranthaceae	*Socratea vertina*	Manalo 2	Liana[l]	not eaten
Malvaceae	*Grewia tuleariensis*	Hazofoty	Arborescent shrub[l]	not eaten
Malvaceae	*Grewia* sp. 2	Lava ravy	Tree[l]	not eaten
Moraceae	*Ficus menabensis*	Nonokamboa	Tree[l]	not eaten
Olacaceae	*Olax andronensis*	Bareraky	Tree[l,f]	not eaten
Olacaceae	*Ximenia perrieri*	Kotro	Arborescent shrub[l]	not eaten
Passifloraceae	*Adenia subssifolia*	indeter.	Liana[l]	not eaten
Plumbaginaceae	*Plumbago aphylla*	Fizolotsora, motemote	Herb[l]	not eaten
Salvadoraceae	*Salvadora anguistifoia*	Sasavy	Tree[l]	not eaten
Salvadoraceae	*Azima tetracanthra*	Tsingilo	Arborescent shrub[l]	not eaten
Solanaceae	*Solanum hyppophaenoides*	Hazon'osy	Tree[l]	not eaten
Zygophyllaceae	*Zygophyllum dipauperatum*	Folatatao	Herb[l]	not eaten

[a] l = leaf, fl = flowers, f = fruit, s = seed.