
BEHAVIOR, THERMAL PREFERENCE, AND RANGING PATTERNS OF THE CRITICALLY ENDANGERED MADAGASCAR SPIDER TORTOISE DURING A CYCLONE

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Abstract.—We surveyed an area of high Spider Tortoise (*Pyxis arachnoids*) density in southwest Madagascar in February 2012 during a cyclone event. Over a 10-day period, we recorded behavior associated with environmental conditions (temperature, humidity, and cloud and vegetation cover) of 198 Spider Tortoises. In addition, we monitored movements of six adult tortoises (3♂, 3♀) using radiotelemetry and the temperature preferences of two individuals (1♂, 1♀) using dataloggers. During this cyclone event, tortoises behaviorally thermoregulated to near 30 °C and 78% humidity, and altered their activity as the storm progressed from being buried to emerging to forage. Tortoises tended to bury themselves in areas of relatively dense vegetation cover (approx. 60%) when humidity and cloud cover were low, and were more often found on the surface, often eating, during precipitation in relatively sparse vegetated cover (approx. 45%). While subadults were typically found resting on the surface, females were usually found buried and males were found above-ground and walking. Concordantly, males moved more and used greater areas than females (mean distance moved = ♂ 256 m vs. ♀ 127 m; mean area used = ♂ 4,463 m² vs. ♀ 1,516 m²) and behaviorally thermoregulated within a narrower temperature range (mean thermal range: ♂ 14.4 °C vs. ♀ 30.0 °C). Though limited in duration, this is the first detailed information on the behavior, thermal preferences, and ranging patterns for wild Madagascar Spider Tortoises and suggests an interplay between extreme weather and behavior in this species.

Key Words.—behavioral thermoregulation; home range; *Pyxis*; radiotelemetry; thermal ecology

INTRODUCTION

Environmental conditions impact daily and seasonal activity in most animals, but are distinctly influential on ectothermic animals (Huey 1982; Brown and Weatherhead 2000). Ectotherms show strong ecological associations with weather because both their behavior and physiology is determined by their environment (Huey and Stevenson 1979). Seasonality dictates when an ectotherm undergoes hibernation, aestivation, reproduction, foraging, and even digestion (Wright and Cooper 1981; Blem et al. 1986; Huey and Kingsolver 1989; Adolph 1990; Cunningham et al. 2009). However, many ectotherms exploit environmental perturbations to accomplish relatively rare behavioral activities such as annual mating congregations or migration events (Wilson 2005; Dodd et al. 2006; Pike 2008; Williams et al. 2009). Therefore, the movements and behavior of ectotherms during regular or unpredictable weather

patterns are of interest for a complete ecological understanding.

The ecology of the Madagascar Spider Tortoise (*Pyxis arachnoids*), listed as Critically Endangered by International Union of Conservation of Nature and Natural Resources (2014. The IUCN Red List of Threatened Species, version 2014.2. Available from www.iucnredlist.org. [Accessed 4 August 2014]) is widely regarded as under-researched (Durrell et al. 1989; Leuteritz and Walker 2008; Pedrono 2008; Walker and Rafeliasoa 2012). This species is becoming increasingly rare as a result of habitat loss, largely due to charcoal production and subsistence agriculture (Harper et al. 2007; Walker et al. 2014). Yet, detailed knowledge of Spider Tortoise ranging patterns, thermal preference, and much of their behavior remains unknown. The Spider Tortoise is endemic to the dry coastal spiny forests of southwest Madagascar (Bour 1981) and appears to have strongly environmentally dependent behaviors, usually going through a period of

aestivation during the dry season from April to October (Pedrono 2008; Walker et al. 2008; Currylow 2012). The species is one of the smallest tortoise species in the world at approximately 11 cm straight-line carapace length (SCL), and based on this, it has been presumed that Spider Tortoises exhibit low dispersal behavior and maintain relatively small home ranges (Walker 2010, 2012). However, there is speculation that heavy precipitation can increase Spider Tortoises activity levels (Pedrono 2008), suggesting that tortoises may require more ranging habitat area than previously expected. To conserve or restore appropriate Spider Tortoise habitat, more detailed information on their ecology, including ranging requirements, weather-related activities, and thermal preferences are needed. We undertook a brief and opportunistic field study to investigate the behavior of a sub-species of Spider Tortoises (*P. a. arachnoides*) within the center of the range of the species in southwestern Madagascar. During a single cyclonic event while conducting a broader study at our field site (Walker et al. 2014), we aimed to: (1) characterize Spider Tortoise activity with relation to sex, age class, microhabitat variables, and weather; (2) determine thermoregulatory preferences; and (3) obtain preliminary movement data for the species.

METHODS

Study site.—We studied tortoise in a 10.2 km² patch of southern dry forest habitat near Toliara, in southwestern Madagascar. The area comprises patchy xerophytic scrub (Fenn 2003) and supports one of the densest populations of *P. a. arachnoides* within the range of the species (Walker et al. 2008). Historically, the forest scrub was dominated by species in the families of Euphorbiaceae and Didiereaceae, but much of the habitat of the region has been severely altered over the past 40 y due predominately to fuel wood harvest for charcoal production and livestock grazing (Jesu and Schimmenti 1995; Harper et al. 2007; Walker et al. 2012a). Annual rainfall in the habitat peaks at around 350 mm and is concentrated in the period from December to March (Durrell et al. 1989; Jesu and Schimmenti 1995).

Cyclone description.—Our study overlapped with Intense Tropical Cyclone Giovanna (9–21 February 2012). On 14 February 2012, Giovanna made landfall on the east side of Madagascar and traversed the island to the Mozambique Channel before beginning a wide u-turn around the southwestern coast, encompassing our study area. The Toliara weather station near our study site reported a local average rainfall of 18.7 mm in 24 h. On 18 February, Giovanna moved eastwards alongside the southern tip of Madagascar, began to weaken to a tropical depression on 20 February, and dissipated late

on 21 February. We used storm path and site-proximity data to break up survey dates into three “storm timeframes” for analysis: (1) early-storm = 11–13; (2) mid-storm = 14–16; and (3) late-storm = 17–20 February. We continually monitored storm temperature and humidity at the survey site using a HygrochronTM iButton temperature and humidity datalogger (model DS1923-F5#, Maxim Integrated Products, Inc., Sunnyvale, California, USA) beginning 12 February 2012. This logger was set to record temperature and humidity every hour and was affixed low on vegetation to collect the ground microclimate comparable to that which tortoises experience.

Species monitoring.—From 11 February through 20 February 2012, we located Spider Tortoises by systematic meandering line-transects within 1-ha plots (following Walker et al. 2008). Each time an animal was encountered, we recorded its age/sex class (male, female, or unsexable sub-adult) and behavior. We grouped behaviors into six Activity Class categories that best matched the observation including: buried (found buried in leaf litter or soil), resting (resting on the soil surface in open), in vegetation (resting in or under vegetation), eating, digging, or walking. We used a Kestrel[®] 3000 pocket weather meter (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA) to record ground temperatures (°C) and humidity (%) at the tortoise location. We also recorded the presence or absence of precipitation and obtained visual estimates of vegetation and cloud cover (in 10% intervals following Walker et al. 2012b).

We selected six adults (three ♂ and three ♀) to be repeatedly relocated every 1–3 d. A radio transmitter (RI-2C, Holohil Systems, Ltd., Carp, Ontario, Canada) was epoxied to the carapace and was ≤ 5% of the total body weight of the tortoise. We then located radio-telemetered animals four more times (totaling five locations each) through the duration of the cyclone. We were careful to minimize disturbance of the tortoises during relocations, and recorded each activity class and associated microclimatic conditions. We also chose two of the radio-telemetered individuals (one of each sex) to carry a Thermochron[®] iButton temperature datalogger (model DS1921G-F5#, Maxim Integrated Products, Inc., Sunnyvale, California, USA). The iButtons continually recorded the preferred temperatures of those two animals every three hours.

Analyses.—We tested assumptions of normality and equal variances of the data (e.g., behavior by date, presence of precipitation, storm timeframe, and age/sex class, and environmental data) and used *t*-tests to compare temperatures and humidities recorded at tortoise locations against ambient. For the non-parametric analyses, we used Chi-square analyses

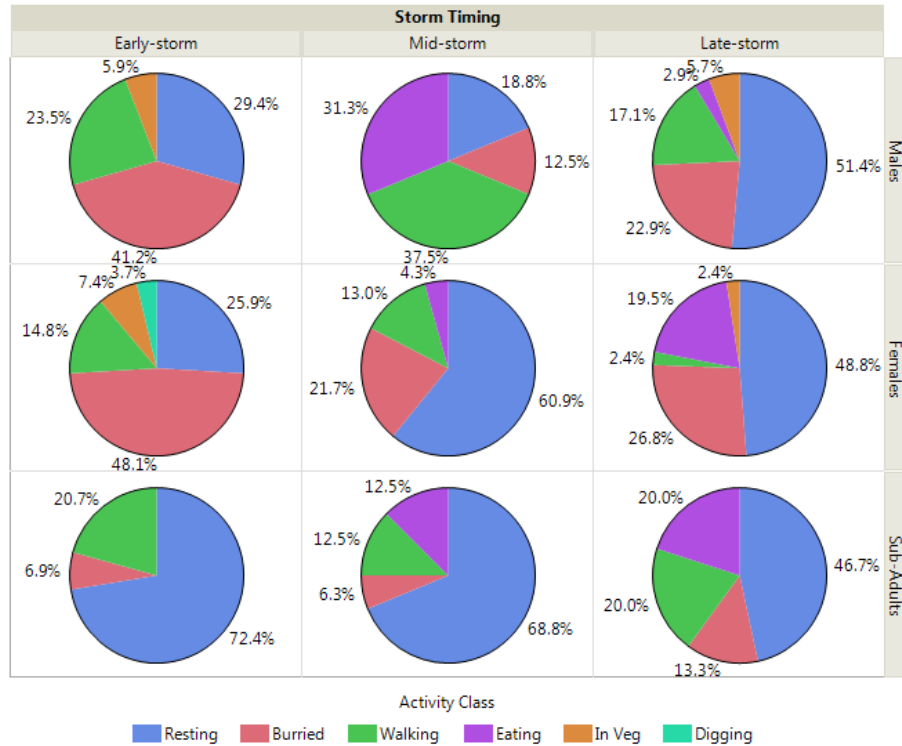


FIGURE 1. Percentages of observed behaviors (activity classes) by age/sex class (male, female, or sub-adult) of Spider Tortoises (*Pyxis a. arachnoides*) in southwestern Madagascar over the course of a cyclone (early-storm = 11–13, mid-storm = 14–16, and late-storm = 17–20 February 2012). Percentages represent the proportion of the observed behavior within the class.

followed by correspondence analyses or generalized linear mixed models (GLMMs). For the GLMMs, we used individual ID as the random subject effect to avoid pseudoreplication (e.g., repeated measures of tracked animals or data from dataloggers). Where GLMMs yielded significant results, we followed with Tukey’s HSD post-hoc analyses to determine the specific significant effects of the model. We used JMP® Pro 11.0.0 software (SAS Institute Inc., Cary, North Carolina, USA) to run all statistical analyses. Significance was determined at $P \leq 0.05$. For radio-telemetered tortoises, we used ArcGIS 10.2 software (ESRI, Redlands, California, USA) to calculate distances and total areas used (minimum convex polygons) by each animal. We report only summary statistics (means and ranges) on the ranging patterns due to the limited duration of the study and resulting restricted dataset.

RESULTS

During surveys 11–20 February 2012, we found 198 Spider Tortoises (57♂, 81♀, 60 sub-adult). We relocated (radio-tracked) six of those tortoises (three ♂, three ♀) every 1–3 d for four more observations each (222 tortoise data points total). The Hygrochron™, which measured environmental variables hourly, logged 202 temperature and 202 humidity readings. The two

button temperature loggers deployed on tortoises (1♂, 1♀) profiled an additional 283 tortoise-temperature data points over the course of this study.

Activity.—We collected behavior data representing 219 tortoise observations (68 ♂, 91 ♀, 60 sub-adult) of the total 222 tortoise observations in this study as three activity class observations were not recorded. We found only one animal digging, so it was left out of the analyses; however, we included this data point in the figure for reference. Participation in activity classes differed significantly ($\chi^2 = 24.11$, $df = 6$, $P < 0.001$). Aside from resting most of the time (53% of all observations), tortoises were often found buried early-storm (28% of observations), and then were often found walking and eating as the storm progressed (22% and 15% of observations respectively). We also found a significant differences in behavior between the sexes and subadults ($\chi^2 = 12.81$, $df = 6$, $P = 0.046$; Fig. 1).

There was a significant difference in the percentage of Spider Tortoise activities depending on presence or absence of precipitation. During rain, tortoises were more often found resting or eating, whereas they would more often be found walking or buried below soil when there was no rain ($\chi^2 = 8.99$, $df = 3$, $P = 0.029$). We also found significant differences in behavior associated with

TABLE 1. Daily mean carapacial temperatures recorded using iButton temperature loggers affixed to the carapace of a single male and single female Spider Tortoise (*Pyxis a. arachnoides*) during a cyclone in southwestern Madagascar. Temperatures were recorded every three hours from 12–20 February 2012.

Date	n	♂ Mean Temp		♀ Mean Temp		Thermal Range	
		(Min–Max)	SD	(Min–Max)	SD	♂	♀
12-Feb.	27	27.5 (22.0–34.0)	4.4	27.3 (21.5–43.5)	7.7	12.0	22.0
13-Feb.	32	29.2 (23.0–37.5)	4.7	34.3 (23.0–56.0)	11.3	14.5	33.0
14-Feb.	32	27.6 (21.5–33.5)	4.2	33.0 (22.0–51.5)	10.4	12.0	29.5
15-Feb.	32	26.9 (20.5–37.0)	5.1	31.8 (20.5–54.5)	11.3	16.5	34.0
16-Feb.	32	27.6 (19.0–39.0)	6.8	32.8 (19.5–59.0)	13.1	20.0	39.5
17-Feb.	32	28.0 (22.5–34.5)	4.1	33.6 (22.5–54.0)	11.4	12.0	31.5
18-Feb.	32	29.8 (25.5–37.0)	4.0	34.1 (26.0–54.5)	10.1	11.5	28.5
19-Feb.	32	25.8 (19–33.0)	5.0	26.5 (18.0–42.0)	7.2	14.0	24.0
20-Feb.	32	22.2 (14.0–31.0)	6.0	25.0 (14.0–42.0)	10.0	17.0	28.0
Mean		27.2 (20.8–35.2)	4.9	30.9 (20.8–50.8)	10.3	14.4	30.0

variations in humidity, vegetation cover, and cloud cover ($F_{5,37} = 7.80$, $P < 0.001$). Tortoises were often found eating or resting above ground when humidity was elevated (82.1–83.8%, SE = 1.5–3.7) as opposed to being found buried or in vegetation when humidity was lower (66.0–71.6%, SE = 1.9–4.5). The mean percent of vegetation cover (61.4% SE = 2.6) was significantly higher in areas where tortoises were found buried and was lower (45.1% mean vegetation cover, SE = 3.1) where they were found walking ($F_{5,123} = 4.80$, $P = 0.001$). When the mean cloud cover was low (38.4%, SE = 3.2), tortoises were often found buried, but when mean cloud cover was high (73.0%, SE = 9.8), the tortoises were more likely to be found significantly more often eating ($F_{4,6} = 6.08$, $P = 0.022$).

Weather and temperature preferences.—Over the course of the storm, the Hygrochron™ environmental datalogger recorded temperatures ranging from 20.6–45.0 °C and humidity from 23.8–100%. When limited to temperatures and humidities recorded only within an hour of tortoise encounters (i.e., excluding those times not comparable to tortoise behavior observations), the averages were 26.4 °C (20.6–34.6 °C, SE = 0.4) and 82.2% (40.9–99.2%, SE = 2.1). Those environmental readings were significantly different from tortoise-location ground temperatures (mean = 30.4 °C [24.5–37.3 °C], SE = 0.2; $t = 9.50$, $df = 258$, $P < 0.001$). However, tortoise-location humidities were not distinct from the environmental humidity readings (mean = 79.6% [40.6–100%], SE = 1.2; $t = -1.07$, $df = 257$, $P = 0.284$), but raw data were bimodal in distribution, concentrating at upper and lower quartiles of 94.2% and 64.3 %.

The mean tortoise-location temperatures began significantly higher averaging 33.3 °C (SE = 0.4) early-storm, then dipped mid-storm and late-storm (to 28.8 °C, SE = 0.3 and 29.8 °C, SE = 0.3 respectively; $F_{2,2} = 42.80$, $P < 0.001$). Humidities recorded at tortoise locations were also significantly different ($F_{2,2} = 51.89$, $P < 0.001$), beginning low at 63.4% (SE = 2.0) early-storm, rising to 81.5% (SE = 1.6) mid-storm, and continuing to rise to 89.3% (SE = 1.5) late-storm.

We found no significant differences between classes in the preferred ground temperatures ($F_{2,2} = 0.861$, $P = 0.439$) or ground humidities ($F_{2,2} = 1.47$, $P = 0.231$). However, we did find differences in the finer-scale range in temperatures recorded by the iButton temperature loggers from the two monitored individuals. While the female averaged only slightly warmer carapacial temperatures (31.0 °C) than the male (27.2 °C), she exposed herself to a much broader thermal range in temperatures each day (daily thermal range_(max-min) = 30.0 °C vs. 14.4 °C; Table 1). The female had pointedly higher average daily maximum carapacial temperatures of 50.7 °C while the male only averaged 35.2 °C, despite having been exposed to the same environmental conditions (they were never found more than 1,230 m from one another).

Movements.—Tracked tortoises moved an average distance between relocations (every 1–3 days) of 48 m (range = 1–142 m). The mean total area used by each tortoise during the cyclone period was greater than expected at 2,989 m² (0.3 ha) and the mean total distance moved was 191 m. Overall, males on average moved more than twice the distance of females (♂ 256 m, range = 160–326 m; ♀ 127 m, range = 61–234 m) yet

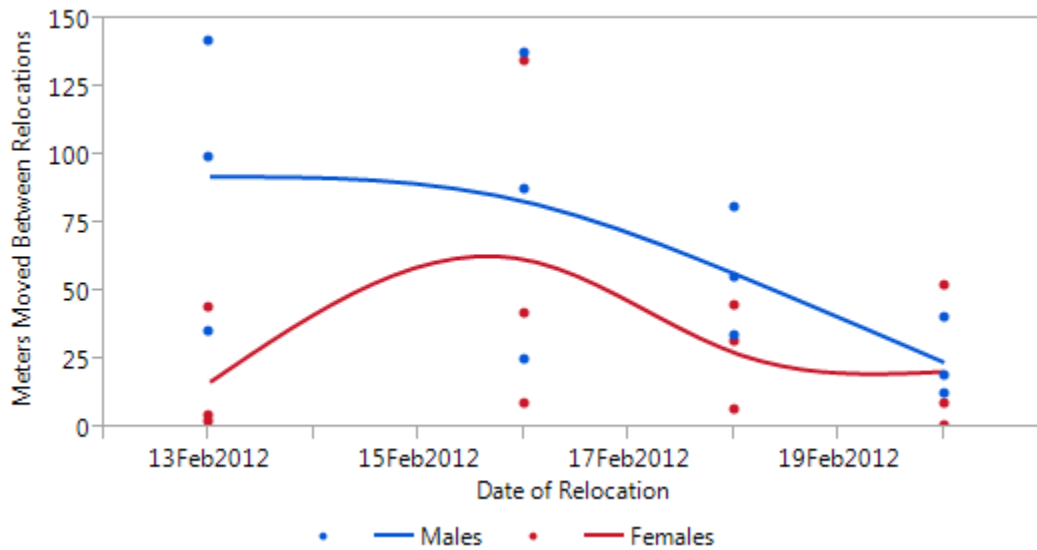


FIGURE 2. Distances traveled (in meters) between radio-locations by three female and three male Spider Tortoises (*Pyxis a. arachnoides*) during a cyclone event in southwest Madagascar in 2012. Trend lines included for ease of interpretation.

decreased movements over the storm period (Fig. 2). Concordantly, males used areas approximately three times larger than that of females (♂ 4,463 m², range = 1,172–7,314 m²; ♀ 1,516 m², range = 147–3,855m²).

DISCUSSION

Our study provides the first data on the behavioral thermoregulation and ranging patterns of this species in the wild, showing the species is more vagile than anticipated and that there are detectable sex differences in response to environmental conditions. Pedrono (2008) speculated that Spider Tortoises are most active during rain, and we indeed found that tortoises were initially buried, then began to emerge and as the cyclone progressed. The shift to becoming active at the surface, often for eating and walking, was associated with less densely vegetated areas, higher cloud cover, higher ground humidity, and presence of precipitation. Yet, the tendency for Spider Tortoises towards less vegetative cover (31–40%) has previously been recorded only during the dry season when tortoises were suspected to have to leave dense cover in search of new food sources (Walker et al. 2008). In general, the tortoises favored more densely-vegetated areas (approximately 60% vegetation cover) only to bury themselves during low cloud cover and low humidities.

The buried behavior was not equally distributed across the classes. Female Spider Tortoises were more often found buried than males. It has been shown that female Gopher Tortoises (*Gopherus polyphemus*; Landers et al.

1980) and Painted Turtles (*Chrysemys picta*; Rowe and Dalgarn 2009) seek out stable temperatures underground while waiting for air temperatures to become favorable and energetically preparing for (or recovering from) nesting forays. However, reproductive behaviors in the Spider Tortoise are currently undescribed; how thermal preferences influence reproductive and movement behaviors within classes should be further investigated.

There have been several studies in other ectotherms on specific behavioral modulation associated with thermoregulation through the use of available thermal environments (Hertz and Huey 1981; McMaster and Downs 2006; Currylow 2011). In the present study, tortoises had access to a range in environmental temperatures during the storm event (averaging 27–36 °C), but they sought out (preferred) average temperatures of 30 °C. The relatively uniform preferred temperature is rather surprising given the range in temperatures tortoises exposed themselves to during our study (as represented by data obtained from the two Spider Tortoises that carried iButton temperature loggers). Interestingly, preferred daily mean temperature ranges differed between the two tortoises by an average of more than 15 °C. This is unexpected because the animals remained relatively proximal and were therefore exposed to the same ambient environmental conditions. The extraordinary range in temperatures Spider Tortoises will prefer or tolerate we see here demonstrates the considerable effectiveness of behavioral thermoregulation within microclimates.

Further research on the ecological impacts of this behavioral plasticity should be investigated.

Prior to this study, it was presumed that Spider Tortoises maintain relatively small home ranges with low dispersal rates (Walker 2010). We found tortoises would move straight line distances of 142 m in only 1–3 days and use areas more than 0.7 ha in just over one week, much higher than anticipated from a decade of mark-recapture surveys on the population (pers. obs.). In other terrestrial turtle species, it has been observed that tropical thunderstorms trigger migration events (Dodd 2001; Aresco 2005; Schofield et al. 2010). Although the movements we observed may be abnormal due to the storm conditions, cyclones of similar magnitude are nearly an annual occurrence in the area and therefore it is not unlikely that these animals use similar areas annually or throughout the active season, perhaps even depending on extreme weather events (e.g., Currylow 2012). For many other turtle species, sex differences in movement trends are often attributed to males actively seeking mating opportunities or females moving to nesting grounds. We observed male Spider Tortoises walking more often than either females or subadults, and saw that females moved, on average, only half as far as the males. Perhaps these trends are tied to yet undescribed reproductive timing events. Additionally, it is worth noting that the areas used by the tortoises in such a short timeframe were so large, habitat requirements for this species may be underestimated, and limits on conservation areas may impact recovery efforts.

Here, we report the first recorded movements of wild Spider Tortoises along with detailed temperature preference and associated behavior. Despite the limited duration of our study, we provide detailed data and present expanded trends in activity, thermoregulation, and vagility of this understudied species. We hope this study may serve as a springboard for additional studies on Spider Tortoise ecology and that these data can aid in conservation management decisions.

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