Turtles on the Brink in Madagascar: Proceedings of Two Workshops on the Status, Conservation, and Biology of Malagasy Tortoises and Freshwater Turtles
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Ecological Husbandry and Reproduction of Madagascar Spider (*Pyxis arachnoides*) and Flat-tailed (*Pyxis planicauda*) Tortoises

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Abstract. – Tortoises of the genus *Pyxis* have limited ranges along the southwestern coast of the island of Madagascar. The genus includes *P. planicauda* and *P. arachnoides*. Both species are listed on CITES Appendix I and have been assessed as Critically Endangered for the IUCN Red Data List in 2008. Previously, large numbers of both species were exported from Madagascar during 2000 and 2001. A naturally low reproductive rate and an increased rate of habitat loss have generated concern over the status of these species in the wild and in captive collections. Both species are native to tropical dry forests with pronounced wet and dry seasons. An understanding of the climatic and environmental conditions experienced by these species in the wild is important in the establishment of a successful captive breeding program. Replicating the seasonal cycles and maintenance of a dry season aestivation period for adults appears important for successful reproduction in captivity. *Pyxis* eggs typically undergo an extended embryonic diapause that likely corresponds to the lengthy dry season in their native range. High hatching rates have been achieved in several captive colonies by exposing fertile eggs to cooler and drier conditions. A shift back to warmer and more humid conditions appears to trigger, or reinitiate embryonic development. An embryonic diapause controlled by environmental cues may serve to synchronize and delay hatching until the following wet season. Soil temperature data collected at three sites in Madagascar provide guidance for incubation protocols in captive collections. Current conservation measures include AZA studbooks and Species Survival Plans. Long-term success of existing assurance colonies will require continued cooperation between zoological institutions and private breeders.

Key Words. – Reptilia, Testudines, Testudinidae, climate, captive breeding, egg, embryonic diapause, incubation, *Pyxis arachnoides*; Spider Tortoise, *Pyxis planicauda*, Flat-tailed Tortoise, Madagascar

The genus *Pyxis* includes two species of tortoise, *Pyxis planicauda* (Kapidolo, or Flat-tailed Tortoise) and *Pyxis arachnoides* (Kapila, or Spider Tortoise), that are endemic to the southwestern coast of Madagascar. *Pyxis arachnoides* includes three subspecies, *P. a. arachnoides*, *P. a. brygooi*, and *P. a. oblonga*. The northern species, *P. planicauda*, is restricted to the few remaining remnants of dry deciduous forest in the western portion of the island near Morondava, whereas *P. arachnoides* is confined to the coastal spiny forest of the southwest (Pedrono 2008). All taxa within this genus have been assessed as Critically Endangered under the International Union for Conservation of Nature (IUCN) Red Data List and are listed on the Convention on International Trade in Endangered Species of Flora and Fauna (CITES) Appendix I. A naturally low reproductive rate and increased rates of habitat loss and harvesting have heightened concerns over the status of these species in the wild and in captive collections. An understanding of the climatic and environmental conditions in the native habitat is important for the creation of successful *ex-situ* breeding programs. Duplication of seasonal patterns appears critical for successful reproduction in captivity (Loehr 2001; Gibson and Buley 2004; Pearson 2006; Mislin and Eberling 2009).

Loss of habitat has caused a dramatic reduction in the historical range of *P. a. arachnoides* and *P. a. brygooi* (Walker 2010; Walker and Rafeliarisoa 2010). It is likely that *P. a. oblonga* will also show evidence of a reduction in range when surveys are completed (Walker et al., this volume). *Pyxis planicauda* is under similar habitat pressures, but has always had a much more limited range (Pedrono 2008). Both *Pyxis* species are also under pressure from collection for the international pet trade, as well as for local consumption (Behler 2002; Pedrono 2008). CITES quotas issued by the government of Madagascar in 2000 and 2001 resulted in the export of thousands of *P. arachnoides* and *P. planicauda*, which significantly exceeded the quotas (CITES 2000; Walker et al. 2004; Pedrono 2008). As many as 4000 *P. planicauda* may have been exported during this time (Leuteritz et al. 2008). As a result of these exports, captive groups of Spider and Flat-tailed Tortoises have been established in many zoological institutions and private collections outside of Madagascar.

Captive reproduction of *Pyxis* has often proved problematic, with either adults failing to reproduce, or the occurrence of high juvenile mortality rates (Razandrimamilafiniarivo et al. 2000; Loehr 2001; Gibson and Buley 2004). An important component of a conservation strategy for *Pyxis* species is the establishment of viable *ex-situ* assurance colonies using founder stock exported from Madagascar during 2000 and 2001. Successful reproduction in *ex-situ* colonies depends upon the understanding of the native environment and natural history of these enigmatic tortoises.

By comparing the climatic patterns of *ex-situ* colony sites with those of the native habitats, it is possible to match temperature and rainfall patterns using a combination of outdoor and indoor facilities. Climate variables play an important role in the annual cycle of *Pyxis* species in the wild. Establishing a similar annual cycle in captivity is a significant factor in successfully reproducing these species. Incubation of eggs must also take into consideration the climate variables in the native environments due to the embryonic diapause that delays the hatching of *Pyxis* eggs. Diapause is a period of natural delay in egg development that occurs in response to regularly recurring periods of adverse environmental conditions, usually seasonal cold periods; diapause is subsequently broken when warm seasonal periods recur and egg development resumes and continues (see Ewert and Wilson 1996). Soil temperature data from the native environment have provided important guidance in determining proper incubation temperatures and temperature cycles. Incubation temperatures are critical not only for successful hatching, but also for sex determination, since it is likely that *Pyxis* species have some form of temperature-dependent sex determination.

METHODS

Climate Matching. — Flat-tailed Tortoises are restricted to the few remaining patches of tropical dry deciduous forest on the western coast of Madagascar north of Morondava (Young et al. 2008). This forest type has a closed canopy during the wet season with lush vegetative growth, which is in stark contrast to an open canopy during the harsh dry season. A deep leaf litter layer provides shelter for the tortoises during the prolonged dry season and associated drought. Most activities take place during the relatively short wet season, while the dry season is spent in some form of aestivation under the leaf litter. The wet season extends from roughly October to May and the dry season spans the remainder of the year (Pedrono 2008).

The three subspecies of Spider Tortoise occur along the southwestern coastline in more open habitats characterized by tropical spiny forest and other scrubby coastal areas dominated by plants in the Didieraceae and Euphorbiacae families. Spider Tortoises occur in generally drier habitats than Flat-tailed Tortoises, but they also experience pronounced wet and dry seasons and aestivate during the dry season buried in leaf litter or sandy soil (Pedrono 2008).

When establishing a breeding colony of any species, it is important to understand the ecological constraints and influences on a species in its native range. Species adapted to certain distinct climatic cycles, for instance, may have difficulty adjusting to, or reproducing successfully, in captive situations that are dramatically different. In 2002, I acquired a group of *P. planicauda* and *P. arachnoides* and housed them near Gainesville, Florida, USA. At that time very little had been published on the ecology of these species in the wild, or on their husbandry in captivity. Valuable information was available in the annual reports of the European Studbook for *P. arachnoides* (Loehr 2001). Anecdotal information suggested that the captive husbandry of *P. planicauda* was not significantly different from that used for *P. arachnoides* that was being bred in Europe. The European breeders had documented the aestivation behavior of *P. arachnoides*, and had applied seasonal temperature and humidity changes to stimulate the adults to breed and successfully incubate eggs (Loehr 2001).

To establish the proper captive environment that would reflect the seasonal variation of the native range, I acquired climate data averages for two locations within the range of *Pyxis* to compare with the climate averages for Gainesville, Florida. Climate data were acquired from weather stations located at the airports at Morondava (Weather Underground, 2010a) and Tulear (Weather Underground, 2010b) in Mada-

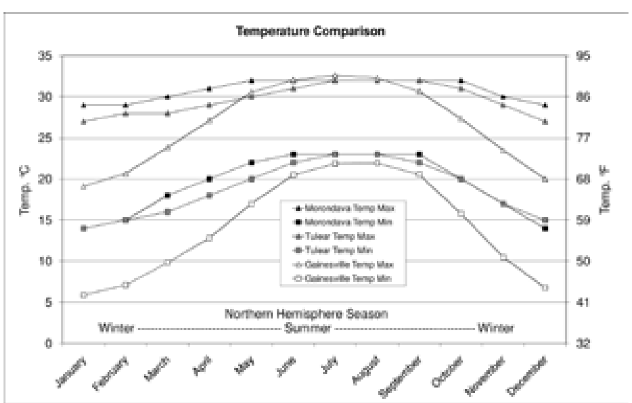

Figure 1. Comparison of monthly average daily maximum and minimum air temperatures for Morondava and Tulear, Madagascar, and Gainesville, Florida, USA. Horizontal axis represents month for Gainesville (northern hemisphere) data only. Morondava and Tulear (southern hemisphere) data have been shifted by six months to align data by season instead of calendar month.

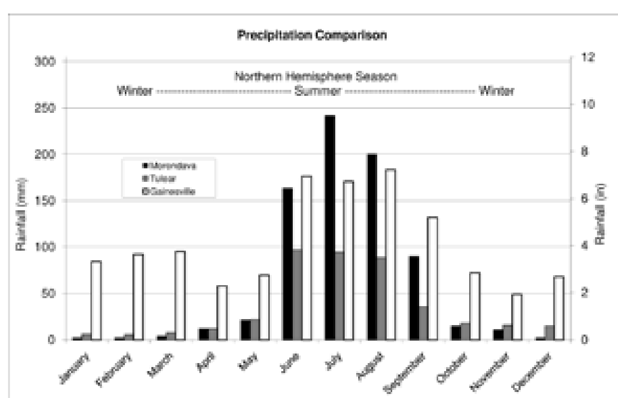

Figure 2. Comparison of monthly average precipitation for Morondava and Tulear, Madagascar, and Gainesville, Florida, USA. Horizontal axis represents month for Gainesville (northern hemisphere) data only. Morondava and Tulear (southern hemisphere) data have been shifted by six months to align data by season instead of calendar month.

gascar, and Gainesville (Southeast Regional Climate Center, 2010) in the USA. Morondava is within the range of *P. planicauda* and Tulear is within the upper third of the range of *P. arachnoides*. Gainesville is located in the northern hemisphere, while the native range of *Pyxis* is located in the southern hemisphere. Consequently, there is a six month shift in the wet and dry seasons between Madagascar and Florida. To compensate for this, the data from Morondava and Tulear were shifted by six months to allow direct comparison of the wet and dry seasons rather than by calendar months (Figs. 1, 2).

Temperatures in the summer, or wet season, are very similar between all three locations. The mean maximum and minimum temperatures for the months of May through September in Gainesville are similar to the temperatures for the months of November through March in Morondava and Tulear. However, the winter season temperatures in Gainesville are lower than the corresponding dry season temperatures in the native range for both species.

Likewise, rainfall amounts are very similar during the summer wet season, particularly during June through August (December – February in the southern hemisphere) with Tulear having the lowest levels of precipitation. During the winter dry season, precipitation in Gainesville declines, but is much higher than either site in Madagascar. Both Morondava and Tulear receive minimal amounts of rainfall during the dry season and experience warm and very dry winters with hot and wet summers. Gainesville has much cooler and wetter winters, but also has hot and wet summers. Both regions of the world have summer weather patterns that are frequently dominated by tropical cyclones or tropical waves causing widespread and intense rainfall events. Duplication of the Madagascar wet season is particularly easy in Florida, especially in years with significant tropical cyclone activity.

Based on the climate comparisons, the *Pyxis* group was set up in Gainesville in outdoor enclosures from May to November to take advantage of the warm summer temperatures, rainfall, and sunlight. From November to May, the tortoises were housed indoors in a climate controlled environment with low humidity and fluctuating daily temperatures. Daytime high and nighttime low temperatures were kept within the range of their native environment.

Annual Cycle. — As part of their adaptation to survival in an extreme environment, both *P. arachnoides* and *P. planicauda* undergo a period of dormancy or aestivation as environmental temperatures decrease and rainfall ceases (Kuchling and Bloxam 1988; Walker et al. 2010). This behavior is even seen in captive born juvenile tortoises. In captivity, tortoises burrow into the substrate and can remain in the same location for weeks at a time. This behavior has also been observed in European collections (Loehr 2001).

Rainfall, or wetting of the enclosures, stimulates tortoise activity on both a seasonal and daily basis. Aestivation gradually ends with an increase in rainfall, or misting of enclosures. Mating begins early in the wet season and tapers off in late summer. In captivity, the egg-laying period for *P. arachnoides* and *P. planicauda* typically begins in July with a peak in mid-September. Egg-laying may even extend into the dry season and fertile eggs have been produced as late as February.

The eggs of tropical tortoise species from less seasonal environments, such as *Chelonoidis carbonaria*, require about 120–130 days of incubation at moderate temperatures (29°C) before hatching. *Pyxis* eggs in contrast can take over 300 days to hatch, depending on the incubation protocol (Razandrimamilafiniarivo et al. 2000). The eggs of *P. planicauda* and *P. arachnoides* both undergo a diapause during development that corresponds to the dry season in their native environment. The diapause occurs at an early stage of embryogenesis, before the embryo can be seen by candling the egg. If *Pyxis* eggs in the wild hatched without this delay in development, the hatchlings would emerge during the height of the dry season in a very harsh environment. By delaying development through diapause, *Pyxis* eggs hatch during the following wet season, when there is abundant food and moisture (Gibson and Buley 2004). Understanding this complex embryonic development process is critical to the successful hatching of *Pyxis* eggs in captivity.

Egg Incubation. — Incubation of *Pyxis* eggs has always been deemed a difficult and tricky process. Initial successes with *P. planicauda* eggs at the Chelonian Captive Breeding Centre in Ampijoroa, Madagascar, depended upon allowing eggs to incubate in ground nests (Razandrimamilafiniarivo et al. 2000). This allowed the seasonal climate effects to influence the development of the eggs. At the Jersey Zoo, the Durrell Wildlife Conservation Trust (DWCT) successfully hatched *P. planicauda* eggs by allowing the eggs to remain in the same conditions as the adults, which were subjected to an artificially replicated version of their natural environment that was complete with wet and dry seasons (Gibson and Buley 2004).

Some of the early successes in Europe with hatching *P. arachnoides* were based on cooling the eggs at some point during the incubation process (Loehr 2001). Zovickian (2003) was able to successfully hatch both species of *Pyxis* in the United States by adapting a protocol that had been successful in hatching the eggs of *Astrochelys radiata,* which involved cooling eggs that appeared to have entered diapause. *Astrochelys radiata* is sympatric with *P. arachnoides*; therefore, it may not be coincidental that *A. radiata* eggs may also undergo diapause. Adams and Zovickian (unpubl. data) have noted that there may be a seasonal effect on whether or not *A. radiata* eggs enter a diapause phase during artificial incubation.

To try and replicate the seasonal and diurnal temperature cycles that *Pyxis* eggs encounter in nature, I set up an incubator using a foam ice chest heated with a section of Flexwatt heating tape (Flexwatt Industrial Sales, Maryville, TN, USA) coupled with a thermostat capable of two temperature set points. Initial temperature settings were based on information from the Knoxville Zoo (M. Ogle, pers. comm.), W. Zovickian (pers. comm.), and Loehr (2001). Daytime temperatures were initially set to approximately

31°C (88°F) with the temperature set to drop overnight to 26°C (78°F). Eggs from both species of *Pyxis* were incubated under the same conditions. Eggs were placed in trays filled with vermiculite dampened with water at a 1:1 ratio by weight. The trays were placed inside ventilated plastic shoeboxes and then placed into the incubator, and kept at these warm temperatures for eight to 12 weeks.

While I assumed that cooler temperatures followed by warmer temperatures serves to break the embryonic diapause in *Pyxis* (as opposed to cooler temperatures causing diapause), the role of low soil moisture followed by higher soil moisture may also play a role in this process. To simulate the cooler temperatures of the dry season, the incubation media was allowed to slowly dry out and the eggs were subjected to a cooler period of temperatures after the period of warm conditions. To achieve this, the incubating eggs were removed from the incubator (after 8–12 weeks) and allowed to remain at room temperature that fluctuated between 20–24°C (68–75°F) for approximately six to eight weeks. After this period of cooler temperatures and drier substrate, the eggs were misted and returned to the warm incubator using the same initial temperatures. The eggs and incubation media were subsequently misted on an approximately weekly basis.

RESULTS and DISCUSSION

With very few exceptions, all fertile eggs hatched successfully using this or similar protocols. The protocol was modified after some years to lower the maximum daily temperature to approximately 30.5°C (86.9°F), reduce the drop in temperature at night to approximately 26.5ºC (80°F), and shorten the length of the initial phase of incubation to four to seven weeks. Although other breeders have reported needing to cool and re-warm eggs a second time to break the diapause, it was rarely necessary in this collection.

Using this technique, 26 *P. arachnoides* (52%) hatched from 50 eggs. The majority (71%) of the 24 eggs that did not hatch failed during the first warm phase or cooling phase of incubation due to infertility. Infertile eggs are usually readily apparent within the first six weeks of incubation when eggs are candled. Infertile eggs display discolorations and opaque layers within the fluid, unlike fertile eggs that remain relatively clear prior to the cessation of diapause. Of the 10 *P. planicauda* eggs produced between 2002 and 2009, all were fertile and all hatched successfully.

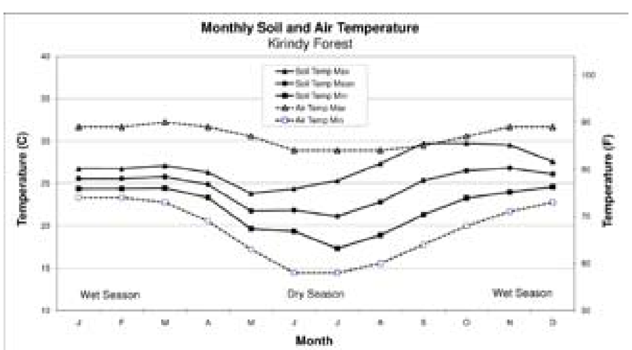

Figure 3. Monthly average daily maximum, mean, and minimum soil temperatures at Kirindy Forest, Madagascar. Monthly average daily maximum and minimum air temperatures recorded at the airport in Morondava, Madagascar.

Eggs were candled frequently during incubation to track their development. The end of diapause was determined by the sudden appearance of the embryo or the characteristic ring of blood vessels that surrounds the embryo. In *P. arachnoides*, diapause ended after an average of 25 days (n = 23; range = 13–57 days) after the eggs were returned to warmer and moister conditions. Diapause in *P. planicauda* eggs ended after an average of 14 days (n = 10; range = 0–32 days). Once embryonic development resumed, *P. arachnoides* eggs hatched in an average of 92 days (n = 23; range = 82–126 days), while *P. planicauda* eggs hatched in an average of 86 days (n = 10; range = 73–97 days).

Total incubation times ranged from 192 to 303 days (mean = 247) for *P. arachnoides* and 213 to 275 days (mean = 240) for *P. planicauda*. The lengthy total incubation periods observed in *Pyxis* are due to the extended diapause, with the actual development phase being approximately the same length as for other tortoise species. Other collections have had success hatching both *P. arachnoides* (Ogle 2006) and *P. planicauda* (Gibson and Buley 2004; Mislin and Eberling 2009) with similar warm-cool-warm cycles during incubation.

Sex ratios among the hatchlings produced here appeared to be skewed along taxonomic lines and a high proportion of the hatchlings had split or extra scutes on the carapace. Nearly all of the *P. a. brygooi* and *P. a. arachnoides* appeared to be males based on the development of secondary sexual characteristics, primarily the lengthening of the tail. However, the *P. planicauda* hatchlings appeared to be female based on tail length and about half had extra or split carapace scutes. Assuming that *Pyxis* have temperature-dependent sex determination, and that shell abnormalities may be related to high incubation temperatures, it is likely that the incubation temperatures initially used were too high. The most recent eggs have been incubated at slightly lower maximum temperatures resulting in normal carapacial scutes in the hatchlings recently produced.

Soil Temperature Data. — Given the complexity of artificial incubation in *Pyxis,* there is a need for more accurate information on incubation conditions in the wild. Fortunately there are now field data available from Madagascar that provide information on the daily and seasonal variation in soil temperatures. Temperature data were collected with HOBO® data loggers (Onset Computer Corporation, Bourne, MA, USA) at three locations: 1) Kirindy Forest, Menabe, within the native range of *P. planicauda*; 2) Village des Tortues, Ifaty, within the range of *P. a. brygooi*; and 3) Chelonian Captive Breeding Centre, Ampijoroa, outside the native range of *Pyxis,* but where *P. planicauda* eggs have been successfully incubated in ground nests.

Figure 3 displays the monthly averages of the daily maximum, minimum, and mean soil temperatures that were collected 3 cm below ground within the Kirindy Forest. The placement of the data logger by DWCT personnel reflected a potential *P. planicauda* nesting site. For comparison, monthly averages of the daily maximum and minimum air temperatures recorded at the Morondava airport (40 km away) are also included. The data show that soil and air temperatures have a much greater daily range in the dry season than the wet season. Nighttime low air temperatures in the dry season are much lower than daytime highs, which are reflected in the soil temperatures; although the soils do buffer the temperature changes to some extent. If egg deposition patterns are similar between the wild and captivity, then eggs would be laid from the middle of the wet season into the early dry season. The lowering of temperatures in the first half of the dry season and the rising of temperatures in the second half of the dry season appear to be the environmental cues that break diapause in *Pyxis*.

The data from Kirindy provide valuable information to guide incubation protocols for *P. planicauda* in captivity. Temperatures during the cooling phase of incubation should range from about 17°C (63°F) to 25°C (76°F) on a daily basis to mimic the dry season temperatures that appear to be required to break diapause. Monthly average soil temperatures during the late dry season, when the embryos resume developing, range from daytime highs near 30°C (86°F) to overnight lows near 21°C (70°F) rising to 24°C (75°F) later in the dry season. This would suggest a maximum incubation temperature of 30°C (86°F) with an overnight drop in temperature of 5–10°C (10–15°F) after diapause is broken.

The data from Village des Tortues in Ifaty (Fig. 4) were collected by the Turtle Survival Alliance (TSA) within the *P. a. brygooi* enclosure. This location shows a similar dry season cooling phase that presumably provides the environmental cue to break diapause in *P. arachnoides*. The wet season temperatures at this site are much higher than those in the Kirindy Forest, which may be related to the effect of solar radiation on the soil temperatures. During the wet season, the tropical dry forest would have a denser canopy that would block direct solar radiation, while the spiny forest in the range of *P. arachnoides* typically has more open soil and less leaf litter. Bailey (*pers. comm.*) measured surface soil temperatures at Ifaty as high as 57°C (135°F) in direct sunlight in January 2009. It is likely that nesting females would choose nesting sites that would provide a proper microclimate for incubation that would prevent eggs from overheating during the wet season temperature peaks.

Based upon the data from Ifaty, the cooling phase of incubation should range from about 20°C (67°F) to 23°C (73°F) on a daily basis. As the dry season progresses, soil temperatures increase gradually. When the rains begin in November, soil temperatures range from average highs near 32°C (90°F) to overnight lows near 27°C (81°F). In captivity, it is likely that *P. arachnoides* is more tolerant of higher incubation temperatures than *P. planicauda*. *Pyxis planicauda* does appear to be more prone to extra carapacial scutes than *P. arachnoides* when incubated at temperatures approaching 32°C (90°F).

At Ampijoroa (Fig. 5) the data logger was buried by the TSA within the *P. planicauda* enclosure where active nests were located, and where successful hatching had occurred. These data are very similar to the seasonal pattern and daily temperatures recorded at Kirindy. At Ampijoroa, however, the nighttime low temperatures in the dry season are not as low as in the Kirindy Forest. Overnight lows averaged only about 21°C (71°F), but daytime highs still reached 25°C (76°F). It appears that the temperatures were still low enough to break diapause in *P. planicauda,* as evidenced by the many successful nests at the Chelonian Captive Breeding Centre (Razandrimamilafiniarivo et al. 2000).

Of the 19 successful hatchings of *P. planicauda* at the Chelonian Captive Breeding Centre between 1995 and 1999, 18 of the eggs hatched between 10 November and 26 December (Razandrimamilafiniarivo et al. 2000). By counting backwards from the hatching dates at Ampijoroa, it can be estimated that embryonic development there resumed in late August and September. Figure 5 shows a marked increase in soil temperatures during that time period, lending support to the theory that cool temperatures followed by rising temperatures cause *Pyxis* eggs to break diapause and resume development. It is also interesting to note that at the point in the dry season when temperatures are rising, there is very little precipitation; therefore, an increase in soil moisture may not play a role in ending

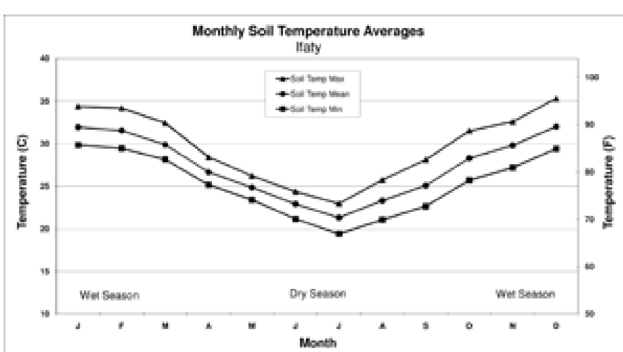

Figure 4. Monthly average daily maximum, mean, and minimum soil temperatures at the Village des Tortues in Ifaty, Madagascar.

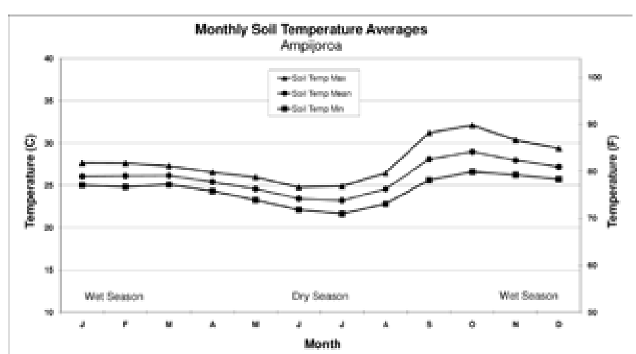

Figure 5. Monthly average daily maximum, mean, and minimum soil temperatures at the Chelonian Captive Breeding Centre in Ampijoroa, Madagascar.

diapause in *P. planicauda* eggs. In my breeding colony, the eggs of *P. planicauda* required about 86 days to develop once diapause was broken and embryonic development resumed, with eventual successful hatching (Fig. 6).

Ex-situ Population Management. — The Association of Zoos and Aquariums (AZA) maintains the North American Regional Studbooks for *P. planicauda* and *P. arachnoides* (Castellano and Behler 2003, 2004; Ogle 2009a, b) as an *ex-situ* conservation action for these critically endangered tortoises. The studbooks track the captive population and maintain birth and death records. Breeding recommendations for the captive population are included in the Species Survival Plans (SSP) and are based on genetic and demographic analyses (Ogle and Sullivan 2013a, b). Relatively few private collections are included in the studbooks and the SSPs, which is unfortunate, since the majority of *Pyxis* in the U.S. are in private collections.

In order for *ex-situ* assurance colonies to succeed in the long term, a base of genetic diversity must be preserved by producing offspring from the wild caught animals exported from Madagascar in 2000 and 2001. Mortality of the wild caught animals over time will continue to reduce the number of potential genetic founders. Juvenile *Pyxis* are rarely seen in the commercial trade. Considering the large numbers of *P. planicauda* and *P. arachnoides* that have been imported into the U.S., captive born offspring should be commonly available in the commercial trade if private collections were successfully breeding *Pyxis*. It is likely that many collections simply are not able to produce fertile eggs, or cannot hatch fertile eggs due to the complex incubation requirements.

Private collections must be encouraged to participate in the AZA studbook program to increase the number of potential founders in the managed population. Whenever possible, information on breeding techniques and incubation strategies must be shared among institutions and private collections in order to increase reproduction of these species in captivity.

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Résumé

Les tortues du genre *Pyxis* ont des territoires restreints le long de la côte sud-ouest de l'île de Madagascar. Le genre comprend *Pyxis planicauda* et *Pyxis arachnoides*. Les deux espèces sont toutes classées en Annexe I du CITES et ont été évaluées En Danger Critique d'Extinction pour la Liste Rouge de l'UICN en 2008. Un grand nombre d'individus des deux espèces ont été exportés de Madagascar en 2000 et 2001. Un taux de reproduction naturellement bas et un accroissement de la vitesse de la perte d'habitat ont attiré l'attention sur le statut de ces espèces à l'état sauvage et dans les groupes en captivité. Les deux espèces sont natives des forêts sèches tropicales avec une saison humide et une saison sèche prononcées. La compréhension des conditions climatiques et environnementales rencontrées par les deux espèces dans la nature est essentielle à l'établissement d'un programme de reproduction en captivité efficace. Reproduire les cycles saisonniers et maintenir la période d'estivation durant la saison sèche apparaissent importants pour une reproduction réussie en captivité. Les œufs de *Pyxis* passent typiquement par une diapause embryonnaire prolongée qui semble correspondre à la longue saison sèche de leur lieu d'origine. Des taux d'éclosion élevés ont été obtenus dans

Figure 6. Captive-born hatchling Spider Tortoise, *Pyxis arachnoides brygooi* (**left**) and Flat-tailed Tortoise, *Pyxis planicauda* (**right**). Photos by Daniel Pearson.

de nombreuses colonies en captivité par l'exposition d'œufs fertiles à des conditions plus fraîches et plus sèches. Le retour à des conditions plus chaudes et plus humides semble alors déclencher voire réinitialiser le développement de l'embryon. Une diapause embryonnaire contrôlée par des indicateurs environnementaux peut aider à synchroniser ou retarder l'éclosion jusqu'à la prochaine saison humide. Des données sur la température du sol recueillies dans trois sites à Madagascar sont utilisées pour établir les protocoles d'incubation dans les groupes en captivité. Les mesures de conservation actuelles comprennent le stud-book de AZA et les Plans de Survie d'Espèces. Le succès à long terme des colonies souches nécessitera la coopération continue entre les institutions zoologiques et les éleveurs privés.

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