

Activity Budget of the Impressed Tortoise, *Manouria impressa* (Günther, 1882), in Phu Luang Wildlife Sanctuary, Thailand

PRATYAPORN WANCHAI^{1,2}, CRAIG B. STANFORD³, ART-ONG PRADATSUNDARASAR², KAMPANAT THARAPOOM⁴ AND KUMTHORN THIRAKHUPT^{2*}

¹Biological Science Program, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND

²Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND

³Department of Anthropology, University of Southern California, Los Angeles, CA 90089, USA

⁴Department of Biology, Faculty of Science, Silpakorn University, Nakhon Pathom, 73000, THAILAND

* Corresponding author. E-mail: kumthorn.t@chula.ac.th

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ABSTRACT.— The activity budget of the impressed tortoise, *Manouria impressa* (Günther, 1882), was studied at Phu Luang Wildlife Sanctuary, Loei Province, Thailand, from January 2010 - October 2011. A total of fourteen *M. impressa* individuals, consisting of ten adults (five males and five females) and four juveniles, were radio-tracked. Hiding was the most frequently observed activity in both the wet and dry seasons. The frequency of active behavior in the wet season was higher than in the dry season. Tortoises were found to be active at ambient temperatures ranging from 12.0 °C - 30.0 °C, and a relative humidity from 60% - 100%. The year-round averages for air temperature and relative humidity for activity in males, females and juveniles were not significantly different. For all individuals, there was no significant difference in temperature between each active behavior. Two cases of nesting were also observed.

KEY WORDS: Radio-tracking, home range, *Manouria impressa*

INTRODUCTION

The impressed tortoise, *Manouria impressa* (Günther, 1882) (Reptilia: Testudines), is distributed throughout the montane areas of Southeast Asia, including Myanmar, Thailand, Laos, Vietnam, Cambodia and Malaysia (Ernst and Barbour, 2001, Fritz and Havas, 2007). Within Thailand this species is found in the mountains of northern, northeastern and western Thailand (Thirakhupt and van Dijk, 1994; Cox et al., 1998). The IUCN Red List (2000) classifies *M. impressa* as a vulnerable species and it is protected under Appendix II of CITES. In Thailand, the impressed tortoise is a protected species under wildlife conservation law whilst the Office of Natural Resources and

Environmental Policy and Planning have classified it as an endangered species.

This species appears to be rare in its natural habitat due to habitat destruction, poaching for food and collecting for the pet trade (van Dijk and Palasuwan, 2000). However, it is difficult to maintain in captivity and has only recently been captive-bred. The natural history of *M. impressa* is poorly known, and most recently accepted data have been based on short term field studies, with no long term study of its ecology in the wild being available. McMorris and Burns (1975) reported that *M. impressa* spends much of its time hiding under leaf litter, and Nutaphand (1979) reported that they are active during the rainy season (May - October) when they eat grass shoots and look for mates. In contrast,

Weissinger (1987) reported the species is only active during the rainy season and Chan-ard et al. (1996) reported that, for the *M. impressa* kept in an enclosure at Phu Luang Wildlife Research Station, they usually entered brumation during November and emerged after the first substantial rain, which usually falls in late February. Based on a study of six *M. impressa* (four males and two females) in the Central Cardamom Protected Forest on the Cardamom Mountains in southwest Cambodia from September 2007 - March 2008, Koulang (2008) reported that the mean ambient temperature near the hiding place was $23.9 \pm 1.8^\circ\text{C}$ (range of 20.0°C - 29.2°C), whilst that at the microhabitat of the hiding place was $20.6 \pm 1.0^\circ\text{C}$ (range of 18.0°C - 22.7°C). Normally, the microhabitat temperature is significantly lower compared to the ambient temperature of the hiding places.

The purpose of this study was to describe the annual activity patterns and any differences in activity between the wet and dry seasons, and the preferred microhabitat of *M. impressa*. This study provides new basic information on its ecology and behavior that could be used for captive breeding and conservation management.

MATERIALS AND METHODS

Study Sites.— The study was carried out in Phu Luang Wildlife Sanctuary (PLWS), located in the south of Loei Province in the Northeast of Thailand at $17^\circ 3' - 17^\circ 24' \text{N}$ and $101^\circ 16' - 101^\circ 21' \text{E}$. PLWS covers an area of 897 km². The climate is characterized by a rainy season (May – October) and a dry season that is further subdivided into the cold-dry (November – February) and hot-dry subseasons (March – April). The sanctuary contains various forest

types, including dry deciduous dipterocarp, mixed deciduous, dry evergreen, montane evergreen and coniferous forests, plus tropical grassland. This study was conducted at 900 – 1400 m above mean sea level (amsl) (Chan-ard et al., 1996).

Radiotelemetry.— Animals were radio-tracked from January 2010 through to October 2011 inclusive. A total of 14 *M. impressa* individuals comprised of ten adults (five males and five females) and four juveniles (Table 1) were tracked using radio-transmitters (148 MHz). The post-attachment transmitter weights for adults and juveniles were 35 g and 25 g, respectively, and so did not exceed the recommended guideline of 5% of the body weight (White and Garrott, 1990). Each tortoise was located 6 – 10 times per month by direct observation, using an ATS receiver (Model FM16) and a handheld ATS 3 element folding Yagi antenna. When a tortoise was located, the activity when first seen was recorded in terms of being active or inactive, where the active state was defined into one of the seven categories of (1) walking, (2) eating, (3) basking (staying on the forest floor, fully exposed to the sun, usually with limbs spreading wide and neck stretching out), (4) resting (immobile; staying in the open or in partial cover, plastron touching the ground, neck and limbs mostly extended), (5) soaking (sitting in a shallow stream or swamp), (6) courting/mating (male following a female, circling around her, and mounting or attempting to mount), and (7) nesting (female building or guarding a nest). Individuals hiding under leaf litter or rocks and fallen branches were classified as “inactive”.

TABLE 1. Home range sizes and specimen data for 13 *M. impressa* radio tracked individuals at Phu Luang Wildlife Sanctuary.

Sex or age class	n	Carapace length (cm)	Plastron length (cm)	Body mass (kg)
Male	5	25.8 ± 1.9	24.9 ± 2.5	2.5 ± 0.6
Female	5	27.1 ± 2.4	25.6 ± 2.8	3.0 ± 0.7
Juvenile	4	18.0 ± 1.3	17.8 ± 1.3	1.2 ± 0.2

n = number of tortoises

Analysis of the data.— The percentage of active and inactive periods were estimated and categorized with respect to whether in the wet (May – October) or dry (November – April) season. The difference in the percentage of active and inactive periods between the sexes, age classes and between the wet and dry seasons were analyzed using ANOVA, accepting significance of differences at the $p < 0.05$ level. The mean annual temperature, mean relative humidity and rainfall at the study site were obtained from the nearby ranger weather station (1–3 km from the field site). In addition, the ambient temperature and relative humidity were also recorded at the position where tortoises were located using a thermo-hygrometer at 1 m above the forest floor. The differences in mean ambient temperature and relative humidity between adults and juveniles, and between the wet, cold-dry and hot-dry seasons were analyzed using ANOVA using the SPSS 11.5 for Windows software and accepting significance of differences at the $p < 0.05$ level.

RESULTS

The air temperature, as obtained from nearby ranger weather station ranged from 6.5 – 33.0 °C (Mean ± SE = 19.9 ± 1.72 °C)

with an average temperature during the wet, cold-dry and hot-dry seasons of 21.7 ± 0.3 °C, 15.3 ± 0.4 °C and 22.8 ± 0.5 °C, respectively. The relative humidity at the study site ranged from 60 – 100%. The average (± SE) relative humidity in the wet, cold-dry and hot-dry seasons were 85.2 ± 0.4%, 66.2 ± 0.4% and 78.6 ± 0.6%, respectively. The average air temperature and relative humidity during the rainy and hot-dry seasons were both significantly higher than those in the cold-dry season (ANOVA, $p < 0.05$).

The air temperature and relative humidity were also recorded at the precise position where tortoises were located, so as to allow the importance of any potential microhabitat-dependent variations to be evaluated. The mean ambient temperature and relative humidity for each activity are shown in Table 2. Active tortoises were found at ambient temperatures ranging from 12.0 – 30.0 °C (mean ± SE = 22.8 ± 0.14 °C) and a relative humidity from 60 – 100% (mean ± SE = 82.2 ± 0.5%). However, large numbers of individuals were inactive (hiding) in the same period when the temperature and humidity ranged from 11.7 – 27.5 °C (mean ± SE = 20.10 ± 0.13%) and 60 – 100% (mean ± SE = 75.7 ± 0.4%), respectively. For all individuals, there was no significant difference in the temperature between each active behavior. However,

TABLE 2. Mean (\pm SE) air temperature and relative humidity (RH) during *Manouria impressa* activity in Phu Luang Wildlife Sanctuary (PLWS), Loei Province, Thailand from January 2010 to October 2011 inclusive.

Sex or age class (n)	Activity																							
	Walking			Resting			Eating			Basking			Soaking			Mating			Nesting			Hiding		
	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)	Temp	RH	(n)
Male (n = 5)	23.2 \pm 0.2 (N = 38)	82.6 \pm 1.2 (N = 38)	22.0 \pm 0.3 (N = 54)	81.3 \pm 1.3 (N = 54)	23.4 \pm 0.6 (N = 9)	84.2 \pm 2.0 (N = 9)	24.4 \pm 0.8 (N = 5)	79.0 \pm 4.5 (N = 5)	22.2 \pm 0.5 (N = 25)	85.0 \pm 1.5 (N = 25)	23.6 \pm 1.0 (N = 8)	79.5 \pm 2.0 (N = 8)	22.9 \pm 1.5 (N = 4)	82.5 \pm 3.2 (N = 4)	19.6 \pm 0.2 (N = 271)	77.0 \pm 0.7 (N = 271)								
Female (n = 5)	23.6 \pm 0.4 (N = 39)	80.6 \pm 1.4 (N = 39)	22.7 \pm 0.3 (N = 51)	82.1 \pm 1.1 (N = 51)	23.7 \pm 0.7 (N = 12)	82.1 \pm 1.1 (N = 12)	25.2 \pm 1.0 (N = 5)	79.0 \pm 3.7 (N = 5)	21.7 \pm 0.4 (N = 19)	84.7 \pm 1.0 (N = 19)	23.6 \pm 1.0 (N = 8)	79.5 \pm 2.0 (N = 8)	22.9 \pm 1.5 (N = 4)	82.5 \pm 3.2 (N = 4)	19.7 \pm 0.2 (N = 319)	74.8 \pm 0.6 (N = 319)								
Juvenile (n = 4)	22.7 \pm 0.8 (N = 13)	83.3 \pm 3.5 (N = 38)	22.9 \pm 0.6 (N = 14)	80.1 \pm 1.9 (N = 14)	24.0 \pm 0.7 (N = 4)	82.8 \pm 2.3 (N = 4)	-	-	23.0 \pm 0.6 (N = 8)	81.8 \pm 3.7 (N = 8)	-	-	-	-	21.9 \pm 0.3 (N = 141)	75.1 \pm 0.9 (N = 141)								

N = total number of observations

basking tended to occur at the highest mean ambient temperatures (25.2 °C and 24.4 °C for males and females, respectively). The mean air temperature and relative humidity during the observed hiding behavior was significantly lower than that during the periods of activity (ANOVA, $p < 0.05$).

Activity Level.— There were no significant differences in activity budgets between males and females ($p = 0.48$) but there were significant differences between adults and juveniles. Adults tended to be more active than juveniles either both all year-round ($p = 0.04$) and in the wet season ($p = 0.02$) but not in the dry season (Table 3).

In both the wet and the dry seasons, the majority of individuals observed were inactive. However, the frequency of active behavior in the wet season was higher than in the dry season (all $p < 0.05$). There were no significant differences between the activity level of males and females in the wet season ($p = 0.52$) but males tended to be more active than females and juveniles during the dry season (Table 3).

Activities varied by season (Fig. 1). Hiding was the most frequently observed activity for tortoises in all seasons, followed by walking and resting. During the cold-dry season (November – February), most individuals were hiding and no movement was observed for any individual during December and January. Most tortoises remained hidden until February when they emerged from their shelters as the first rain arrived (Fig. 2). However, if the rain did not continue for several consecutive days, the tortoises remained in their shelter and did not emerge until the subsequent hot-dry season. In the hot-dry season (March and April), most of the tracked tortoises emerged from their shelter and became active. Substantial rain arrived in April and continued for several days, and mushrooms, the main diet of *M. impressa* in this study, were available at this time. Of the activities; walking, resting, basking, eating and mating were the main activity observed in this month. In May, which is usually the first month of the rainy season, many species of mushrooms were available. Activity levels, and

TABLE 3. Proportion of active and inactive *Manouria impressa*, as percentage of observations, all year-round and in the wet or dry season in Phu Luang Wildlife Sanctuary (PLWS)

Sex or age class (n)	Year-round		Wet season (May-October)		Dry season (November-April)	
	Active (%)	Inactive (%)	Active (%)	Inactive (%)	Active (%)	Inactive (%)
Male (n = 5)	33.1 (N = 153)	67.0 (N = 310)	44.6 (N = 116)	55.4 (N = 144)	18.2 (N = 37)	81.8 (N = 166)
Female (n = 5)	31.2 (N = 145)	68.8 (N = 320)	43.0 (N = 116)	57.0 (N = 154)	14.9 (N = 29)	85.1 (N = 166)
Juvenile (n = 4)	21.8 (N = 41)	78.2 (N = 147)	29.6 (N = 29)	70.4 (N = 69)	13.3 (N = 12)	86.7 (N = 78)

N = total number of observations

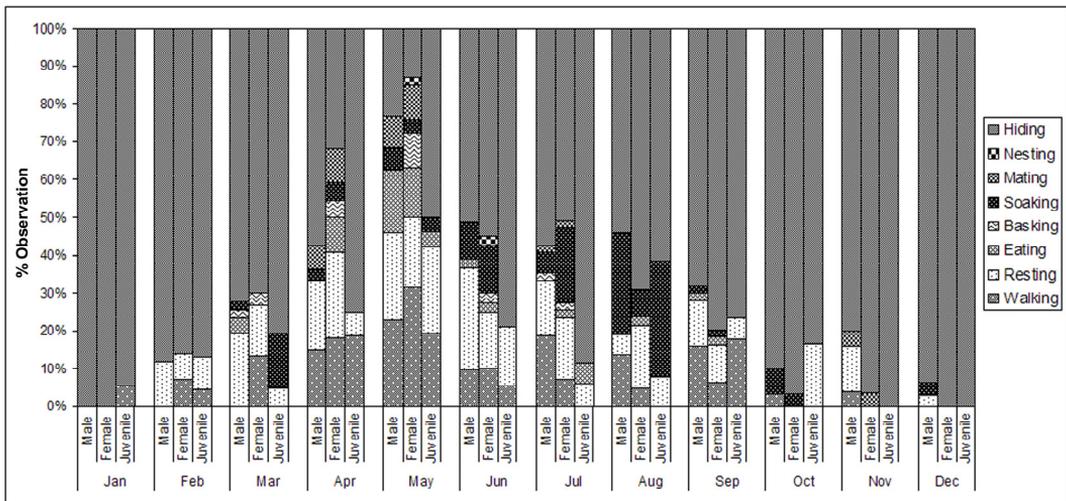


FIGURE 1. Frequencies of the different observed activities of male, female and juvenile *Manouria impressa* all year-round in Phu Luang Wildlife Sanctuary (PLWS), Loei Province, Thailand.

especially walking, resting, eating, basking and mating, also peaked in this month. By late September tortoises became less active, which coincides with when many species of mushrooms were no longer available. In October, when the temperatures were lower and mushrooms were not available, most tortoises became inactive.

Types of activities.— Feeding behavior was observed during March – September but peaked in May, when a high abundance and diversity of mushrooms were available. *M. impressa* in this study fed on at least eight different species of forest mushrooms and were not found to consume any other vegetation or fruit. Basking behavior was only seen in adults and was observed from March through July. Soaking was found in all seasons but the proportion of observations of this behavior was highest in the rainy season during July and August. Courting and mating were observed in all seasons but peaked in the rainy season. At the beginning of the rainy season in May 2010, one male was found mating with a

female and 4 days later the same male was found mating with another female. Re-mating between the same male and female was also observed but in different years and not in the same year.

Two cases of nesting were also found in this study. Nest building was first seen on May 4th, 2011, where a female was collecting plant materials next to the nest, back sweeping while backing towards the nest. On May 10th the female was still collecting new materials for the nest building and on May 16th she was still beside the nest. On May 19th the female had left the nest and the nest was investigated. The nest was situated in bamboo forest on a hill slope at 1375 m amsl. Its site was close to a bamboo grove and was shaded from direct sunlight. Most nest materials consisted of dry bamboo leaves and the female also used this material to cover her eggs. The diameter of the nest was 100 cm and the height was 25 – 30 cm. Damaged and broken eggs were found in the nest and the clutch size was estimated at 8 – 10 eggs. The second nest was found while a female

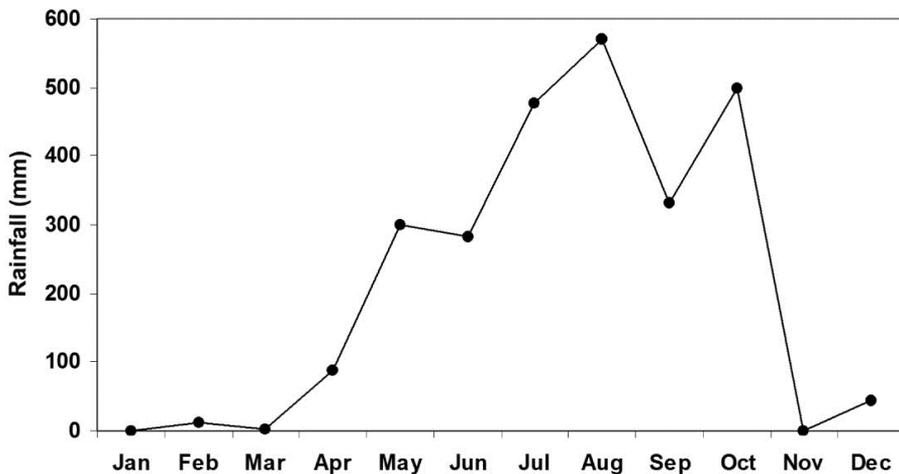


FIGURE 2. Total rainfall at Phu Luang Wildlife Sanctuary (PLWS), Province, Thailand from January 2010 - October 2011.

was guarding it on June 28th, 2011. The female sat on the nest and displayed aggression towards the observers. The nest was located in montane forest mixed with bamboo on a sloped area near the top of the mountain at 1400 m amsl. The nest site was similar to that of the first female, but the composition was quite different, consisting of small sticks and leaf litter. The diameter of the nest was about 100 cm and the height was 40 – 45 cm. Clutch size was estimated at 8 – 10 eggs, but all the eggs were broken. The female did not guard the nest the next day but still spent time near to the nest, 5 to 10 m away. Both nests were presumably destroyed by predators, since eggshells were found inside and beside the nest.

DISCUSSION

M. impressa in this study were active when the ambient temperature and relative humidity ranged from 12.0 – 30.0 °C (mean = 22.8 °C) and 60 – 100% (mean = 82.2%), respectively, and they were inactive at temperature and humidity ranges from 11.7

– 27.5 °C (Mean = 20.1 °C) and 60 – 100% (Mean = 75.7%), respectively. Similarly, Koulang (2008), who studied six *M. impressa* at the Central Cardamom Protected Forest on the Cardamom Mountains of southwest Cambodia from September 2007 – March 2008 inclusive, reported that the range of ambient temperature and relative humidity near the position where *M. impressa* were located was 20.0 – 29.2 °C (Mean = 23.9 °C) and 60 – 96% (Mean = 85%), respectively. Although most activities occurred in every season, there were seasonal differences in the relative frequencies of activities. Hiding is the main activity of tortoises in all seasons. This result was similar to that reported by Koulang (2008) in that *M. impressa* spent more time hiding than walking or any other activities. Our results also agreed with that reported by McMorris and Burns (1975) and Weissinger (1987), who reported that *M. impressa* spent most of its time hiding under leaf litter and was active during the rainy season.

There were no nocturnal observations in this study. However, Koulang (2008) suggested that *M. impressa* may be more active at night. Also Chan-Ard et al. (1996) reported that *M. impressa* seems to be more active at twilight and during rain showers. For adult tortoises, feeding occurred more frequently in the wet season, during March-September, especially in May. This difference presumably reflects the availability of food. Seasonal change may affect food plant availability for tortoises. Many species of mushrooms were easily found in May – July. In contrast, during the dry season, there are very few edible mushrooms available. The first observation of basking occurred in March, perhaps due to their attempt to raise or regulate body temperature after the hiding period. The tortoise might require more basking time to reach a body temperature that would enable them to feed and digest food (Joshua et al., 2010). Elevating body temperatures via basking should enhance the feeding rate (Spencer et al., 1998), digestion, metabolism and activity, all of which would help tortoises capitalize on the food available in the spring. For juveniles, they simply did not venture into open areas and that may be a strategy for predator avoidance. However, the hiding places of juveniles were frequently located in unshaded areas where sunlight can enter during the day and may provide basking opportunities.

The nesting ecology of *M. impressa* is not well documented. No previous study has documented natural nests, with most studies based upon captive tortoises. McMorris and Burns (1975) found that a female laid 17 eggs while Cox et al. (1998) reported that females laid about a dozen eggs per clutch. The eggs are laid in a shallow cavity and then covered with leaves. Only one example of nesting ecology in a natural habitat of this

genus was previously available, where it was reported that *M. emys emys* nesting occurred in July during the monsoon period (Mortensen, 2004), where the nest was situated on top of a small hill in the secondary forest, with half the perimeter being the edge of a steep slope and the rest moderately sloped to almost flat. Both nests of *M. impressa* in this study were located on a sloped area and near bamboo grove. This location may have been selected to ensure that the nest was protected against flooding and runoff during heavy rainfalls.

A congeneric species, *M. emys phayrei*, appears to be different in some activity patterns. Wanchai (2007) reported that during the wet season, (May - October) *M. emys phayrei* adults were mostly found eating. This too may be because of food availability and *M. emys phayrei* eats many kinds of plant foods which were easily found in the forest throughout the rainy season, especially the bamboo shoot. In addition, many kinds of mushroom at PLWS which are the main diet of *M. impressa* are available for only a short term period during May to July. Therefore, the longer inactive period of *M. impressa* should be suitable for their survival as they can save their energy during food limitation.

During the cold-dry season, both adult and juvenile tortoises spent the majority of their time hiding. This may be an adaptation to the lack of resources in the dry season (November - April). The inactive period is usually interpreted as a mechanism for energy conservation that reduces metabolic rate when little food is available (Gregory, 1982). Activity patterns of turtles and tortoises influenced by seasonal change and other environmental factors have been reported by several authors. In cold months, the yellow-margined box Turtle, *Cuora flavomarginata* is less active and reduces

foraging (Lue and Chen, 1999). The extreme continental climate of central Asia (hot and dry summer followed by a very cold winter) limits the activity of the steppe tortoise, *Testudo horsfieldi*, to within the spring only (Lagarde et al., 2003).

In this study, in late February (end of the cold-dry season) when the first rain arrived and the temperature rose, some *M. impressa* tortoises emerged from their hiding places. Rain might alter established periods of activity and tortoises respond by becoming active. However, mushrooms were not available during this month, and most tortoises retreated into their shelter. This result is similar to that reported by Chan-ard et al. (1996) who observed that *M. impressa* kept in the enclosure at PLWS usually emerged from brumation after the first substantial rain. The beginning of activities following the first rain is also reported in *Gopherus berlandieri* (Rose and Judd, 1975) and the Egyptian tortoise, *Testudo kleinmanni* (Geffen and Mendelssohn, 1988). Most tortoises were active during April due to two major factors: rising temperature and availability of mushrooms.

M. impressa at PLWS used hiding places, such as burrows, under fallen branches, under rocks and shallow streams, to avoid extreme heat. Use of burrows and shelters has been experimentally demonstrated to reduce evaporative water loss in many reptiles. The reason for the observed *M. impressa* soaking in shallow streams might not only be associated with thermoregulation. Many times tortoises were observed to be submerged in shallow streams or swamps covered by litter with only their nose exposed. From this position it is camouflaged and so potentially may be to avoid detection by predators. Another possible indirect benefit is that being submerged might also help get rid of ticks.

All of the tortoises in this study had many ticks on their carapace and softer parts of the neck and legs. All the examined ticks (20) were found to be *Amblyomma geoemydae*, a widespread tortoise and turtle tick in South and Southeast Asia (Robbins et al., 2006). Mortensen (2004) suggested that submersion in *M. emys emys* might help it to reduce the tick load.

In conclusion, this study provides new information of the life history of *M. impressa* that has refined our understanding of this species. Because Impressed tortoises are difficult to maintain in captivity, with almost one hundred percent mortality during the adaptation process to captivity, then data from their natural habitat are important. Such data would likely be of great benefit in, if not essential to, establishing suitable husbandry protocols and conservation programs.

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LITERATURE CITED

- Chan-ard, T., Thirakhupt, K. and van Dijk, P.P. 1996. Observations on *Manouria impressa* at Phu Luang Wildlife Sanctuary, northeastern Thailand, Chelonian Conservation and Biology. 2: 109-113.
- Cox, M., van Dijk, P.P., Nabhitabhata, J. and Thirakhupt, K. 1998. A photographic Guide to Snakes and other Reptiles of Thailand and South-East Asia. Bangkok: Asia Books. pp. 144.
- Ernst, C.H. and Barbour, R.W. 2001. Turtles of the World. Washington, D.C: Smithsonian Institution Press. pp. 313.
- Fritz, U. and Havas, P. 2007. Checklist of Chelonians of the World. Vertebrate Zoology 57: 149-368.
- Geffen, E. and Mendelssohn, H. 1988. Home range use and seasonal movements of the Egyptian tortoise (*Testudo kleinmanni*) in the northwestern Negev, Israel. Herpetologica. 44: 354-359.
- Gregory, P.T. 1982. Reptilian hibernation. In: Gans, C. and Pough, F.H. (Eds.). Biology of the Reptilia. New York: Academic Press. pp. 53-154.
- IUCN Red List of Threatened Species (2000). Impressed Tortoise (*Manouria impressa*) <http://www.iucnredlist.org/apps/redlist/search>, Published 2000. Accessed 5 March 2012.
- 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.
- Koulang, C. 2008. Behavioural Ecology of Impressed Tortoises, *Manouria impressa* (Günther, 1882) Via Radio Telemetry Study. MSc thesis, Department of Biodiversity Conservation, The Royal University of Phnom Penh. pp. 72.
- Lagarde, F., Bonnet, X., Corbin, J., Henen, B., Nagy, K., Mardonov, B. and Naulleau, G. 2003. Foraging behavior and diet of an ectothermic herbivore: *Testudo horsfieldi*. Ecography. 26: 236-242.
- Lue, K.Y. and Chen, T.H. 1999. Activity, Movement Patterns, and Home Range of the Yellow-Margined Box Turtle (*Cuora flavomarginata*) in Northern Taiwan. Journal of Herpetology. 33: 590-600.
- MCMorris, J.R. and Burns, D.M. 1975. Notes on *Geochelone impressa*. Chelonia. 2: 5-7.
- Mortensen, K.H. 2004. The tortoise *Manouria emys emys*: behavior and habitat in the wild. MSc thesis, University of Southern Denmark. pp. 100.
- Nutaphand, W. 1979. The Turtles of Thailand. Bangkok: Siamfarm Zoological Gardens. pp. 222.
- Robbins, R.G., Phong B.D., McCormack, T., Behler, J.L., Zwartepoorte, H.A., Hendrie, D.B., and Calle, P.P. 2006. Four new host records for *Amblyomma geoemydae* (Cantor) (Acari: Ixodida: Ixodidae) from captive tortoises and freshwater turtles (Reptilia: Testudines) in the Turtle Conservation Center, Cuc Phuong National Park, Vietnam. Proceedings of the Entomological Society of Washington. 108: 726-729.
- Rose, F.L. and Judd, F.W. 1975. Activity and Home Range Size of the Texas Tortoise, *Gopherus berlandieri*, in South Texas. Herpetologica. 31: 448-456.
- Spencer, R.J., Thompson, M.B. and Hume, I.D. 1998. The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*. Comparative Biochemistry and Physiology. 121: 341-349.
- Thirakhupt, K. and van Dijk, P.P. 1994. Species diversity and conservation of turtles of western Thailand. Natural History Bulletin of the Siam Society. 42: 207-259.
- UNEP-WCMC Species Database: CITES-Listed Species. Impressed Tortoise (*Manouria impressa*) <http://www.cites.org/eng/resources/species.html>, Published 1 July 1975. Accessed 5 March 2012.
- Van Dijk, P.P. and Palasuwan, T. 2000. Conservation status, trade, and management of tortoises and freshwater turtles in Thailand. In: van Dijk, P.P., Stuart, B.L., and Rhodin, A.G.J. (Eds.). Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs. 2: 137-144.
- Wanchai, P. 2007. Radio-telemetry Study of Home Range Size and Activities of the Black Giant Tortoise, *Manouria emys phayrei* (Blyth, 1853). MSc thesis. Department of Biology, Faculty of Science, Chulalongkorn University, Thailand. pp. 84.
- Weissinger, H. 1987. Maintenance of *Manouria impressa*, Günther (1882). Elaphe. 9: 9-10.
- White, G. and Garrott, R. 1990. Analysis of Wildlife Radio-tracking Data. San Diego, Academic Press. pp. 383.