REPTILES & AMPHIBIANS

Recent Demographic Survey of the Radiated Tortoise (*Astrochelys radiata*) in Southwestern Madagascar

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Abstract.—Effective management strategies for at-risk chelonian populations require sound knowledge of population demographics. Previous research on the Critically Endangered Radiated Tortoise, *Astrochelys radiata* (Shaw 1802), revealed a trend of increasing male bias in the sex ratio and a concomitant decrease in the proportion of juveniles in Lavavolo, southern Madagascar. This location is one of the few remaining sites with a high concentration of this species and was last studied ten years ago. The aim of our study was to provide an updated snapshot of Radiated Tortoise demographics at Lavavolo, which, when combined with previous studies, will provide insight into changes over 20 years (1999–2019). Additionally, we provide the first assessment on the impact of soil types (calcareous, ferruginous, and sandy) on the distribution of individuals across the site. We used mark-recapture data to determine the sex ratio, age structure, and distribution of size classes. Overall, the study site contained mostly adults (76.87%) with only a few juveniles (23.13%). Though the proportion of juveniles is low, it has increased over the last ten years. However, the sex ratio has become increasingly skewed towards males, 1.8:1. We did not find any significant difference in sex ratios between soil types, but there were significant differences in the distribution of size classes, with the smallest size class 0–8 cm most prevalent in sandy soil and the juvenile size class 17–24 cm most frequent in ferruginous soil. Most juvenile size classes were less common than expected on the calcareous soil. In general, populations located on calcareous soil appear to be more vulnerable, potentially due to the long-term existence of poaching activities in this habitat.

The current era is described as the sixth extinction event (Purvis et al. 2000) driven by land use change and overexploitation (Hilton-Taylor 2000), with hunting a major anthropogenic driver of biodiversity loss (Bennett et al. 2007). This biodiversity crisis does not spare reptile populations, such as chelonians, the oldest reptile group (Bonin et al. 1998). Slow, not very aggressive, easy to capture, and providing abundant meat, oil, and fat, chelonians have been and still are a source of food in much of the world (Bonin et al. 1998). Since 1600, 11 species of tortoises have become extinct due to slaughter for meat (Honegger 1980). Indeed, 51.9% of the categorized global chelonian diversity is considered threatened (CR + EN + VU), making chelonians the second most threatened vertebrate taxa on the planet after primates (Rhodin et al. 2018).

Madagascar counts nine native chelonian species, with five of them endemic (Pedrono 2008), including the Radiated Tortoise, *Astrochelys radiata* (Shaw 1802), in the southern dry spiny thicket (Glaw and Vences 2007). Primary threats facing this species include high levels of poaching associated with the local bush meat trade and habitat loss (Raxworthy and Nussbaum 2000; Rioux Paquette et al. 2009; Walker et al. 2014; Ganzhorn et al. 2015; Manjoazy et al. 2017). As intense as habitat degradation is in some areas, the main threat to the persistence of the Radiated Tortoise is overexploitation (O'Brien 2002). Radiated Tortoises are extensively collected for food and the local, national, and international pet trade (O'Brien et al. 2003). The people of southwest Madagascar appreciate the tortoise meat during the Christmas and Easter holidays, with another peak of consumption thought to coincide with Independence Day (Pedrono et al. 2000; Manjoazy et al. 2017). Since 1975, increasing demand for tortoise meat and derived products on the international market resulted in the species being listed on Appendix I of CITES. The status of the species continues to deteriorate, and the IUCN Red List classifies the Radiated Tortoise as "Critically Endangered" (Leuteritz and Rioux Paquette 2013), possibly becoming extinct in twenty years (Hudson 2013).

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The persistence of the Radiated Tortoise in different areas of the species' distribution is dependent upon the regional human populace (Rioux Paquette 2008). For instance, local people from the Tandroy and Mahafaly tribes have taboos or *fady* that prohibit them from eating or touching Radiated Tortoises, thus providing a form of protection for the species in the respective areas (Raxworthy and Nussbaum 2000; Lingard et al. 2003). However, human populations in the northeastern and southeastern range of the tortoise (Raxworthy and Nussbaum 2000) and immigrant populations do not adhere to these fady, resulting in the exploitation of the Radiated Tortoise as a source of food or for the international pet trade (Raxworthy and Nussbaum 2000; O'Brien et al. 2003; Irwin et al. 2010). Lavavolo, a village whose local population belongs to the Tagnalana tribe who also hold a fady against touching tortoises, was previously identified as one of the remaining strongholds for Radiated Tortoises (Castellano et al. 2013), with a mean density of 14.5 tortoises/hectare during the wet season (Nambinina et al. 2022). Unfortunately, people immigrating from other regions exploit tortoises in the culturally protected areas, with commercial harvesters from Toliara and Taolagnaro transporting tortoises by oxcart and fishing boat (Lingard et al. 2003). Thus, significant declines have been noted in the places where the fady once protected Radiated Tortoises (O'Brien et al. 2003).

Though Lavavolo's Radiated Tortoise population remains intact, the demographic sustainability of the species may be under threat. Maternal body size is a significant contributor to variations in reproductive output (Wallis et al. 1999), with large females producing heavier and larger eggs (Hammer 2015). Unfortunately, immigrating human populations appear to be harvesting females disproportionately, leading to changes in the demographics of the remaining tortoises (Castellano et al. 2013; Rafeliarisoa et al. 2013). For instance, the Lavavolo population exhibited a male-biased sex ratio between 1999 and 2009, increasing from 26.3% male (Leuteritz et al. 2005) to over 50% (Castellano et al. 2013) of the adults. This unequal sex ratio has been attributed to large females being preferentially targeted because they provide more meat and sometimes contain eggs (Leuteritz et al. 2005).

Similarly, between 1999 and 2009 there were dramatic changes in the juvenile population. In 1999, over half of the observed individuals in Lavavolo were juveniles (Leuteritz et al. 2005), possibly a byproduct of high hunting pressure as adults are favored for the bush meat trade (Leuteritz et al. 2005). In 2009, ten years later, the proportion of juveniles dropped to 14.2% and 16.6% along two sampling transects in Lavavolo (Castellano et al. 2013). A similarly low proportion of juveniles, 12.5%, was also observed in 2011 in Lavavolo (Rafeliarisoa et al. 2013). Two conflicting explanations have been presented to explain the low numbers of juveniles at Lavavolo. One possibility is that these low juvenile numbers were the result of illegal collection for the international pet trade that preferentially targets young individuals, whose small size makes them easier to conceal at security checks and customs controls as they are smuggled out of the country (Pedrono 2008; Rafeliarisoa et al. 2013). This is supported by the absence of observed individuals in the smallest size class (≤ 5 cm) or between 10.1–15 cm from surveys in 2009 (Castellano et al. 2013). Alternatively, the juvenile tortoises observed by Leuteritz et al. (2005) may have grown into larger size classes. This appears to be supported by associated data on the increased size of Radiated Tortoise individuals in Lavavolo, with average straight carapace lengths (SCL) increasing from 19.2 cm in 1999 (Leuteritz et al. 2005) to 30.1 and 30.4 cm in 2009 (Castellano et al. 2013). This could reflect a decrease in bushmeat harvesting between these study periods (Castellano et al. 2013).

Lastly, ecological factors can influence demography; edaphic variation is known to affect the distribution of individuals across their available habitat for multiple tortoise species. For example, Desert Tortoises (*Gopherus agassizii*) are more frequently found in loamy soils and avoid stony soils (Andersen et al. 2000). Similarly, the density of *A. radiata* populations in Lavavolo differs depending on the soil type (Rasoma et al. 2010; Nambinina et al. 2022). During the wet season, the highest densities were recorded in ferruginous soil followed by the sandy soil, with the lowest population densities on the calcareous soil (Nambinina et al. 2022). Soil type can even influence where nests are made, such as seen in Gopher Tortoises (*G. polyphemus*), which select bare sandy soil over clay or loamy soil nesting sites (Jones and Dorr 2004; Lamb et al. 2013). A difference in densities and nesting locations could potentially influence population parameters.

Since unbalanced sex and age demographics can impact population vital rates, reduce the effective population size, and lead to decreased genetic variability and reduced recruitment (Gibbs and Amato 2000; Skalski et al. 2005; Grayson et al. 2014), it is crucial to maintain accurate estimates of population size and structure to assess the status of a species (Chase et al. 1989). Therefore, the aim of our study is to provide an updated snapshot of Radiated Tortoise demographics at Lavavolo, which, when combined with previous studies, will provide insight into changes over 20 years (1999–2019). These data, which include sex ratio, age class, and body size, will be used as parameters to reassess population health at this stronghold.

Methods

Study site.—We conducted this study in southwest Madagascar at Lavavolo (-24.640808, 43.934300), located in the rural commune of Itampolo, approximately 150 km southeast of Toliara. Vegetation at this site is characterized by *Adansonia* sp. (Baobab), *Alluaudia ascendens*, *Didierea trollii* (Octopus Tree), *Euphorbia* sp. (Spurge), *Jatropha mahafalensis* (Nettlespurge), and *Kalanchoe beharensis* (Velvet-leaf; Leuteritz 2002). Lavavolo contains three geological facies: sandy soil, ferruginous soil, and calcareous soil. Dry forest is distributed on the sandy and ferruginous soils, and xerophytic bush on the calcareous soil (Rasoma et al. 2010).

Sampling protocol.—We sampled tortoises from July–September and November–December of 2018, and March–April 2019. During the sampling periods, we conducted intensive searches for tortoises along three 1,000-m transects oriented in a north–south direction, one on each soil type (Fig. 1). Given mean Radiated Tortoise home range sizes of 2.02 ± 2.22 ha for males and 1.53 ± 1.07 ha for females (Rasoma et al. 2013), we ensured transects were at least 200 m apart to avoids recapturing an individual from one habitat in another (Ranivoarivelo 2011). For our study, transects were separated by at least 500 m. Upon locating a tortoise, we captured individuals by hand, and recorded the geographic location using a Garmin Map64s GPS handheld unit, at which time we marked and measured all individuals. We individually numbered tortoises by filing notches in the marginal scutes and the nuchal scutes with a rectangular file using a numbering system similar to that developed by Cagle (1939). This system of marking is permanent and adapted for long term surveys. Marginal plates are marked by a rectangular notch and from left to right are assigned the numbers 1, 2, 4, 7, 10, 20, 40, and 70 and the nuchal plates are numbered from left to right 100, 200, 400, 700, 1,000, 2,000, 4,000, and 7,000. The addition of the numbers gives a multitude of possible combinations. Example individual number 287 obtained by incision of the scutes 200 + 70 + 10 + 7.

A study in 2011 (Rafeliarisoa et al. 2013) used the curved carapace length (CCL) measurement. Measuring the CCL does not require expensive calipers and is something that can be done in the field with a simple tape measure. Therefore, we also measured CCL with a tape measure, though there is no species-specific equation to convert between CCL and straight carapace length making it challenging to compare data from Rafeliarisoa et al. (2013) and this study to previous studies. Using the minimum size of adults as set by Rafeliarisoa et al. (2013), CCL of 33 cm, we established seven size classes. Specifically, the classes 0–8 cm, 9–16 cm, 17–24 cm, and 25–32 cm are juveniles and 33–40 cm, 41–48 cm, and 49–56 cm are the adults. Sex was determined by secondary sexual characteristics with males having concave plastrons, thicker and longer tails, deeper anal notches, and more protruding gular scutes (Leuteritz 2002).

Statistical analysis.—We used R-4.0.3 for all statistical tests (R Core Team, 2020) and used the same significance level for all tests ($\alpha = 0.05$). We used Chi-squared tests of independence to identify if the sex ratio, and size class differed significantly between soil types.

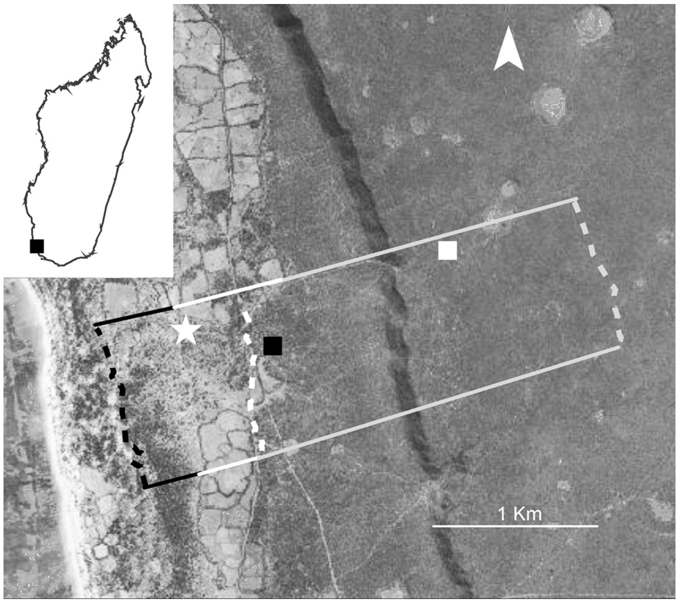

Figure 1. The dashed lines represent the locations of the transects in Lavavolo, Madagascar. The star indicates the village of Lavavolo. The solid lines demarcate changes in soil types: black is sandy soil, white is ferruginous soil, and grey is calcareous soil. The black square indicates the beginning of transect T084 from Rafeliarisoa et al. (2013), the white square indicates the beginning of the Lavavolo transect surveyed in Leuteritz et al. (2005) and Castellano et al. (2013). Map generated by Cynthia Frasier.

Results

We marked a total of 147 tortoises with 34 juveniles and 113 adults. Of the adults, there were 41 females and 72 males. The sex ratio was biased in favor of males (1.8:1). The mean CCLs were 47.34 ± 4.49 cm, 39.48 ± 3.54 cm, and 18.93 ± 9.25 cm for males, females, and juveniles, respectively. The proportion of males, females, and juveniles on each soil type are listed in Table 1. Chi-squared tests showed that sex ratios ($\chi^2 = 0.08$, df = 2, p = 0.95) were not significantly different between soil types. However, the size classes varied significantly with soil type ($\chi^2 = 25.48$, df = 12, p = 0.01). In particular, there were significantly more juvenile individuals of the size class 0–8 cm in the sandy soil and of the size classes 9–16 and 17–24 cm in the ferruginous soil than was expected (Fig. 2, Table 2). There

Table 1. Total numbers, percentage of males, females, and juveniles per soil type.

Soil Type	N	% Males	% Females	% Juveniles
Sandy	57	49.12	26.32	24.56
Ferruginous	59	47.46	27.12	25.42
Calcareous	31	51.61	32.26	16.13

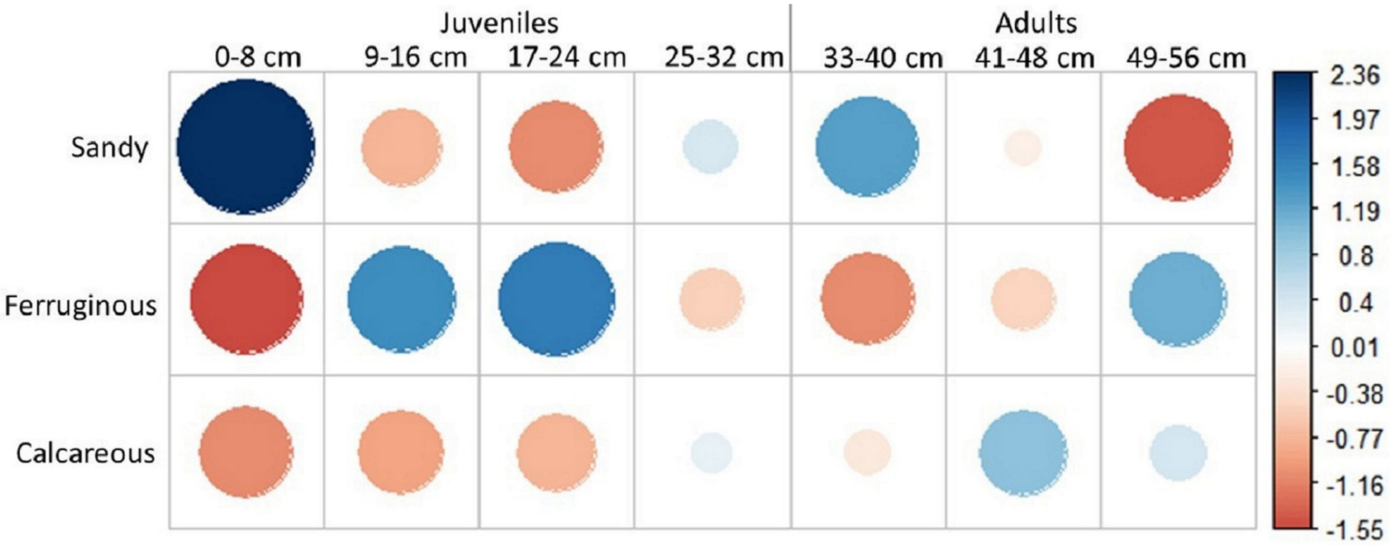

Figure 2. Pearson residuals for each size class according to soil type. For the colored circles, the larger and darker the circle, the greater percent this variable contributed to the Chi-square value. Created by Andrée Nambinina.

Table 2. Numbers of individuals in size classes (cm) in each soil type.

	Juveniles				Adults		
Soil type	**0-8**	**9-16**	**17-24**	**25-32**	**33-40**	**41-48**	**49-56**
Sandy	6	3	0	6	20	12	11
Ferruginous	0	8	3	4	11	11	22
Calcareous	0	1	0	3	7	9	10

were fewer individuals than expected in the three smallest size classes on calcareous soil. Additionally, sandy soil had fewer adult individuals of the size class 49–56 cm.

Discussion

The present study showed that the Radiated Tortoise population in Lavavolo consists mainly of adults (76.87%), with juveniles poorly represented (23.13%). However, the percentage of juveniles has nearly doubled since the previous estimate from 2011 (Rafeliarisoa et al. 2013), which may suggest an improvement in recruitment over the last decade, though this would need to be verified through additional surveys. The adult sex ratio has become increasingly male-biased over the past twenty years, 1.4:1 in 1999 (Leuteritz et al. 2005), 1.6:1 on average in 2009 (Castellano et al. 2013), and 1.8:1 on average for the present study.

Size and age classes—. The lower proportion of juveniles observed by Castellano et al. (2013), Rafeliarisoa et al. (2013), and this study, in comparison to the proportion from 1999 (Leuteritz et al. 2005), is likely due to a combination of factors, the most conspicuous being poaching around Lavavolo. Tortoise eggs are collected for consumption, while juvenile tortoises were the most confiscated age class in seizures made by customs services (Pedrono et al. 2000; Rougier 2015). Additionally, small juvenile tortoises are known to have high death rates due to fire, trampling by cattle, and hunting by the native mongoose *Galidictis grandidieri* (Andriatsimietry et al. 2009). The dramatic changes in the proportion of juveniles over a 20-year period, with a three-fold decline from 1999 to 2011, and then a nearly two-fold increase from 2011 to 2019 (Leuteritz et al. 2005; Rafeliarisoa et al. 2013; this study), indicate the need for continued monitoring of this long-lived species. Without continued surveillance of this species, we will be unable to establish baseline demographic patterns, which are critical for assessing population stability.

Previous demographic studies (Leuteritz et al. 2005, Castellano et al. 2013, Rafeliarisoa et al. 2013) of Radiated Tortoises in Lavavolo did not consider the different soil types as we did in the present study. While there were no discernable differences in sex ratios based on soil types, there was a difference between size classes based on soils. This difference is most evident for juveniles on the sandy and ferruginous soils, where some juvenile classes were present, but absent in other habitats (Table 2). In the sandy soil, there were more small juveniles of 0–8 cm, while the large juveniles of 17–24 cm dominated the ferruginous soil type. It is conceivable that opportunistic passersby played a role in this size class distribution, as the road leading to Toliara passes through the ferruginous soil type, and, while traveling, people collected the smallest individuals to carry with them (Fig. 1; Ranivoarivelo 2011). Alternatively, the higher concentration of the smallest juvenile class on the sandy soil may be suggestive of higher nest concentrations there with larger juveniles migrating to the ferruginous soil where there were more individuals than expected in the size classes spanning 9–24 cm (Fig. 2). Excavating the sandy soil could be easier for females, while the hardness of the ferruginous and calcareous soils can be a disadvantage (Rasoma et al. 2010), though verification of nests in calcareous soil is still necessary. Similar behavior has been noted for the Gopher Tortoise (*Gopherus polyphemus*) where the female tortoises emigrate in search of higher quality habitat that offers suitable nesting areas (Folt et al. 2021). It may prove necessary to protect the sandy and ferruginous soil habitats where there are more juveniles.

Sex ratio—. Sex ratio is an important biological index because the proportion of males and females can affect reproductive success. In Lavavolo, the population appears to be heavily disturbed with a large imbalance in the number of males compared to females. The most common explanation invoked for this imbalance is that it is the result of poachers choosing female individuals rather than males as adult females are appreciated for their more tender meat (O'Brien 2002). This suggestion has been questioned as it is unlikely that poachers would pass up a tortoise just because it is male (Rioux Paquette et al. 2009). Therefore, alternative explanations for this male-biased sex ratio should be explored to ensure that conservation efforts accurately target the drivers of this skew. For example, the skewed sex ratio may reflect a sampling bias favoring males. Male Radiated Tortoises are known to have larger ranges during the wet season with the means of 2.25 ± 2.18 ha in the littoral forest and 1.35 ± 1.12 ha in the limestone, as they look for mates (Rasoma et al. 2013), and thus are easier to observe (Hailey 1988). Moreover, it was noted that Radiated Tortoises exhibit male-biased dispersal behavior with females more often staying in their natal areas (Rioux Paquette et al. 2010). If true, the immigration of new females to Lavavolo would be rare and natural processes may not correct the sex ratio even if poaching and habitat loss stopped, making it critical to protect existing adult females. However, there are not yet any comprehensive studies about female philopatry for this species.

The male-biased sex ratio could also be due to differences in survivorship of males and females. In African Leopard Tortoises (*Geochelone pardalis*), females experience high mortality due to mating (Willemsen and Haley 2001). Though female mortality events related to mating have not been reported for the Radiated Tortoise, the courtship behavior of males, the larger sex, includes biting, ramming, pushing, and trying to lift females using their gular scutes (Leuteritz and Ravolanaivo 2005). The skewed sex ratio at Lavavolo may result in extensive harassment of female Radiated Tortoises, reducing female survivorship. This has been noticed for Hermann's Tortoise, *Testudo hermanni*, where populations with severely male-biased sex ratios had lower female survival rates due to intensive harassment of females (Hailey and Willemsen 2000; Golubovic et al. 2018).

Instead of adult female survivorship, the skewed sex ratio could be attributed to sex-biased survivorship of hatchlings or possibly the driving force of the skew even precedes hatching and is linked to maternal behavior. In captive studies of the Radiated Tortoise, it has been shown that this species exhibits temperature-dependent sex determination (TSD), with lower incubation temperatures producing males and higher incubation temperatures producing females (Kuchling et al. 2013). For the Emydinae subfamily, Bull et al. (1982) postulated that female turtles may compensate for climate change through nest site selection related to shade provided by vegetation (Bull et al. 1982). In this study, most Radiated Tortoise juveniles were found on the sandy and ferruginous soils where vegetation was denser and nests plausibly cooler, possibly indicating a preference for nesting in these areas versus on calcareous soils.

Though the concentration of Radiated Tortoises at Lavavolo is one of the highest throughout the species' distribution range (Rafeliarisoa et al. 2013), the demographics have become increasingly male-biased over the past 20 years, possibly compromising the long-term population viability at this site. This is further exacerbated by unbalanced juvenile classes which may indicate future declines in recruitment. What is more disheartening is that other regions within the Radiated Tortoise's range are experiencing more dramatic reductions in their tortoise populations. Lavavolo is in a zone (between the Onilahy River and Linta River) where the poaching threat level is only moderate (Walker 2010), and the presence of NGOs such as the Madagascar Biodiversity Partnership and Conservation Fusion may serve to dissuade illegal collection. Understanding the intricacies of Radiated Tortoise ecology at strongholds like Lavavolo is crucial to the continued existence of this species.

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