The tortoise *Manouria emys emys*: behaviour and habitat in the wild

M. Sc. Thesis

by

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Dedicated to the memory of

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i. Landskildpadden *Manouria emys emys*: naturlig adfærd og habitat

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Resumé

Landskildpadden *M. e. emys* er som mange af dens beslægtede asiatiske arter udryddelsestruet. Gennem de seneste årtier har udviklingen i Sydøstasien resulteret i et større pres på bestandene som følge af skovrydning og indfangning til kæledyrsindustrien.

Fælles for de fleste asiatiske skildpaddearter er at der vides meget lidt om deres naturlige adfærd og krav til habitattyper. Dette gør sig også gældende for *M. e. emys*, om hvilken der indtil nu kun er publiceret én artikel af begrænset omfang (Lambert and Howes, 1994).

Målet med dette specialeprojekt var således at øge vores viden omkring adfærd og habitat i naturen. Herunder artens eventuelle tilpasningsevner i et af mennesket forstyrret habitat. Feltarbejdet foregik i Tabin Wildlife Reserve beliggende på østkysten af det nordlige Sabah, Borneo. Området består af 120.000 ha lavlands regnskov, som for størstedelen har været et tidligere skovbrugsområde. Centralt beliggende i området er et 15.000 ha uberørt område (Core Area) omgivet af det resterende sekundære regnskov. Al skovning ophørte i 1984 og området er således under regenerering.

To perioder på i alt seks måneder, fordelt mellem foråret 2002 og foråret 2003 udgjorde feltarbejdet. Her fandt jeg 13 individer, hvoraf 12 blev udstyret med radiosendere og fulgt mellem 1 og 67 dage. Skildpaddernes geografiske positioner blev registreret vha. en håndholdt GPS modtager og gemt til senere analyse af daglige bevægelser og home range. Daglige bevægelser varierede mellem 0 og 390 meter i lige linie mellem to punkter. Enkelte skildpadder udstyredes foruden radiosender med en trailer tråd, som blev trukket ud efter skildpadden. Tråden blev indsamlet og længden målt, hvorved det viste sig at distancen reelt tilbagelagt var gennemsnitlig 87% længere end den lige linie. Dette skyldes områdets meget kuperede terræn og skildpaddens afvigelser fra den lige linie mellem to punkter. Ud fra GPS koordinaterne er home range størrelsen blevet estimeret for otte af de moniterede dyr. Estimaterne ligger mellem 0,01 km^2 og 1,81 km^2 baseret på en parametrisk metode, som beregner en 95% konfidens ellipse omkring koordinaterne.

Skildpaddernes fødevalg blev studeret ved direkte observationer, eller hvis tydelige spor (eks. fodspor eller bidemærker) af en fouragerende skildpadde var til stede. I alt blev 22 planter registreret, hvoraf 15 tilhørte slægten *Alocasia*. To svampe blev spist af et af individerne men

arterne kunne ikke identificeres, da svampene var enkeltstående og blev slugt hele. Derud over blev urter af familierne Begoniaceae, Melastomataceae, Marantaceae, Woodsiaceae og Zingiberaceae registreret med en enkelt plante fra hver. Der blev ikke registreret animalske fødeemner og ingen indtagelse af vand. *M. e. emys* er ud fra resultaterne af denne undersøgelse herbivore generalister med en mulig specialisering i *Alocasia*. Et interessant aspekt af denne specialisering er at *Alocasia* planter indeholder calcium oxalater, som fremkalder stærke allergiske reaktioner hos eks. køer, får eller hunde. Ved indtagelse af calcium oxalater hæver svælget, hvilket i yderste konsekvens kan medføre kvælning. Der blev ikke konstateret sådanne effekter på skildpadderne.

Aktivitets mønsteret viste sig meget svært at kvantificere ud fra direkte observationer. Skildpadderne holdt ganske enkelt op med deres igangværende aktivitet, så snart min tilstedeværelse blev dem klar. En ny metode blev derfor taget i brug, hvor en aktivitetsmåler (ActiTrac®) blev limet på skjoldet af to skildpadder. Skildpadderne viste stor individuel variation i total aktivitet. En lå stille i 17 dage kun afbrudt af 40 minutters fouragering, mens den anden typisk vandrede op til flere hundrede meter om dagen. For begge individer fandtes en foretrukken aktivitets periode i de tidlige eftermiddagstimer. På dage med maksimaltemperaturer overstigende ca. 29°C i skyggen sås dog ofte en inaktiv periode midt på dagen.

Temperatur- og luftfugtighedsmålinger viste, at skildpadderne oftest foretrak et mikroklima omkring 26°C med en relativ luftfugtighed overstigende 90%. Gemmesteder såsom under væltede træer eller i meget tæt bevoksning var klart foretrukne.

Kvalitative vurderinger af habitatet viser at *M. e. emys* trives i de sekundære såvel som primære skovområder. Faktisk blev de fleste skildpadder fundet i de sekundære områder af reservatet, hvilket dog er et resultat af større søgeaktivitet i disse områder fra min side. Det fortæller dog stadig, at skildpadderne trives i de tidligere skovbrugsområder. To ting syntes at være nødvendige for forekomsten af skildpadder; skygge og høj luftfugtighed.

En redebygning blev observeret i juni 2002. Reden blev konstrueret over tre dage, hvorefter hunnen forlod stedet. Den blev senere gravet op af et formodentligt mindre pattedyr, og indholdet af alle 10-12 æg blev spist.

ii. Abstract

During six months of field work in Tabin Wildlife Reserve, Sabah, Borneo a total of thirteen Asian Brown tortoises (*Manouria emys emys*) were encountered. Straight-line carapace lengths ranged between 38 cm and 49 cm and body mass between 8.75 kg and 17.25 kg.

Twelve tortoises were fitted with radio transmitters and followed for various lengths of time (1-67 days). The study animals' locations were determined using a handheld GPS receiver. From the locations obtained, daily movements and home range estimates were calculated. Daily movements (beeline) ranged between 0 and 390 meters. However, the tortoises illustrated considerable latitude in their traverses. Actual distance traveled was measured using a trailer thread on five occasions and exceeded the beeline distances on average by 87%. Home ranges were estimated for eight animals using the confidence ellipse method. Estimates ranged between 0.01 km^2 and 1.81 km^2. Estimates based on the convex polygon method are also reported and ranged between 0.002 km^2 and 0.51 km^2.

Tortoise diet revealed new plant species not reported before. Of the 22 plants collected 15 belonged to the genus *Alocasia*. In addition, two unidentified fungi were eaten along with herbs from the families Begoniaceae, Melostomataceae, Marantaceae, Woodsiaceae and Zingiberaceae. No animal matter was observed to be eaten. The study animals were found to be generalist herbivores with a possible specialization towards *Alocasia*. The toxic properties of calcium oxalate contained in *Alocasias* do apparently not have the same effect (irritation and swelling of tissue) on tortoises as in mammals. Drinking or licking dew off the vegetation was not observed.

Activity measured as movement of the carapace was recorded using ActiTrac® monitors. Two individuals were monitored for one month. An overall unimodal activity pattern was found, though on days where the midday temperature exceeded approx. 29°C a bimodal pattern was often observed. The activity level of the tortoises varied between individuals.

A qualitative assessment of the habitat revealed that the tortoises thrived in regenerating forest with a closed canopy. Humidity around 90% and shade seemed to be essential for suitable tortoise habitat. The lack of tortoises in the palm monocultures surrounding the reserve suggests that clear-cut forestry practices leads to extinction in the affected areas.

One nesting female was observed over three days, while constructing the nest mound.

iii. Abbreviations

CITES	Convention on International Trade in Endangered Species of Fauna and Flora (p. 6)
CCL	Curved carapace length (p. 26)
CEM	Confidence Ellipse Method (p. 19)
CL	Carapace length (p. 2)
CPM	Convex Polygon Method (p. 21)
GIS	Geographical Information Systems (p. 18)
GPS	Global Positioning System (p. 18)
IUCN	International Union for the Conservation of Nature (p. 6)
PL	Plastron length (p. 26)
T_A	Ambient temperature (p. 50)
TL	Tail length (p. 27)
T_M	Microclimate temperature (p. 50)
TWR	Tabin Wildlife Reserve (p. 9)
UTM	Universal Transverse Mercator (p. 18)
VJR	Virgin Jungle Reserve (p. 10)

1 Introduction

Over the last two decades, there has been an alarming decline in the Asian turtle and tortoise populations. Some 75% of the tortoise and freshwater turtles living in Asia are today listed as Critically Endangered, Endangered or Vulnerable (Turtle Conservation Fund, 2002). The primary reasons are the harvesting of animals for the food and pet trade compounded by loss of habitat. This has lead to a worldwide concern about the future of these populations and species. One such species is *Manouria emys emys* (Schlegel and Müller, 1844).

1.1 The tortoise *Manouria emys emys*: a biological review

Taxonomy: (Tewksbury Institute of Herpetology and World Chelonian Trust, 2004)
Phylum: Chordata
Class: Reptilia
Order: Testudines (Turtles, Tortoises and Terrapins)
Family: Testudinidae (Tortoises)
Genus: Manouria
Species: *Manouria emys*
Subspecies: *Manouria emys emys*
Manouria emys phayrei

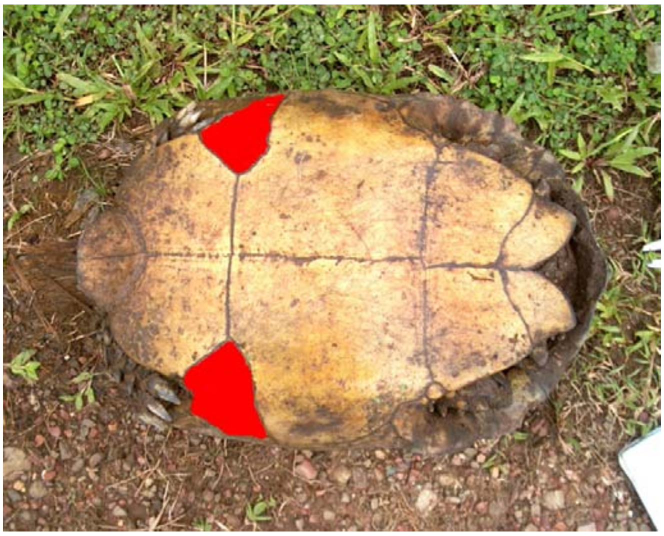


Figure 1.1.1. Ventral view of the tortoise (plastron). Pectoral scute (red) arrangement *of Manouria e. emys*. In *Manouria e. phayrei* the pectoral scutes meet at the midline forming a common suture (figure 1.1.2). Photo: Klaus Høybye-Mortensen

M. e. emys was first described by Schlegel & Müller (1844). They used the name *Testudo emys* and thus placed it in the genus Testudo. Since then changing names have been used until Bour in 1984 (Bour, 1998) finally argued that the species should be put in the genus Manouria, which is now generally accepted in the herpetological society. This genus includes two different species *M. impressa* and *M. emys,* the latter subdivided into *M. emys phayrei* (Blyth,

1853) and *M. emys emys*. For a full historical review on the genus Manouria, see Bour (1998). The genus Manouria is considered the most primitive among the Testudinidae based on cranial osteology, supracaudal division, and their preference for moist forest habitat (Crumly, 1982; Pritchard , 1979).

1.1.1 Distribution

The two *M. emys* subspecies are generally considered to be geographically divided with *M. emys phayrei* ranging from Assam, India to Myanmar, Bangladesh and central Thailand, while *M. e. emys* ranges from Peninsula Malaysia, Sumatra to Borneo (Ernst et al., 2001; Iverson, 1992; Liat and Das, 1999; McKeown, 1990; Moll, 1989; Morgan and Schaffer, 2001; Paull, 1996; Pritchard , 1979; Schaffer and Morgan, *In press*; Wirot, 1979). However, records of specimens having the characteristics of *M. e. emys* are found as far Northwest as Assam, India (Bhupathy, 1994). An intergrade, ranging from southern Thailand to northern Malaysia, between the two subspecies is mentioned by Schaffer & Morgan (2002) (without exact provenience) and by Obst (1983). However, no evidence seems to be present except from one specimen observed in Bangladesh (Das, 1995). The finding of an intergrade in Bangladesh further greys the area. Thus, it seams that a revision of the distribution of *M. emys* is much needed.

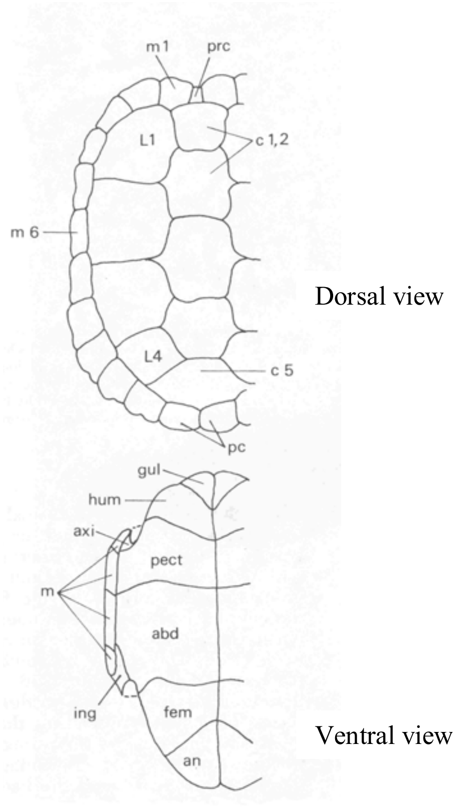


Figure 1.1.2. Horny scutes of *Pseudemys scripta*. abd, abdominal; an, anal; axi, axillary; c, central; fem, femoral; gul, gular; hum, humeral; ing, inguinal; L, lateral; m, marginal; pc, postcentral; pect, pectoral; prc, precentral. m6 is the sixth marginal scute, c5 is the fifth central scute etc. counted from the cranial end (up). Adapted from Porter (1972).

1.1.2 Morphology

M. e. emys is the smaller of the two subspecies reaching about 50 cm carapace length (CL) and 20 kg (in Wirot (1979) up to 31 kg). It is easily distinguishable from *M. e. phayrei* as the pectoral scutes (figure 1.1.2) do not meet at the midline seam of the plastron (figure 1.1.1). *M. e. emys* is commonly known as the Asian brown forest tortoise because of its lighter coloration compared to *M. e. phayrei,* which is referred to as the Asian black forest tortoise. Coloration in *M. e. emys* varies from dark brown (almost black) usually in older animals to light brownish green in younger animals (Das, 1995; Inger and Tan Fui Lian, 1996; Iskandar, 2000; McKeown, 1990; Schaffer and Morgan, 2002; Wirot, 1979).

Scutes are often multi-coloured with the centre having lighter colour than the outer rim (figure 1.1.3). The plastron is normally light brownish/yellowish and sometimes with a distinct pattern of darker colours. The front legs are covered with large scales and have five large claws. Hind limbs have the elephantine shape typical for Testudinidae, with smaller scales relative to the front limbs. Hind limbs end in four large pointed claws. The soles of the hind feet are covered with enlarged conical shaped scales and posteriorly clustered forming a rim (Schlegel and Müller, 1844). This arrangement probably helps the animal when climbing up steep and muddy slopes. Two clusters of enlarged scales are present on both sides of the tail, the median scale being the largest. This gives rise to the name "Six legged tortoise" as it, looking from behind, seems that the animal has four hind legs.

1.1.3 Sexual dimorphism and behaviour

M. e. emys shows little or no sexual dimorphism, though Fife (1989) states that "Sexual morphology is quite evident in *M. e. emys*" without further description. Tail length is usually considered the most distinct character for determining gender in most tortoise species, males having longer and wider tails than females (Auffenberg and Iverson, 1979; Ernst and Babour, 1989; Schaffer and Morgan, 2002). This, however, does not apply to *M. e. emys* (Cox et al., 1998), which is further supported by the statement that "In practice, adults can only be sexed with confidence if they show themselves to possess a penis or lay eggs"(Ernst et al., 2001). Other suggested male characteristics are concavity of plastron (Ernst and Babour, 1989;

Figure 1.1.3 Typical carapace colouration of adult *Manouria e. emys*. Note the radio transmitter posteriorly on the carapace. Photo: Klaus Høybye-Mortensen

Günther, 1864), bulging of the fifth central scute (Morgan and Schaffer, 2001; Schaffer and Morgan, 2002) and narrower carapace. Five different morphological characters were found to distinguish males from females in *M. e. emys* by Aranyavalai (1996). These were; 5th central scute length and width, 4th lateral scute length, abdominal scute width and tail length. Thus, as apparent from the former descriptions, no consensus exists in positively defining sexual dimorphism in *M. e. emys*.

Little attention has been paid to the natural ecology of this species and to date, only one article based on *in situ* observations has been published. In, what shall hereafter be referred to as the "Danum Valley study" (Sabah, Borneo), *one* female *M. e. emys* was radio tagged and followed over a period of 53 days (Lambert and Howes, 1994). From their daily observations, the authors found this animal to range an area of 0.6 km^2. In general, daily movements were less than 200 meters. However, on many days little or no movements were recorded. On nineteen occasions, the tortoise was recorded foraging. Seedlings, herbs, fruit and especially fungi were eaten. This female spent inactive periods under tangles of branches or between the buttresses of large trees. Two male tortoises were recorded trying to mate with the female during the study. Other than that, no social interactions were recorded.

Mating in *M. e. emys* occurs all year round in captivity (Eggenschwiler, 2003; Morgan and Schaffer, 2001). Behaviours associated with mating include "head bobbing", "trailing" and vocalizations. The head bobbing is a common social behaviour among the Testudinidae and most often occur during male-male combat or courtship (Auffenberg, 1977). *M. emys* of both sexes are known to make use of vertical and horizontal head bobbing during non-sexual behaviours. During courtship, only the male employs the head bobbing (McKeown et al., 1991).

Trailing is often employed by the male prior to mounting. This behaviour consists of the male following the female at a close range and at the same pace (Auffenberg, 1977), it is often associated with shell ramming or tapping performed by the male. Whenever the female halts, the male will try to mount her (Mähn, 2001).

During mounting, the male vocalizes in what may be described as rhythmic moanings, grunts or bellows (Lambert and Howes, 1994; McKeown et al., 1991). Both sexes vocalize during courtship, however with different duration and frequency modulation between the sexes (McKeown et al., 1991).

1.1.4 Nesting

The nesting behaviour employed by female *M. emys* is unique for tortoises, as they build a nest mound of leaves and other debris, in which they lay their eggs (Fife, 1989; Glasgow Zoopark, 2003; Iverson, 1992; Jacobsen, 2003; Liat and Das, 1999; Louwman, 1982; McKeown, 1990; McKeown et al., 1991; Moll, 1989; Morgan and Schaffer, 2001; Paull, 1996; Pritchard , 1979; Schaffer and Morgan, 2002; Wirot, 1979). This kind of nest mound construction is also seen in species of crocodiles and some birds, the megapods (Vleck et al., 1984). Until now, no confirmed record of nesting in the wild has been published even though the first anecdotal record dates back to 1901 (Anon., 1901). The back sweeping motions of the front legs for collection of nest materials is also a unique behaviour among tortoises. Most tortoise species lay their eggs in chambers dug out in the bare soil (Ehrenfeld, 1979). A few days prior to the actual oviposition the female will start the construction of a nest mound by scraping debris together using a back sweeping motion of her forelimbs. Before oviposition a shallow depression is formed on top of the mound in which the female will place her eggs (Louwman, 1982; McKeown, 1999; McKeown, 2001).

M. emys lays up to 51 eggs, which is the highest number recorded for any tortoise species (McKeown et al., 1991). When egg laying is completed she will again turn to the back sweeping motions and continue to add debris to the mound. This may last for 2-3 days. The complete nest mound may reach up to 91 cm in height and a diameter of 2,5 meters (Louwman, 1982; McKeown, 1999). During the whole session, the female will guard the nest against potential predators by either trying to push away the intruder or if this fails, lay flat on top of the mound. The guarding behaviour will normally stop after a few days when the female looses interest in the nest mound (McKeown, 2001). However, a record of up to six weeks of nest guarding is also reported (Eggenschwiler, 2003). Artificial incubation (eggs placed in an incubator) lasts between 63–84 days at temperatures ranging between 25.6-28.9°C (McKeown et al., 1991). There are no records of incubation temperatures or period from the wild. Nesting occurs during the months of April, May, June, August and September in captivity (Schaffer and Morgan, *In press*).

Hatchlings of *M. e. phayrei* measure 51-55mm and weigh 50-55gram (Louwman, 1982) and those of *M. e. emys* tend to be somewhat smaller (Schaffer and Morgan, *In press*). Nothing is known about the habits of young and adolescents of *M. emys* in the wild.

1.2 Conservation status

As mentioned earlier, Asian turtles and tortoises are under immense pressure from habitat destruction and human exploitation. *M. emys* is no exception. From most records concerning its distribution and numbers in the wild, it seems to be fragmentally distributed and rather rare where occurring (Moll, 1989). No density estimations exist for this species.

The species is listed in the category Endangered under the criteria A1cd+2cd, on the IUCN red list of threatened species (figure 1.2.1) (IUCN, 2003). This means that the species either have been or is expected to be reduced by more than 50% over ten years or three generations, whichever is the longer (figure 1.2.1). In this case, three generations applies as one generation is considered to be somewhere between 10 and 15 years (Schaffer, pers. comm.). Again, it is evident that human exploitation and habitat destruction is considered the main factors. Until 2000, *M. emys* was listed as vulnerable, by IUCN (1996).

International trade of *M. emys* is also controlled by the CITES appendix II (UNEP-WCMC, 2004). The export quota from Peninsula Malaysia was raised from 200 wild caught individuals in 2001 to 500 individuals in 2002 and 500 in 2003. This seems like a paradox as the species was moved from the vulnerable to endangered red list by IUCN only a year earlier.

Imports of *M. emys* are now totally banned in the European Community (EC nr. 349/2003) but unfortunately, this has just shifted the trade towards Japan and the United States (UNEP-WCMC, 2000).

M. e. emys is locally protected in Sabah, Malaysia under the Wildlife Conservation Enactment 1997, schedule 2 section 25(2) and a licence issued by the director of the Wildlife Department is required to hunt or collect specimens (State of Sabah, 1997).

ENDANGERED (EN) A taxon is Endangered when it is not Critically Endangered but is facing a very high risk of extinction in the wild in the near future, as defined by any of the following criteria (A to E):			
A)	**Population reduction in the form of either of the following:**		
	1)	**An observed, estimated, inferred or suspected reduction of at least 50% over the last 10 years or three generations, whichever is the longer, based on (and specifying) any of the following:**	
		a)	direct observation
		b)	an index of abundance appropriate for the taxon
		c)	**a decline in area of occupancy, extent of occurrence and/or quality of habitat**
		d)	**actual or potential levels of exploitation**
		e)	the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites.
	2)	**A reduction of at least 50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer, based on (and specifying) any of (b), (c), (d), or (e) above.**	

Figure 1.2.1. Criteria to be met for a species to be listed on the IUCN red list as Endangered. *Manouria emys* is currently listed under the criteria A1 cd + 2 cd (bold text). Adapted from IUCN web site (IUCN, 1994)

1.3 Objectives of the present study

As very little is known about the life history of *M. e. emys* in the wild, the objectives of this study cover a broad spectrum. In fact, all information obtained during the study would either be new to science or significantly add to the very limited knowledge of the habits of this species in the wild. Planning fieldwork was indeed a challenge, as no preliminary surveys had been conducted. Consequently, the research had to be based on *ad libitum* data collection in the beginning and then gradually building up the methodology as field experience increased. As the researcher and university staff had little first hand experience with tortoises and radio telemetry in tropical rainforests, many decisions had to be made after initial trials in the field.

Some of the original objectives had to be altered or given up as they proved to be too difficult or time consuming. Especially observations on behavioural elements and other activities where the study animals could see the observer proved to be difficult. Whenever the researcher was spotted by the study animals, they would simply stop whatever they were doing and withdraw into the safety of their carapace. This behaviour normally persisted throughout the entire observation period.

Objectives of the present study are:

- To add to the overall knowledge of the general ecology of *M. e. emys*.
- To study behavioural elements such as foraging, mating and nesting in the wild.
- To study the activity, movements and short term home range of *M. e. emys*. Does environmental factors such as temperature, humidity and water resources have any influence on activity and home range?
- To describe habitat preferences/requirements by measured environmental variables and qualitative descriptions. Does *M. e. emys* tolerate habitat alterations caused by logging activities?

2 Methods

2.1 Research time frame

The fieldwork for this research project was carried out over two periods during 2002 and 2003. First field trip started 26th of March and ended 1st of August 2002. Originally, one field trip lasting six months was set as the time frame. However, half way through it was realized that this time frame was too optimistic. Working single handed in the field not only implies data collection but also logistics such as working out food supplies, equipment maintenance etc. These duties proved to be more time consuming than expected because of the remoteness of the study area.

In addition, shortly after my arrival in Sabah I was informed that obtaining the research permissions would take longer than expected and thus the start of data collection was delayed until 20th of April. This unforeseen delay resulted in too few data being collected during the first field trip.

The second field trip was carried out from 15th of January to 10th of March 2003. Total time in the field summed up to approx. six months, covering the months from January-July when the two field trips are combined.

2.2 Study area: General description

Fieldwork was carried out in Tabin Wildlife Reserve (TWR), a 120,000 ha wildlife reserve in the Malaysian state Sabah, northern Borneo (5°12’N 118°40’E, figure 2.2.1). Nearest town being Lahad Datu, approximately one hour drive by dirt road from TWR. The reserve is administered by Sabah Wildlife Department and Sabah Forestry Department each taking care of their respective areas of interest. TWR has previously been logged extensively and thus the area is a mix of primary and secondary forest. The primary forest consists of one large area in the middle of the reserve, the so-called Core area, and small patches scattered around in the predominantly secondary outer boundaries of the reserve. The Core area is 15,000 ha of undisturbed lowland rainforest 22 km east of Tabin Station. The Core area is only accessible by vehicle from the main logging road, which runs from the western part of the reserve straight east to the Sungai Tabin (sungai is Malay for river). This road has been partly maintained to serve as access for vehicles from the above departments and researchers traveling to the Core area. However, during the first field trip, most bridges had fallen apart and the only way to get to the Core area was by trekking. All other logging roads running through TWR have deteriorated and can now only be followed on foot. Apart from the Core area, seven smaller areas have been left untouched and are referred to as Virgin Jungle Reserves (VJR). For locations see TWR map (figure 2.2.2)

Except from the Core area and the smaller VJR's all other areas of the reserve have been selectively logged during the period 1969-1989 (Ecotone Management, 1998). In 1984, the area was officially appointed a wildlife reserve. Since 1989, no legal logging has taken place (Malim and Mohamed, 1999) and the previously logged areas are now regenerating. Unfortunately, illegal logging has been reported from various areas over time, last known to be the Spring of 2003 in the eastern part of the Core area.

The reserve is delimitated by palm oil plantations on its Southern, Eastern and Western borders. The Northeast is bordered by mangrove forest and the Northwest is a mix of forest and palm oil plantations. In March 2003 a 3.640 ha large wildlife corridor between TWR and Kulamba Wildlife Reserve (north of TWR, figure 2.2.1) was proposed (JICA, 2003). The area consists mostly of freshwater swamp forest around Sungai Segama.

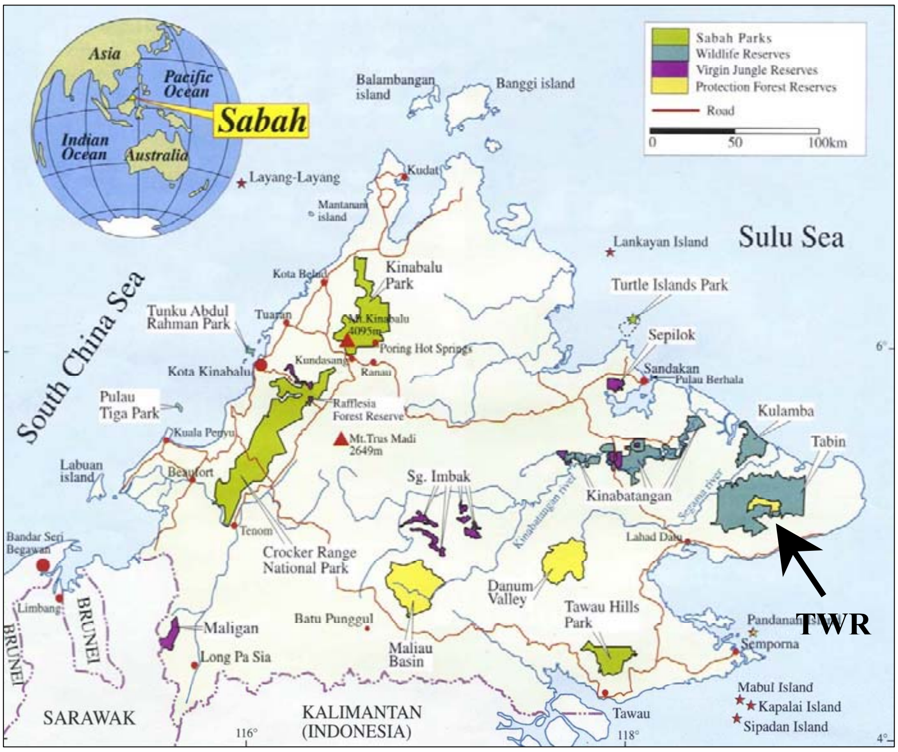


Figure 2.2.1. Map of Sabah. Tabin Wildlife Reserve (TWR) is located in the eastern part of Sabah (arrow). Courtesy of Discovering Sabah.

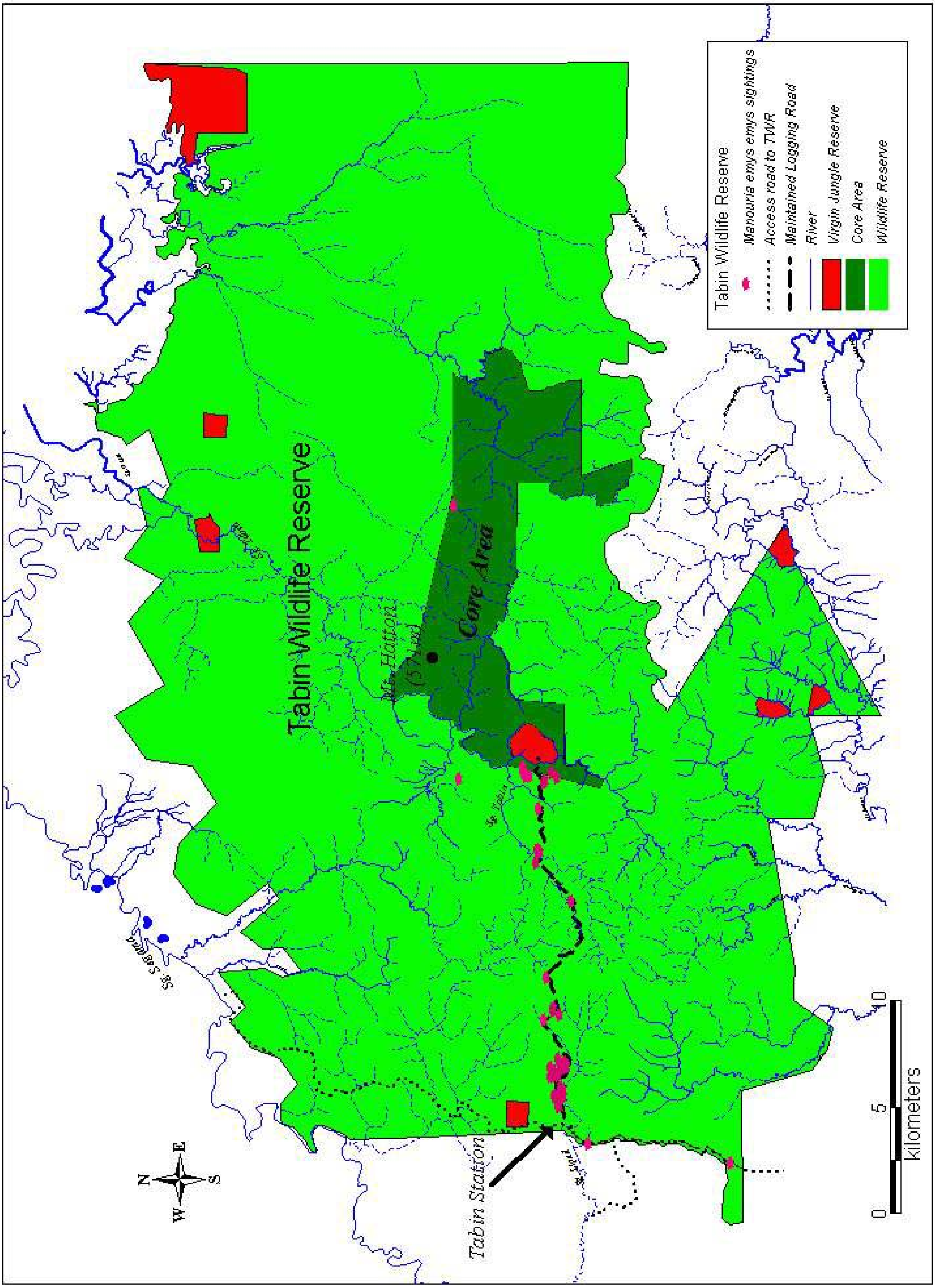


Figure 2.2.2. Map of Tabin Wildlife Reserve. Courtesy of WWF Sabah

2.3 Topography

TWR consists of lowland areas ranging from 80-571 meters above sea level. Mt. Hatton (571 meters) is the highest point (figure 2.2.2, centre). Most areas are dominated by small hills divided by ravines and steep slopes with angles up to 45 degrees being normal. The northeast part of the reserve is mainly lowland swampy areas and the northwest corner consists of limestone formations.

There is an extensive network of waterways, which drains the reserve. Larger rivers such as Sungai Tabin and Sungai Lipad are perennial whereas the smaller streams only rise to contain significant water after heavy rainfalls and during the wet months. All rivers carry water from the area to the adjacent oil palm plantations and thus no pollutants are carried into TWR by surface waters.

There are a number of mud volcanoes and mineral rich springs scattered around TWR. The mud volcanoes are rich in minerals and thus attract a diversity of wildlife (Dalimin and Ahmad, 1999).

2.4 Climate

Sabah and Malaysia in general fall into the Tropical Monsoon type of climate (Ecotone Management, 1998). This type is dominated by two monsoon seasons, one from November until March (the wetter North-east monsoon) and the other in June and July (the drier South-west monsoon). The annual rainfall at Tabin Station and close destinations is shown in figure 2.4.1.

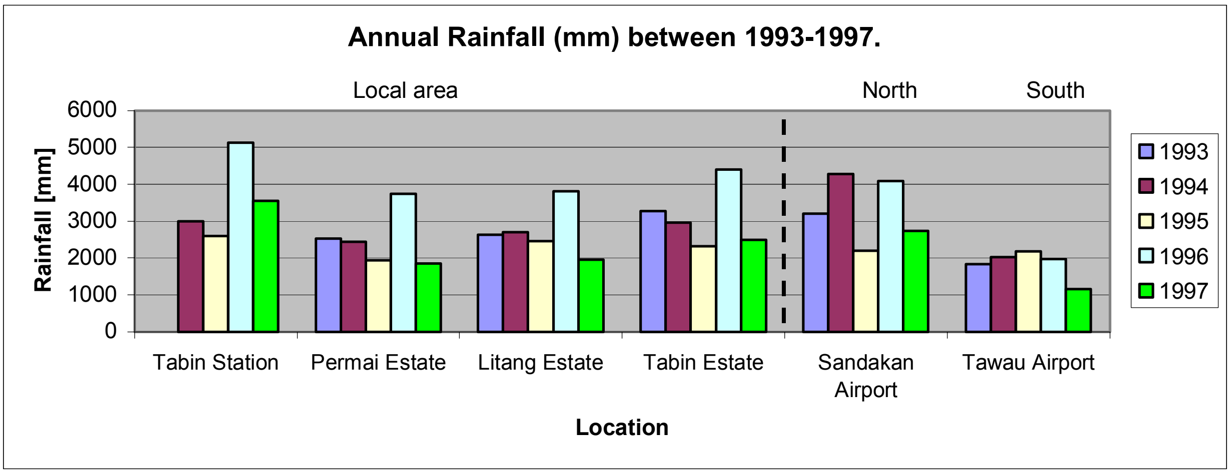


Figure 2.4.1. Annual rainfall between 1993-1997. Note that data from Tabin Station 1993 is missing. From the figure, it is seen that annual rainfall varies considerably within locations and within years. Permai, Litang and Tabin Estate are all surrounding Palm Oil plantations. Sandakan Airport is 150 km north of TWR and Tawau Airport is 80 km south of TWR. Source: Ecotone Management Sdn. Bhd.

Humidity is high throughout the year. The mean annual relative humidity in 1988 was 82.9% (Ecotone Management, 1998). From data collected during this field study, it is seen that the relative humidity very seldomly falls below 90% at the forest floor during daytime. Temperatures measured at Tabin Station from January 1998 until May 2000 are shown in figure 2.4.2. The mean monthly temperature throughout 1990-1997 did not fall below 26.6°C and did not exceed 28.3°C (Ecotone Management, 1998).

Although TWR lies within the area affected by El Niño Southern Oscillation events, no recent signs of wildfires have been found in the reserve. Irregular dry spells do occur and are normally associated with El Niño. Tropical cyclones rarely reach the northern parts of Borneo and no major wind throws are found in TWR.

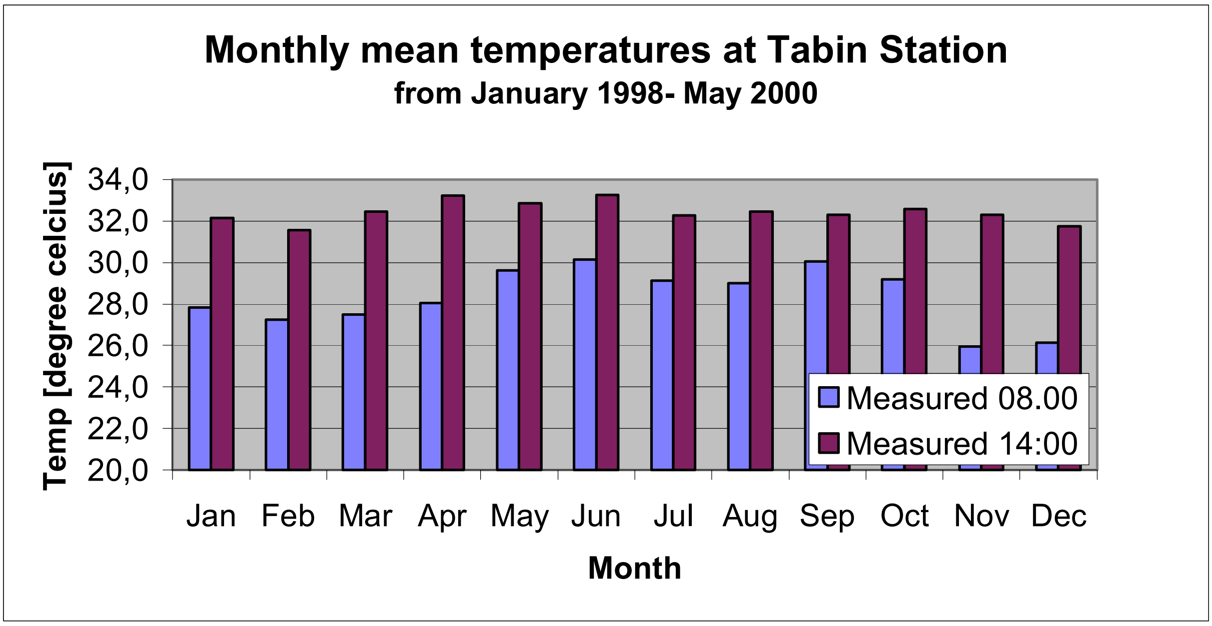


Figure 2.4.2. Monthly mean temperatures measured at Tabin Station during January 1998- May 2000 when the weather station was destroyed by wild elephants.

2.5 Flora

The old lowland forests of eastern Sabah are dominated by the large hardwood species of Dipterocarpaceae e.g. *Dipterocarpus* spp. and *Shorea* spp. (Whitmore, 1984). These trees have high commercial value and thus have been extensively logged in many areas of TWR (Sale, 1994). Only in the VJR's and the Core area does the original tree composition still exist. However, as reported by Kjeldsen (2003), in many places the forest canopy still resembles that of undisturbed forest in complexity.

Typically, the pioneering species have taken over after the removal of the commercial timber. Such species include *Macaranga spp.* and *Mallotus spp.* of the Euphorbiaceae family (Kjeldsen, 2003). These are fast growing trees reaching up to about 6 meters in height. In some places where the forest has been totally damaged from clear-cut practices or along logging roads, the vegetation is dominated by Leguminosae, Rubiaceae, Euphorbiaceae and Zingiberaceae (Sale, 1994). A plant community like that slows down the regeneration of the forest by shading out the slower growing Dipterocarpaceae. Thus, TWR is a mosaic of forest types in different succession states.

In the areas dominated by secondary growth, the lower strata are very dense making trail cutting very time consuming.

2.6 Fauna

The main reason for TWR being declared a wildlife reserve is its faunal diversity.

TWR is home to the three big mammals of Borneo; the Borneo pygmy elephant, only recently proven a subspecies of the Asian elephant and not yet given a scientific name, the Sumatran Rhinoceros (*Dicerorhinus sumatrensis harrissoni*), and the Tembadau or Banteng (*Bos javanicus*), which is a wild ox indigenous to Borneo. It is estimated that TWR holds a population of 250-300 elephants (Sale, 1994) and 8-15 Sumatran Rhinos (SOS Rhino, pers. comm.). Especially the Sumatran Rhinos get a great deal of attention, as TWR is one of the last places on earth with a potential viable population of this highly endangered species. Primates such as Orang utans (*Pongo pygmaeus pygmaeus*), Gibbons (*Hylobates spp.*), Langurs (*Presbytis spp.*) and Macaques (*Macaca spp.*) are frequently spotted, as are Bearded pigs, Sambar deer and Mouse deer. So far, 71 species of mammals have been identified within the reserve with probably more to come (Sale, 1994).

The list of birds consists of 220 species within 42 families. This number is based on limited studies and there is no doubt that the list will grow in the future as research intensifies. As for reptiles, amphibians and other classes little or no research has been done and thus the checklists are incomplete.

A special interest in this study was of course the list of turtles and tortoises. During fieldwork, three species were seen and photographed, either by the author or by SOS Rhino rangers. These are: Malayan softshell turtle (*Dogania subplana*), Spiny Hill Turtle (*Heosemys spinosa*) and the subject of this study the Asian Brown Tortoise (*M. e. emys*). The Asian Brown Tortoise is reported to be “not uncommon” in TWR and “may possibly be of some importance for the herbaceous ground vegetation” by Kjeldsen (2003).

2.7 Recording techniques

2.7.1 Radio telemetry

A key element of this study was the use of radio transmitters. A preliminary search for commercial products revealed that these are expensive and often equipment such as receivers are unhandy and not up to date. Thus we decided to custom build the transmitters to cut the costs and to make a lighter and more handy receiving system. Besides the lower costs, this was also a way for the technical staff at Institute of Biology, University of Southern Denmark of gaining experience in radio telemetry. Both technicians and researcher had no experience using radio tagging so the project was very much in the developing stages in this field. The literature on how to build and use radio tag equipment is plentiful and straightforward for the inexperienced. One reference worth mentioning is “A Manual for Wildlife Radio tagging” by Kenward (2001), which gives a good overview of the methods, problems and solutions.

The most important factor in radio telemetry is the range of which the signals propagate. As this study was conducted in an environment dominated by dense secondary rainforest, it was of great importance that the bandwidth of the signals was chosen to fit this issue. Another concern was the length of the antenna elements. A large unhandy antenna would be undesirable in an environment like that of the study site. Thus, a small antenna was of equal importance. 433.500-433.900 MHz was chosen as this waveband fulfilled both requirements.

As reported by Lambert and Howes (1994) *M. e. emys* sometimes travels up to 300 meters in one day and thus a desirable signal range would be at least this distance. When tested in a dense pine forest in Denmark the signals could clearly be detected at a range of 700 meters. Thirteen transmitters were made. For component diagram, see appendix I. Each transmitter was set to a specific frequency within the above-mentioned band and given a letter of reference (#A-#M). The study animals were named according to the letter of the transmitter attached to their carapace. As tortoises are slow moving animals, a narrow separation of the wavelengths of each transmitter should be sufficient to track individual animals even when positioned close to other transmitters. In order not to confuse signals, transmitters were carefully chosen in such a way that individuals in geographical close proximity had transmitters separated by at least 200 kHz in frequency. Again, tests showed that transmitters were easy to differentiate at a distance of 50 meters placed within an angle of approx. 20°. When placed on a straight-line from the point of reception it was difficult to differentiate the signals. This posed a minor problem, as it was unlikely to occur often in the field.

The transmitters were cast in a two-component epoxy glue to make them waterproof and resistant to wear and tear. The batteries (SAFT 3.6 Volt, T04/8AA lithium cell) were attached in the field to save battery life. A gas driven soldering iron (Portasol Technic, Oglesby & Butler Ltd, Ireland) was used to solder the batteries to the transmitter. The batteries and solder was then covered by several layers of fast potting two-component epoxy glue ("5 Min. Epoxy" from R&G Gmbh, Waldenbuch, Germany) to prevent water from sieving into the battery compartment.

The original design of the transmitters proved to be insufficient as the batteries detached when the tortoises moved through the dense undergrowth. The protecting layers of epoxy were torn off when the tortoises forced themselves under branches and other sturdy elements. Thus, the design was altered by making a full cast of epoxy around the batteries in the same manner as the transmitters. Each transmitter including batteries and glue for attachment weighed approx. 90 grams, which was less than 1% of the total body weight of any individual tortoises which ranged between 10.50 kg and 17.75 kg. No effect on fitness (energy expenditure) is seen as long as a device weighs less than 5% of total body weight in bats (Aldridge and Brigham, 1988; Berteaux et al., 1996), which is often referred to as the "five percent rule of thumb". Flying animals are more susceptible to the extra weight from a transmitter than creeping animals (Kenward, 2001). Thus, the attachment of radio transmitters to the carapace of the study animals was not expected to have any significant effects.

Figure 2.7.1. Tortoise #B with radio transmitter attached. The transmitter is placed posteriorly on the carapace in such a way that the carapace profile is not dramatically altered. This minimizes the likelihood of the transmitter becoming entangled in the vegetation.
Photo: Klaus Høybye-Mortensen

The transmitters were attached to the lower posterior part of the carapace using 5 Min. Epoxy. The epoxy was added little at a time as fast potting epoxies becomes very hot during the potting process. In order not to induce heat damage to the underlying tissue, this practice was undertaken. Handling time when fitting transmitters was approx. 45 minutes. Tortoises were released immediately after handling.

For receiving the pulses from the transmitters a YAESU communications receiver VR-500 (YAESU MUSEN Co. Ltd., Japan) and a three element, 432 MHz, Yagi antenna (Vårgårda Radio, Sweden) were used. With the system weighing only 600 grams and the antenna easily fitting into a standard 35-litre backpack, it was well suited for this kind of fieldwork. One downside though was the receiver's susceptibility to the very moist climate. This caused some instability during the last weeks of the second field trip.

Transmitters were fitted with new batteries in the days before my departure from TWR at the end of the first field trip. Calculations on the transmitters energy expenditure predicted a battery lifetime of at least seven months. As I was expecting to return for my second field trip only six months later, this seemed to be a reasonably safety margin. However, when returning to TWR all the transmitters had run cold and could thus not be located.

2.7.2 GPS and GIS

The use of a Global Positioning System (GPS) greatly enhances the accuracy of geographical measurements such as straight-line distance between two observation sites. However, in a rugged terrain one only gets the beeline distance with the loss of extra meters added by the different contours and wandering traverses of the tortoises. In an area like Tabin Wildlife Reserve, which lacks transect systems for reference, the forest can be virtually impenetrable in many areas and it would be extremely time consuming to approximate or calculate positions.

A handheld GPS reciever (Garmin® eTrex Venture) was used to calculate and save positions. All points used have a minimum accuracy of 20 meters. Positions are given in Universal Transverse Mercator (UTM), Zone 50 northern hemisphere, World Geodetic System of 1984 (WGS 84).

MapInfo Professional® Version 6.5 was used for plotting positions on GIS maps. GIS maps were provided by WWF, Sabah and Sabah Wildlife Department.

2.7.3 Home range

Primary rationale for GPS utilization was to obtain data for home range estimations. The term home range in this context is used according to the definition by Burt (1943) that an animals home range is "the area used by an individual during its normal activities such as food gathering, mating and caring for young".

Using the UTM datum enables the researcher to directly use the single GPS points as XY-coordinates for home range calculations. Where X is the latitudinal coordinate and Y is the longitudinal coordinate of the UTM datum. Home ranges are mapped from the GPS coordinates using MapInfo version 6.5 (IM Systems Inc., 2002; MapInfo Corporation, 2001). For estimation of home range, the confidence ellipse method (CEM) is used, presented by Jennrich and Turner (1969). Their index is specifically designed to measure non-circular as well as circular home ranges. As mentioned previously, virtually nothing is known about the ranging and movements of this species, thus a method not assuming a specific home range shape was chosen. Furthermore, the chosen estimator has a high statistical stability and lack of bias even for small numbers of capture loci (*n*) (Boulanger and White, 1990; Jennrich and Turner, 1969). However, the method has been criticized for its assumptions of bivariate normality around a centre of activity, which is derived from the arithmetic mean (Harris et al., 1990). If this assumption is not met, the estimator will include a too large area (Ackerman et al., 1990). In addition, the loci used for computing the estimate must be free of autocorrelations. Autocorrelations occur if repeated observations are done over a relatively short period (Ackerman et al., 1990). Harris et al. (1990) notes that observations more than twelve hours apart are independent and thus free of autocorrelation. Swihart and Slade (1985) calculated that the minimum interval between independent observations was 270 minutes in their study of the cotton rat (*Sigmodon hispidus*). As the temporal distance between observations in this study varies from one day up to several weeks, it is assumed that this assumption is met.

The index is given by the equation:

$$Home\ \ range = 6\pi |S|^{\frac{1}{2}}$$

where $|S|$ is the determinant of the GPS point covariance matrix

$$S = \begin{pmatrix} s_{xx} & s_{xy} \\ s_{yx} & s_{yy} \end{pmatrix}$$

Defined by the equations

$$s_{xx} = \frac{1}{n-2}\sum_{i=1}^{n}(x_i - \bar{x})^2 \quad , \qquad s_{yy} = \frac{1}{n-2}\sum_{i=1}^{n}(y - \bar{y})^2$$

$$s_{xy} = s_{yx} = \frac{1}{n-2}\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})$$

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}x_i \quad , \qquad \bar{y} = \frac{1}{n}\sum_{i=1}^{n}y_i$$

With this index, an elliptic area based on the covariance matrix of the GPS points is estimated. For more details, see Jennrich and Turner (1969) and Boulanger and White (1990).

In choosing the appropriate method, different considerations have to be made. How large a data set is available and does it meet the assumptions of the method. The data sets from this study only contains between 5 and 17 loci for the individual study animals. This means that other estimators such as the Harmonic mean, Fourier estimator and Kernel, though more stable when dealing with non-normal distributions, become biased because of small sample sizes

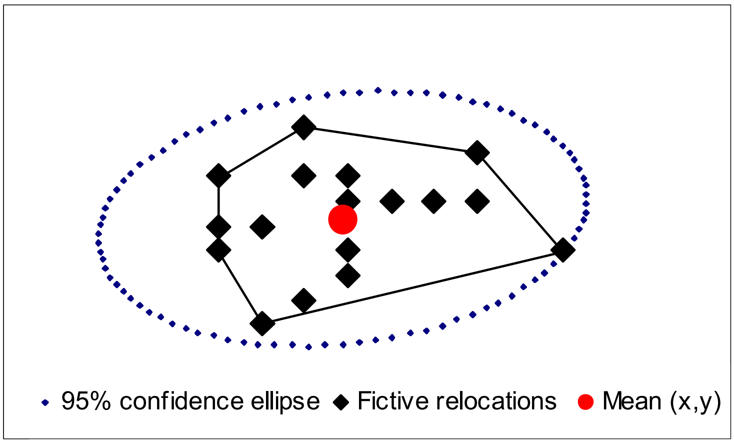


Figure 2.7.2. Difference between the Ellipse method and the Convex polygon method based on 17 fictive loci. The black line represents the Convex polygon

(Boulanger and White, 1990; Harris et al., 1990). The small number of loci also has its disadvantages when using the simplest of models such as the convex polygon method (CPM). With few loci, the risk of underestimating the true home range is greater (Hayne, 1949). One example could be five loci arranged on an almost straight line with a total distance between the loci of one kilometre. Here the convex polygon estimation would be close to zero, even though the animal has travelled one kilometre in a given direction. On the other hand, there is also a risk of overestimating the home range, as occasional “sallies” made by the animal will affect the estimate (Worton, 1995). However, as the CPM is straight forward and one of the most commonly reported estimators it will be presented here to ease the comparison of the present study and others.

Home range was only estimated for study animals with five or more GPS points.

2.7.4 Daily movements

Daily movements are straight-line distances between day-to-day locations/GPS points. Landscape contours and deviations from the beeline path are of course not accounted for by the GPS device. In theory, a study animal could move hundreds of metres in a day ending up only 20 metres from its starting point. When recording the new location the next morning the researcher would only get information about the 20 metres beeline between the two locations. Thus, the daily movements are somewhat underestimated. During the second field trip a trailer thread device was used (figure 2.7.4), revealing the actual path followed by the study animal, which gives a more precise measurement of distance moved between two recorded GPS points. With this method, the thread can simply be collected and the length measured. All distances, except for the trailer thread measurements, were graphically determined using the MapInfo ruler tool.

2.7.5 Activity

To quantify the activity of the study animals a movement sensing system was used. The system is based on a piezoelectric sensor, which records movements (acceleration in two dimensions). The average acceleration in an epoch (a chosen time interval) is then calculated and stored in the memory. The data can then be downloaded to a computer and shown graphically or statistically with customized software. The ActiTrac® monitor (IM Systems Inc., USA) (figure 2.7.3) was

Figure 2.7.3. ActiTrac (middle) and custom made PVC casing (left). The casing was made of two pieces held together by six screws. Data from the ActiTrac could then be downloaded at any time simply by unscrewing the top piece. Scale bar to the right (small square = 1 cm)

used to monitor activity patterns during the second field trip. Two monitors were purchased for this project. As this was a new method, and to my knowledge not previously used for the study of Testudines, the system had to be tested under controlled conditions. Before the second field trip, the monitors were tested at Vissenbjerg Terrarium, Denmark. Two red-footed tortoises (*Geochelone carbonaria*) were chosen as their morphology and movements resemble that of *M. e. emys*. It was tested whether or not the ActiTrac would register movements to the same degree as a human observer (the author). A continuous one-zero focal sampling was used with a one-hour observation period. This setup was chosen because it resembles the way the ActiTrac collects the data (30-second epochs, one-zero sampling for movements). The two data sets were compared in a contingency table and the correlation statistic Φ calculated, which is equivalent to the r calculated for numerical data (see appendix II) (Zar, 1999). From three trials at Vissenbjerg Terrarium, a mean $\Phi \pm$ SD was calculated to be 0.86 ± 0.05. This shows a high correlation between the data sampled by the observer and that recorded by the ActiTrac device. For all three tables, χ_c^2 (Chi-square corrected for continuity) (Zar, 1999) tests lead to rejection of H_0 ($\chi_c^2 = 76.725$, n = 120, DF = 1, $p < 0.0001$; $\chi_c^2 = 97.194$, n = 120, DF = 1, $p < 0.0001$ and $\chi_c^2 = 92.873$, n = 120, DF = 1, $p < 0.0001$). Thus, the two samples are highly dependent. The conclusion was that the ActiTrac would provide an accurate 24-hour movement observer in the field.

As the ActiTrac is placed on the lower caudal side of the carapace (opposite side of the radio transmitter), activity is defined as movement or tilting of the carapace. Movement of legs, tail or head is not registered as long as the carapace acceleration equals zero. The ActiTrac software (IM Systems Inc., 2002) registers activity if the average of a particular data point and the four points before and after that point is above the set activity threshold. For all the activity recordings during this study, the lowest threshold was chosen (×8) as tortoises are generally slow moving (low acceleration).

A waterproof casing was made of PVC to protect the device. The total weight of ActiTrac and casing was 95 grams. The two study animals (#DII and #L) equipped with radio transmitter, ActiTrac and trailer would thus be carrying a load of 210 grams, which was less than 3% of the total body mass of any individual.

2.7.6 Diet

Part of the study was to find out more about the diet preferred by *M. e. emys*. From the literature, it is known that they are predominantly herbivorous but occasionally will eat animal matter (Jacobsen, 2003; Obst, 1986). Whenever a study animal was located, its activity was noted and if eating a sample of the food was taken for identification. The immediate area was searched for any signs of foraging and again samples were taken if any found. This method proved to be no more than moderately successful as only the larger plant species show the bite marks, remainders, and other evidence of tortoises feeding. In the smaller species the entire plant may be eaten leaving no signs for the researcher. This could lead to biased results towards the larger plant species.

Another problem was tracking back the study animals movements. It is virtually impossible to ascertain footprints in the forest floor unless the tortoise has crossed mud pools or places with bare soil. To address this problem a new method was adopted from Moskovits & Kiester (1987) and Legler (1960). In their research on two Amazonian forest tortoises, (*Geochelone carbonaria* and *Geochelone denticulata*) and the Ornate Box Turtle (*Terrapene ornata*) respectively, a trailing system was used to follow the exact movements of single specimens. The idea is to have the tortoise pull a thread after itself revealing its path between to points. The researcher can then follow the thread in search for signs of foraging. In this way, one can focus on the path actually used by the animal and rule out all other places. This way the time wasted in searching places,

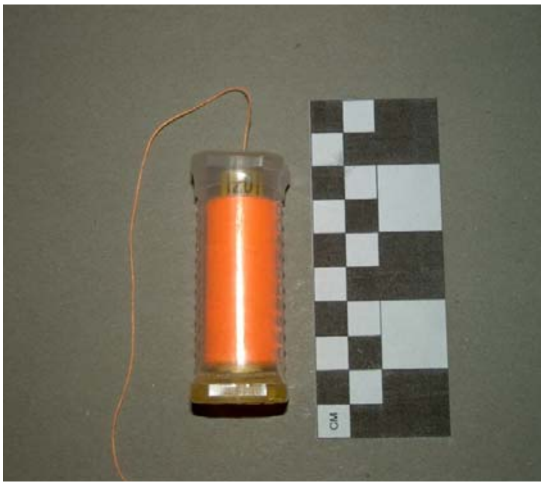


Figure 2.7.4. Trailer. Simply a standard roll of 200 meter cotton thread glued to the bottom of a plastic cylinder. The cylinder was then glued to the carapace and the thread tied to a tree or so. As the tortoise walked the thread was pulled out of the cylinder.

where the tortoise have never set foot is minimised. This simple system proved to be very efficient as day-to-day movements could be followed very precisely.

As the tortoises in this study also would be carrying a radio transmitter and ActiTrac at the same time, the trailer system was somewhat modified to make it smaller and lighter (figure 2.7.4). A standard roll of cotton sewing thread containing 200 meters was used. The roll was cased in a plastic cylinder for protection and glued to the back of the study animal right next to the ActiTrac. The trailing device, including attachment adhesive, weighed approx. 60 grams.

When possible, plants of the genus *Alocasia* were determined using the species and species complexes key presented by Hay (1998). Plants of the family Zingiberaceae were identified by Poulsen (pers. comm.) based on photos. All other plants were photographed and determined to genus or if possible to species at Sepilok Forest Research Center, Sabah.

2.7.7 Behaviour

As previously mentioned, *M. emys* behaviours have been described in different private collections or zoological gardens (Fife, 1989; Glasgow Zoopark, 2003; Louwman, 1982; McKeown, 1990; McKeown et al., 1991; Mitchell, 2003; Mähn, 2001; Schaffer and Morgan, *In press*). The maternal investment associated with the nest building and defence have been described in detail, but only under captive conditions. A major question is to the applicability of captive observations to wild animals. Other behavioural elements such as vocalisations and social interactions have also drawn some attention. However, of all these studies were performed under non-natural conditions. It is known from the Danum Valley study that during the 53 days of observations, only three social interactions were observed (with two different males) and all of these were associated with mating behaviour (Lambert and Howes, 1994).

Normally *M. e. emys* is found as solitary individuals in Tabin Wildlife Reserve. Before the present research was begun, the local rangers from SOS Rhino had observed individuals on a regular basis (Bosi, pers. comm.).

Behavioural elements were recorded whenever an individual animal was observed in the field (*ad libitum*). In a dense forest habitat observations have to be done at a close range as the visibility is very limited. In the disturbed forest, the lower strata are often impenetrable thickets of herbs, lianas and other pioneering species. Thus, observing at distances not disturbing the animals of interest are in most cases impossible. These difficulties were also experienced by Legler during his study on *Terrapene ornate* in Kansas, USA (Legler, 1960)

2.7.8 Temperature

Tinytag Ultra (model TGU-0017 from Gemini Data Loggers Ltd., UK) with internal probe was used to monitor long-term temperature ranges. The temperature range of Tinytag is -40°C - +85°C with a sensor accuracy of ±0.2°C. Loggers were used to monitor temperature fluctuations at 1.5 metres above the forest floor in an area with dense canopy cover (ambient temperature) and microhabitat fluctuations for a typical hiding place (under a fallen tree). Tinytag was also used to monitor temperature in the egg chamber of a nest mound. Logging interval was set according to the desired length of the monitoring period (e.g. minutes interval for the nest mound measurements). The data downloaded from the loggers were analyzed and graphically presented using the software OTLM, version 1.31 by Gemini Data Loggers.

A temperature logger was set up at a camp 21 km inside the reserve in May 2002. On 17th of February 2003, when retrieving the logger, the camp had been destroyed by elephants and the device split apart. All electronic components were missing and thus no data was obtained.

Temperature and relative humidity at tortoise sites/hides was measured using a TempTec™ thermo-hygrometer. The term hide refers to places where the tortoise finds rest under objects such as tree falls, entanglements of vegetation, etc. To obtain microclimatic data the TempTec was left next to the tortoise for at least 15 min. before the temperature and humidity was noted. All temperatures are given in degrees Celsius (°C) and humidity in percentage relative humidity (% RH). Humidity above 90 % RH are listed as >90 %RH as the TempTec range is 20-90 % RH.

2.7.9 Habitat

For every location/GPS position, the type of habitat was noted. An overall qualitative site description was made recording topography, weather and vegetation (e.g. disturbed/undisturbed forest, canopy cover, tree falls, etc). The surrounding habitat was described as either disturbed or undisturbed based on different signs of logging activities such as old logging roads or tree stumps. Canopy cover was divided into three categories: full cover, semi cover and open. A location was noted as full cover if the canopy was dense enough to shade out the majority (>50%) of sunlight. Semi cover was noted if the canopy was broken and sunlight penetrated to the forest floor and open was noted if no canopy existed at all. In addition, it was also noted if the carapace of the study animal was in the shade or not (e.g. basking in a sunlit place to rise the body temperature). The canopy cover is important in body temperature control of poikilothermic animals living in tropical regions. Places with no canopy tend to be very hot (>30°C) (figure 2.4.2) and dry during daytime (Johns, 1997) and will typically lead to heat stress if the animal is exposed for longer periods. Thus, tortoises living in the tropics often face the problem of keeping themselves cool enough as opposed to their relatives living in temperate regions where the problem is keeping sufficiently warm. It was expected that the study animals would spend most of their time in semi- to full-cover habitats to meet their temperature preferences, which are somewhere between 13°C and 32°C (Morgan and Schaffer, 2001; Schaffer and Morgan, 2002).

Distance to nearest water source was noted if less than 50 meters. *M. emys* is said to have a strong commitment to water (Wirot, 1979), and even described as having “amphibian habits” by Obst (1986). Going through the literature, it becomes evident that some controversy exists on this subject as other authors state that *M. emys* is found in the drier parts of the forest (Boulenger, 1912; Cox et al., 1998; de Rooij, 1915). It was also noted whether the tortoise was in or out of water. The term “in water” was defined as water bodies with a clear surface, independent of depth.

2.7.10 Morphometry

Study animals were measured using a flexible measuring tape to nearest half centimetre. Carapace length (CL) was measured as the straight-line distance from the tip of the precentral to the tip of the posterior marginals (figure 2.7.5). Curved Carapace Length (CCL) was measured from precentral scute to postcentral following the curves of the carapace. Plastron Length (PL) was measured as the straight-line distance between the gular and anal scutes. Plastron Width (PW) was measured as the maximum distance perpendicular to the midline seam.

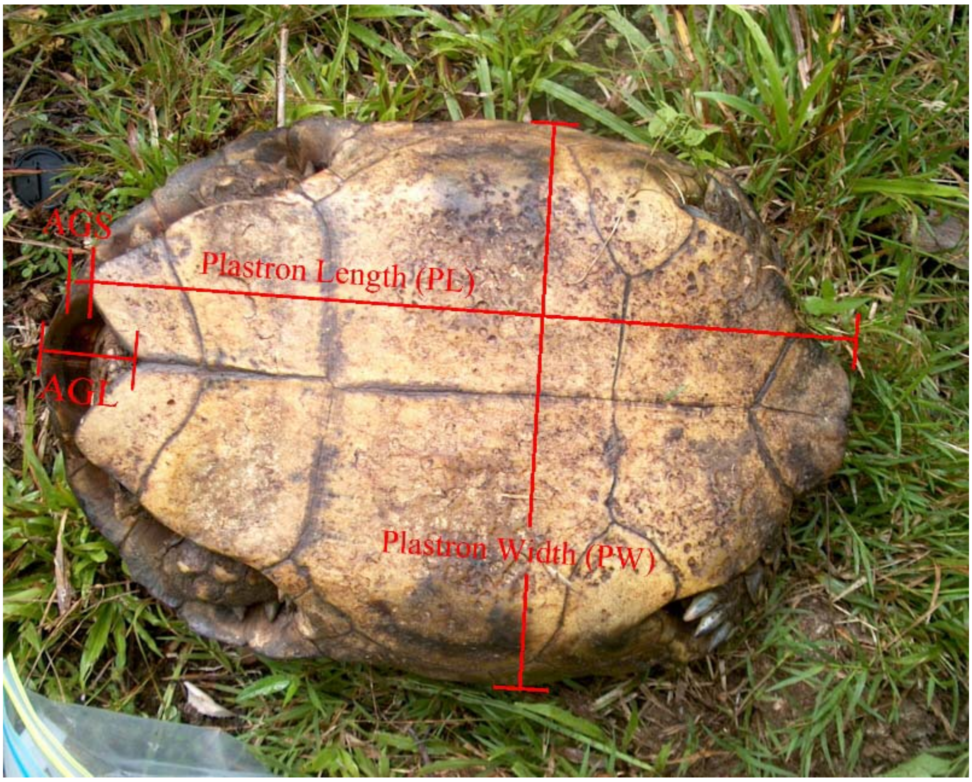


Figure 2.7.5. Morphometry measured on the plastron. Plastron length (PL), Plastron Width (PW), Anal Gap Short (AGS) and Anal Gap Long (AGL)

Tail Length (TL), Anal Gap Long (AGL) and Anal Gap Short (AGS) was measured, using a Vernier Gauge, to nearest millimetre.

TL was measured along the midline from the tip of the tail to the transition between the soft tissue and the postcentral scute.

AGL was measured from the notch between the anal scutes to the postcentral scute. AGS is the shortest distance between the tip of the anal scutes and the postcentral.

The morphometry study conducted in Thailand (Aranyavalai, 1996) only came to my attention after finishing fieldwork and thus no data on the length and width of the fifth central scutes were obtained.

Weight (W) was measured, using a 30 kg spring scale, to nearest 250 grams. A nylon string was tied around the middle part of the tortoise for attachment of the spring scale. Spring scale and tortoise was hung in a nearby tree and the scale was read when it had settled.

For documentation, pictures were taken using a digital camera (HP Photosmart 912). Pictures were taken of morphometric features such as carapace, plastron, scutes, tail etc. Whenever relevant, pictures will be presented to document findings of the present study.

2.7.11 Statistics

For all the parametric tests, the assumptions of normality and homogeneity of variances were tested using SAS. Data sets failing these tests were transformed. If the data still failed normality or homogeneity of variances after transformation, the appropriate nonparametric test were used.

The evaluation of ActiTrac was done by comparing the manually obtained data with the electronic recordings in dichotomous contingency tables. The statistic Φ was calculated using StatView 5.0 (SAS Institute inc., 1998) for each of the three tables (appendix II). Φ is the equivalent to the correlation coefficient r (Zar, 1999). In addition, a χ_c^2 (Chi-square corrected for continuity) test was used to test for independence between the two procedures.

Activity recordings from the ActiTrac were analysed using Oriana 2® Demo version (Kovach, 2004), which is a software, for handling circular distributions. Rao's Spacing Test (test statistic U) was used to test for directedness (Batschelet, 1981). The null hypothesis (H_0) being: The activity is uniformly distributed around a 24-hour circle. Rao's test was chosen as it is specially designed to handle circular data sets, which in this case are represented by time instants. In addition, Rao's test maintains its power even when dealing with multimodal samples (Batschelet, 1981). Mean vector (m) and length of mean vector (r) was used to determine the preferred direction/acrophases and the concentration of activity around m (Batschelet, 1981). Rose histograms of the ActiTrac data was generated in Oriana 2®. Test results are summarised in appendix VII

Temperature measurements were tested using the Mann-Whitney Rank Sum Test. The test for normality failed for all groups and transforming the data did so, violating the assumptions of a parametric test. Thus, a nonparametric test was chosen. Test results summarised in appendix VI.

The home range estimations were tested for correlation against the weight of study animals, length of tracking period and number of relocations. The test performed was Fisher's r to z (Zar, 1999), using StatView 5.0.

For all statistical testing the level of significance was set at $\alpha = 0.05$.

3 Results

3.1 Study animals

On 20th of April 2002 the search for study animals started. First approach was to walk along the main logging road and then cut trails in north-south direction. Nine trails were cut ranging in lengths from 0.5 km – 1.5 km. The search was not set up to be a transect model but merely a random search. As no guidelines for finding this particular species had been published prior to this study different search conditions were tried out. Early morning searches were performed on thirteen occasions with no results. Midday searches were done four times without results and late afternoon searches were done ten times.

Water sources were of great interest because of the habits reported for this species (see section 2.7.9) and areas with small streams or other water bodies were more carefully searched. However, a total of 88 search hours in the forest, from 20th of April until 9th of May, produced no evidence of *M. e. emys* at all.

3.1.1 First sighting

At 10.30 am in the morning of May 10th, the first specimen was found. While hiking between two campsites 21 km inside the reserve, a tortoise was found in a small clearing next to the trail. After weighing and measuring the animal, a transmitter (#F) was fitted to the lower back of the carapace and the tortoise was released. GPS coordinates of the location were recorded for later mapping. The location was on a steep hillside covered with secondary growth. The hill had been extensively logged and was traversed by a network of old logging roads. Except from two huge Menggaris trees (*Koompassia excelsa*) only the buttresses of the once emerging hard wood trees was evident. The forest was dominated by smaller trees reaching about 10-15 metres in height. The canopy was dense and the penetration of sunlight was very limited. The nearest water source was estimated to be at least 50 metres away and was a dried out stream bed with only few bodies of still water. The hill is outlined by tributaries of Sungai Tabin and no springs are present on the hill. Thus, the nearest perennial water sources are at the very bottom of the hill (approx 350 meters downhill).

3.1.2 Morphometry

In the original research proposal a total of ten study animals, preferably five males and five females, was set as a minimum in order to perform statistics with acceptable power. Shortly after starting the fieldwork, the half male half female setup was discarded, as all animals encountered had to be included in the project to at least get enough specimens.

Close up pictures were taken of the carapace scutes for age estimation. Growth ring count is visually estimated from the pictures. Estimates are not given for #C, #E, #DII, #G as growth rings were worn down. #DII had, in addition to worn down growth rings, signs of severe shell rot in the past. Age estimates are presented in table 3.1.2.

Figure 3.1.2. Closeup of fifth central scute (#F). The growth rings are very clear on this specimen. Age estimate is 25 years. Note the anterior part of the scute is broken.
Photo: Klaus Høybye-Mortensen

Animal ID	Age (years)	Mass [kg]	Carapace Length (CL) [cm]	Curved Carapace Length (CCL) [cm]	Plastron Length (PL) [cm]	Plastron Width (PW) [cm]	Anal Gap Short (AGS) [cm]	Anal Gap Long (AGL) [cm]	Tail Length (TL) [cm]	TL/CL
#A	23	13.0	42	47.5	43	32.5	2.1	5.8	10.3	0.25
#B	22	12.5	42	50	43	30.5	1.5	5.6	8.2	0.20
#C		15.0	44.5	49.5	43.5	33	1.4	5.6	10.9	0.25
#D	23	10.5	38.5	43	39	32				
#E		17.25	46.5	53	46	36.5	2.4	7.0	10.8	0.23
#F	25	8.75	38	42.5	36	28	1.8	4.5	8.5	0.22
#G		14.25	46	52	48.5	34	1.6	5.7	11.8	0.25
#H	21	17.0	48	56	46	34	1.1	6.5	8.8	0.18
#I	17	12.5	43	47	43	30	2.4	6.6	9.8	0.23
#J	23	11.25	42.5	46	43	30.5	1.2	5.0	11.7	0.28
#L	28	14.0	49	55.5	47.5	33.5	2.3	6.1	12.7	0.26
#DII		15.0	45	54	47	33	3.0	6.6	11.3	0.25
*	16	9.5	38	42.5	38.5	29	1.7	5.4		

Table 3.1.1. Morphometry data on all *M. e. emys* encountered during this study. The TL, AGS and AGL were not measured for #D as the transmitter failed and the individual was thus only seen once. Simple correlation analysis revealed no results usable for sex determination. * Animal not carrying a radio transmitter. Data not available for cells shaded grey

3.2 Diet

One of the objectives of this study was to establish a list of diet items eaten in the wild. During the first field trip, the method used to obtain these data was simply to search the immediate area when a tortoise was tracked. This method proved to be insufficient as only diet items eaten at the time or shortly before could be found. Therefore, a trailing device was made during the second field trip to enable the researcher to track back the path of the tortoise. Even then, it was very difficult to find traces of tortoises foraging. On a few occasions, direct observations of tortoises eating shoots off small herbs highlighted the problems. No clear signs were left that the herbs had been subject to tortoise foraging. Thus, if not directly observed to be eaten the smaller plants will most likely go unnoticed and consequently not be included in the diet list. When dealing with the larger plants the trailer proved to be a very successful tool as the signs here, were quite clear. The bite marks and imprints in the forest floor from the large pointed nails were obvious and unmistakeable.

When a plant was eaten by the study animals, a sample was brought back to Tabin Station for identification. If possible, the amount of food intake was estimated and an equivalent sample was taken back for weighing. During the study period a total of 22 diet items were collected (table 3.2.1), from seven different plant families. Of the 22 items collected 15 (68%) was of the genus *Alocasia*. Taro or elephants ear, which are the common names of *Alocasias*, are common along the logging roads in TWR. They are subsucculent herbs growing to different sizes depending on species. One species of particular interest is the arborescent (having the shape or characteristics of a tree) giant *Alocasia sarawakensis* (figure 3.2.1). It grows in open areas throughout the reserve and is closely related to anthropogenic activity and other disturbances such as landslips and tree falls. The smaller species of the genus such as *A. scabriuscula* and *A. wongii* were generally found within the forest under ever-wet conditions. When feeding on *A. sarawakensis*, only the leaf blade and petiole (leaf stem) were consumed. In young plants, a stem is not yet present and thus the whole plant was often eaten leaving only the root. As the plants grow bigger, a stem is grown more or less erect, often exceeding 50 cm. This makes it difficult for the tortoises to reach the petiole and they have to stand up against the stem in a vertical position to reach the edible parts (figure 3.2.1). In these cases the base of the petiole will be partly eaten and make up a full meal for the tortoise. On four occasions, the estimated equivalent of what was eaten by the study animals was collected and weighed. Weights were 168 g, 182 g, 187 g and 234 g.

Figure 3.2.1. #A eating *Alocasia sarawakensis*. To reach the leave stems the tortoise has to stand up in an almost vertical position. The stem is always left untouched. *A. sarawakensis* was the preferred food item observed in this study.
Photo: Klaus Høybye-Mortensen

On two consecutive days #L was observed eating mushrooms from the forest floor. In both cases, the mushroom was covered by leaf litter and thus not visible. The mushrooms could not be named as they were both eaten before any documentation such as pictures could be obtained. The flower of a wild ginger (*Etlingera coccinea*) was eaten by #L on one occasion (species confirmed by Poulsen, pers. comm.). The flower has bright red and yellow colours and once noticed by the tortoise, it went straight in the direction in a much-focused manner.

Family	**Species or genus name (Common name)**	**Part(s) eaten**	**Number of collections/ observations**	**Study animals (number of occasions)**
Fungi	Unidentified	Whole mushroom	2	#L (2)
Melostomataceae	*Clidemia hirta* (Koster's Curse)	Shoot	1	#L (1)
Araceae	*Alocasia* sp. Scabriuscula Group (Taro)	Leaf and petiole	6	#C (1), #H (1), #DII (1), #L (3)
	Alocasia sp. (Taro) Group or species unidentified	Leaf and petiole	2	#F (1), #L (1)
	Alocasia sarawakensis (Taro)	Leaf and petiole	7	#A (1), #D (1), #E (2), #I (1), #DII (1), #L (1)
Begoniaceae	*Begonia* sp.	Shoot	1	#L (1)
Marantaceae	*Phrynium* sp.	Shoot	1	#L (1)
Woodsiaceae	*Diplazium esculentum* (Vegetable fern)	Shoot	1	#DII (1)
Zingiberaceae	*Etlingera coccinea* (Wild ginger)	Flower	1	#L (1)

Table 3.2.1 Plant species found to be eaten by the study animals. All plants were identified to at least genus and if possible to species, except for the two fungi eaten by #L.

No animal matter was recorded eaten by any of the study animals during this study. Drinking actively from water bodies or licking dew off objects was not observed.

3.3 Home Range

Relocating the study animals was of great importance in data collection for home range estimation. However, problems in the beginning of the study with the arrangement and attachment of the transmitter batteries lead to the loss of two study animals before any relocations could be obtained. No signals were emitted by the radio transmitters on the days following attachment. This is ascribed to disconnection of the batteries coursed by the animal moving under sturdy objects, e.g. branches or roots. On two occasions, the radio transmitters began emitting signals in a continuous manner. The tortoises were relocated and the problem solved by resoldering the transmitter-battery connection. The new design proved to better withstand the wear and tear from the environment.

During the first field trip, ten animals were radio tagged. Three of those were lost due to transmitter failure. The remaining seven had the batteries changed shortly before my departure from TWR at the end of the first field trip. The battery lifetime was calculated/expected to be at least seven months and should thus be sufficient to keep the transmitters running until my arrival some six months later.

Unfortunately at my arrival for the second field trip no signals were received from any of the seven transmitters. Three transmitters left at Tabin Station were also out of battery. This was of course a major setback as relocations of the study animals was impossible without the transmitters operating.

New study animals had to be found very quickly to make the second field trip at least somewhat successful. After four days search, on a very lucky Sunday, two animals (#DII and #L) were found during a road search. #DII was located a few metres from a recently eaten *Alocasia sarawakensis*. Using *Alocasias* as search image for locating the tortoises again proved efficient. #L was found when crossing the logging road shortly before.

The home range estimates for tortoises relocated five or more times are presented in table 3.3.1. The estimates are highly variable, ranging between 0.01-1.81 km^2 for the confidence ellipse method (CEM). As predicted, the convex polygon method (CPM) produces home range estimates smaller than the confidence ellipse method.

Study animal	**Body mass [kg]**	**Monitor period [days]**	**Number of loci**	**Convex Polygon [km^2]**	**Confidence Ellipse [km^2]**
#B	12.5	64	6	0.11	0.69
#C	15	12	5	0.04	0.07
#E	17.25	36	9	0.002	0.01
#F	8.75	67	9	0.25	1.55
#H	17	23	11	0.01	0.03
#J	11.25	18	9	0.01	0.03
#L	14	37	17	0.51	1.81
#DII	15	31	10	0.05	0.24
Danum Valley	N/A	53	58	0.3	0.97

Table 3.3.1. Home range estimates for the eight individuals followed in this study. Note the differences between the convex polygon and confidence ellipse estimators. The Danum Valley female is included for comparison.

Statistical testing (Fisher's r to z) showed no correlation between the home range estimates (CEM) and body mass ($r = -0.55$, $z = -1.37$, $p = 0.17$), monitor period ($r = 0.63$, $z = 1.67$, $p = 0.10$) or number of loci ($r = 0.55$, $z = 1.38$, $p = 0.17$). Test statistics for both CEM and CPM are reported in appendix V.

From all the coordinates obtained at relocation sites maps could be constructed using MapInfo. As the study animals were found at different sites along the logging road smaller section maps are presented in the following pages. Please note that the section maps (1-5) have different scales. The lines between the loci do not represent the route followed by the individual tortoises. The actual routes followed were not recorded except for cases where the trailer thread method was employed. Additionally, GPS coordinates of the known routes were not recorded due to the difficulties regarding satellite reception.

The confidence ellipses for #L and #DII outlining the home range estimates are shown in figure 3.3.2. These are excluded from the section maps, as they would confuse the picture.

Daily movements ranged from 0 to 390 metres (beeline distance). However, the actual distance travelled exceeded the beeline distance by an average of 87% ± 90 in five cases where the trailer thread was collected and measured (table 3.3.2). A trailer thread of 200 metres proved to be insufficient on a few occasions for #L as this individual had a high level of activity throughout the monitoring period.

Tortoise ID/Date	**Beeline distance [m]**	**Trailer thread distance [m]**	**Difference**
#DII/2-3.02.03	51	98	92%
#L/4-5.02.03	73	102	40%
#L/18-19.02.03	10*	34	240%
#L/2-3.03.03	107	133	24%
#L/4-5.03.03	133	182	37%

Table 3.3.2. Beeline distances between loci on consecutive days and the actual distance travelled based on the trailer thread collected and measured. * Directly measured with measuring tape. Mean difference is 87% ± 90 (SD).

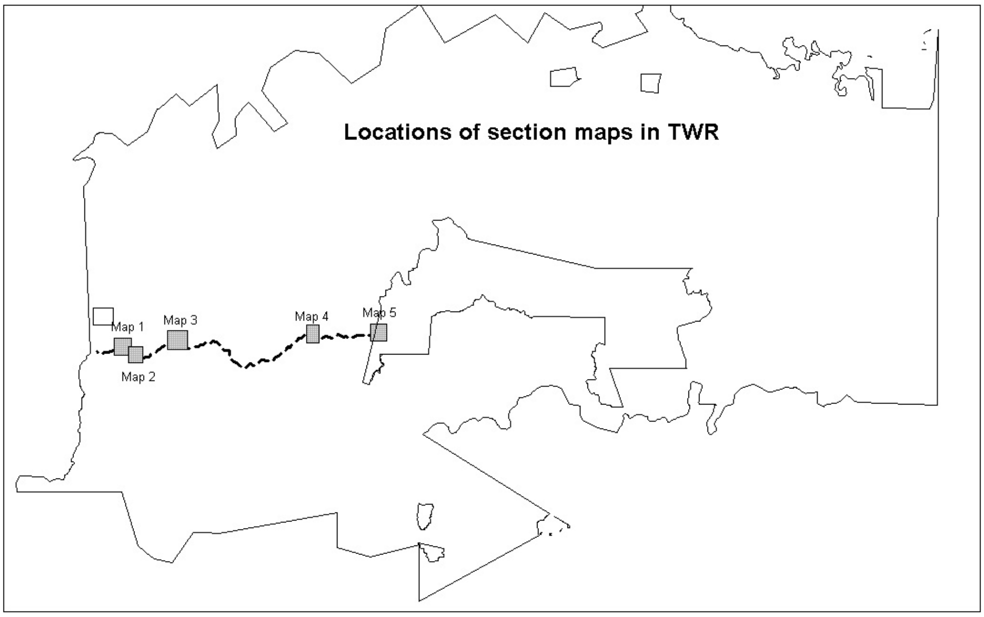
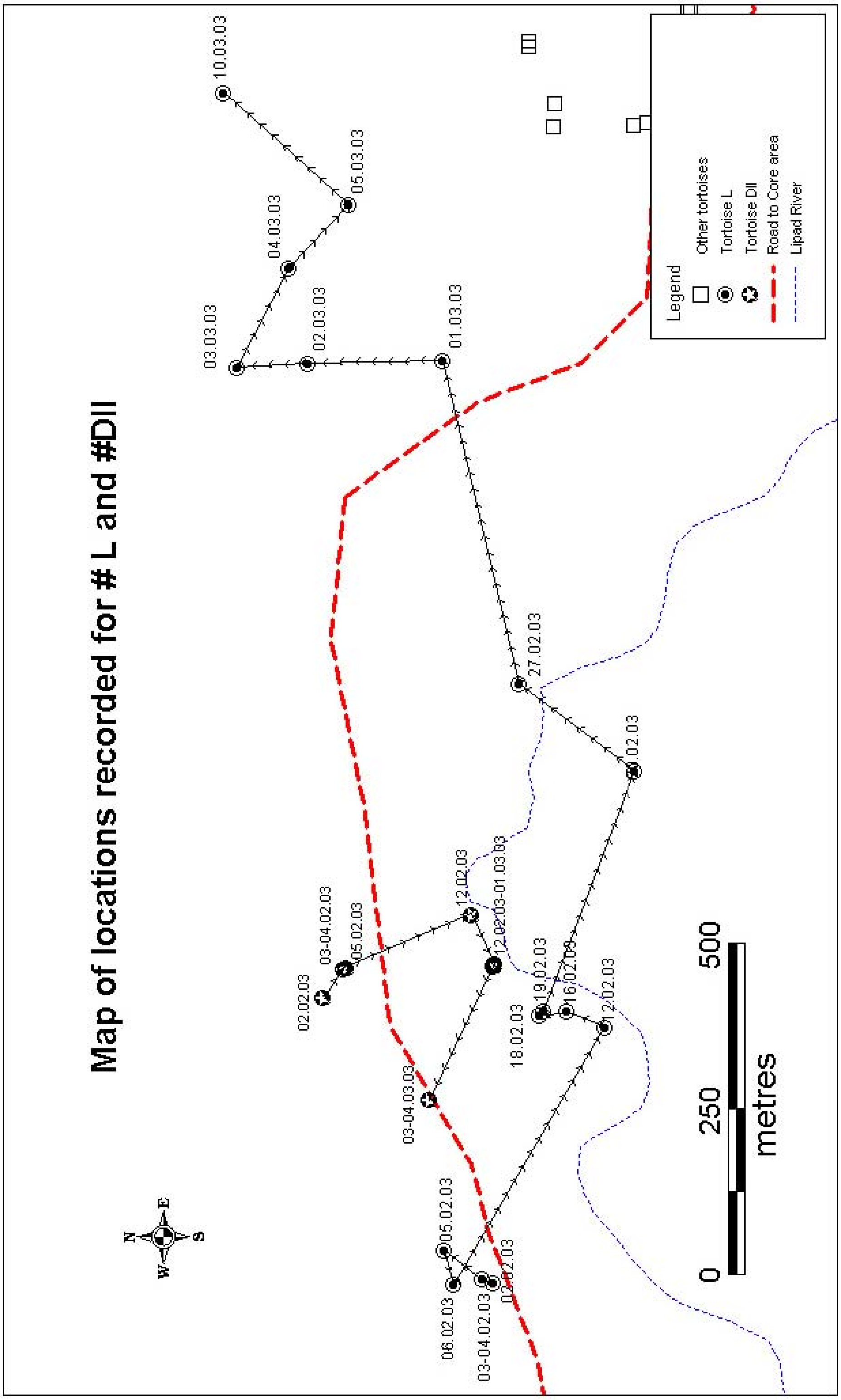
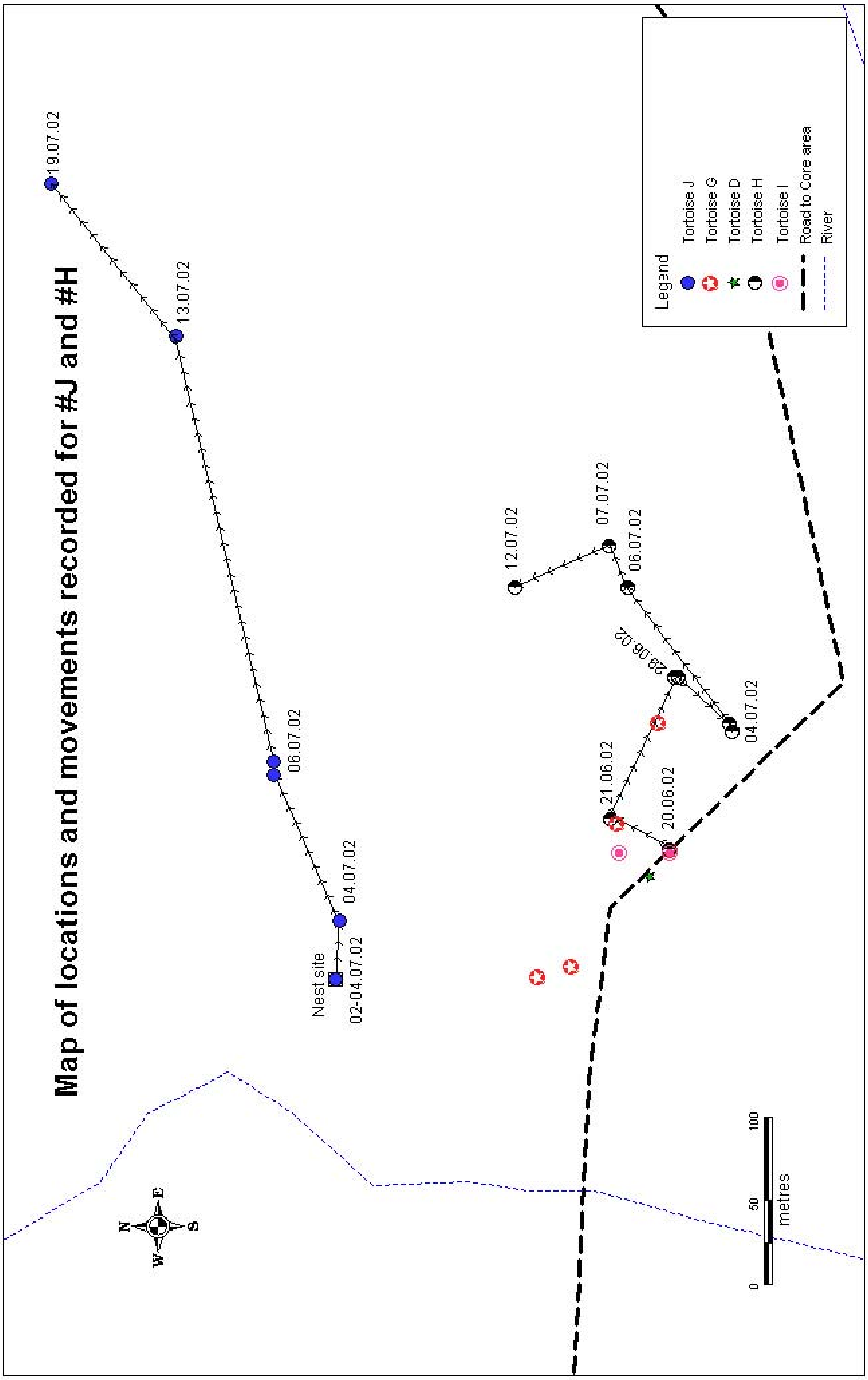


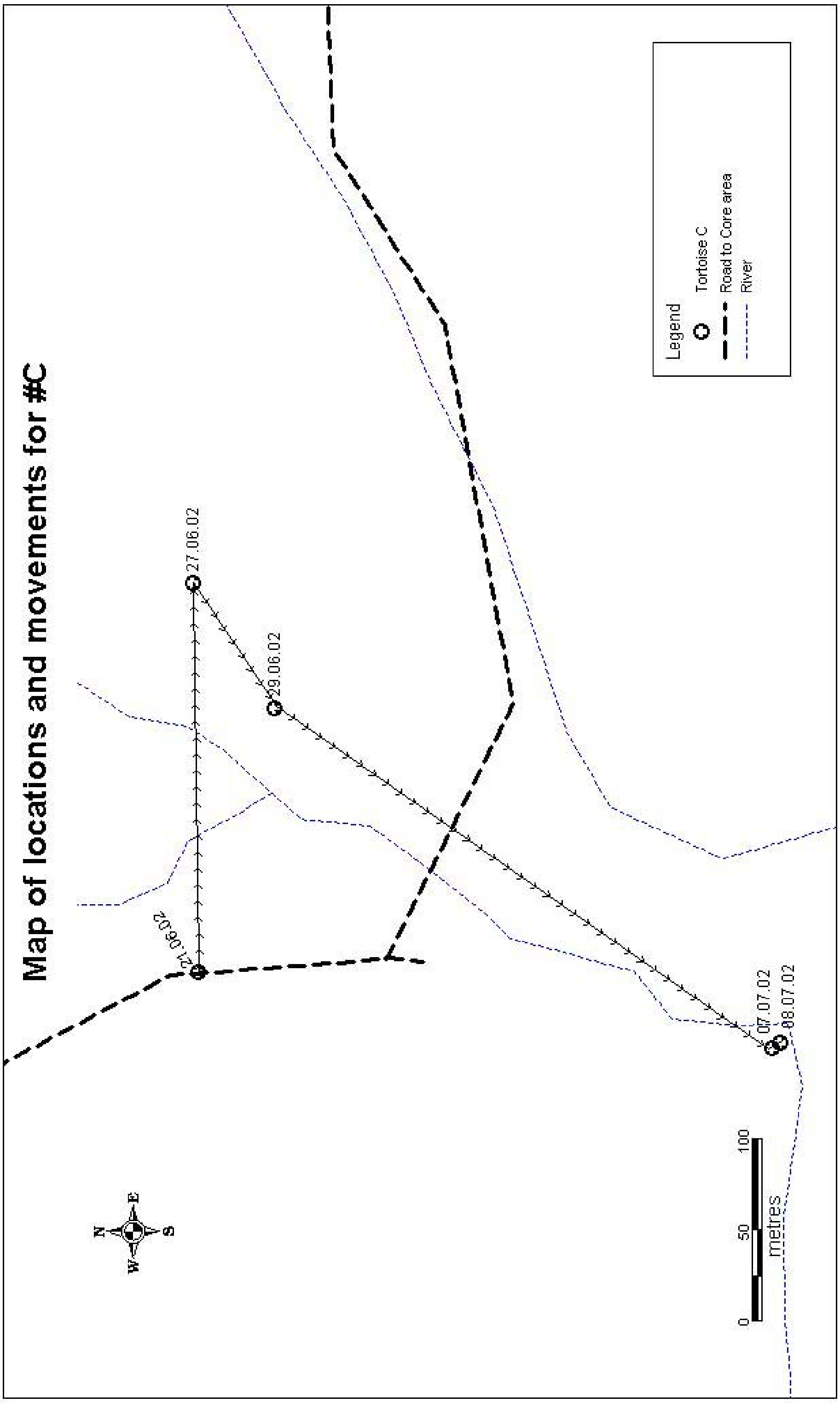
Figure 3.3.1. Map of TWR showing the areas (grey squares) presented in the following section maps (1-5). Note: the section maps have different scales.



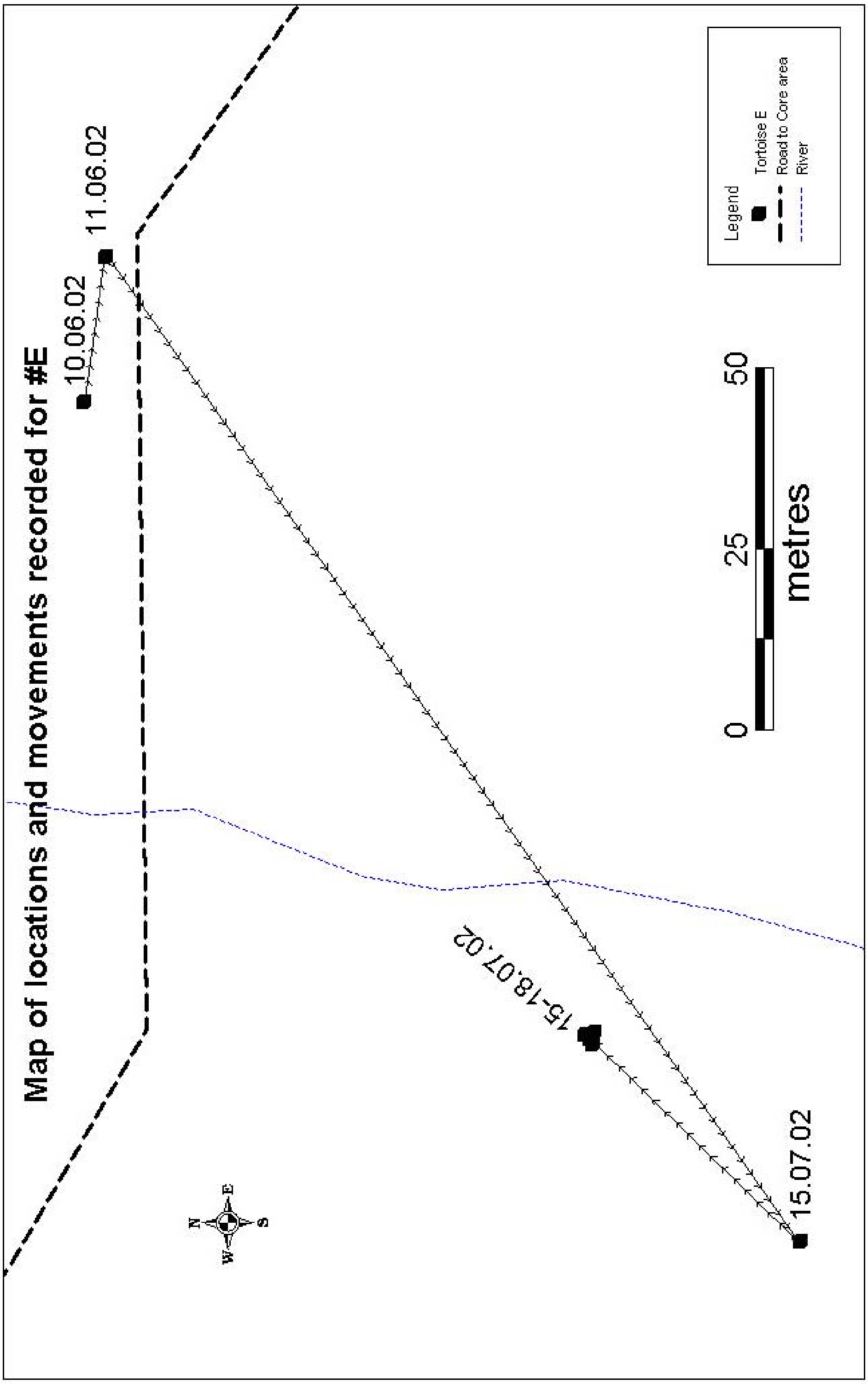
Map 1. The locations where #L and #DI was found during February and March 2003. Lines between locations are direct beeline and not actual routes used by the animals.



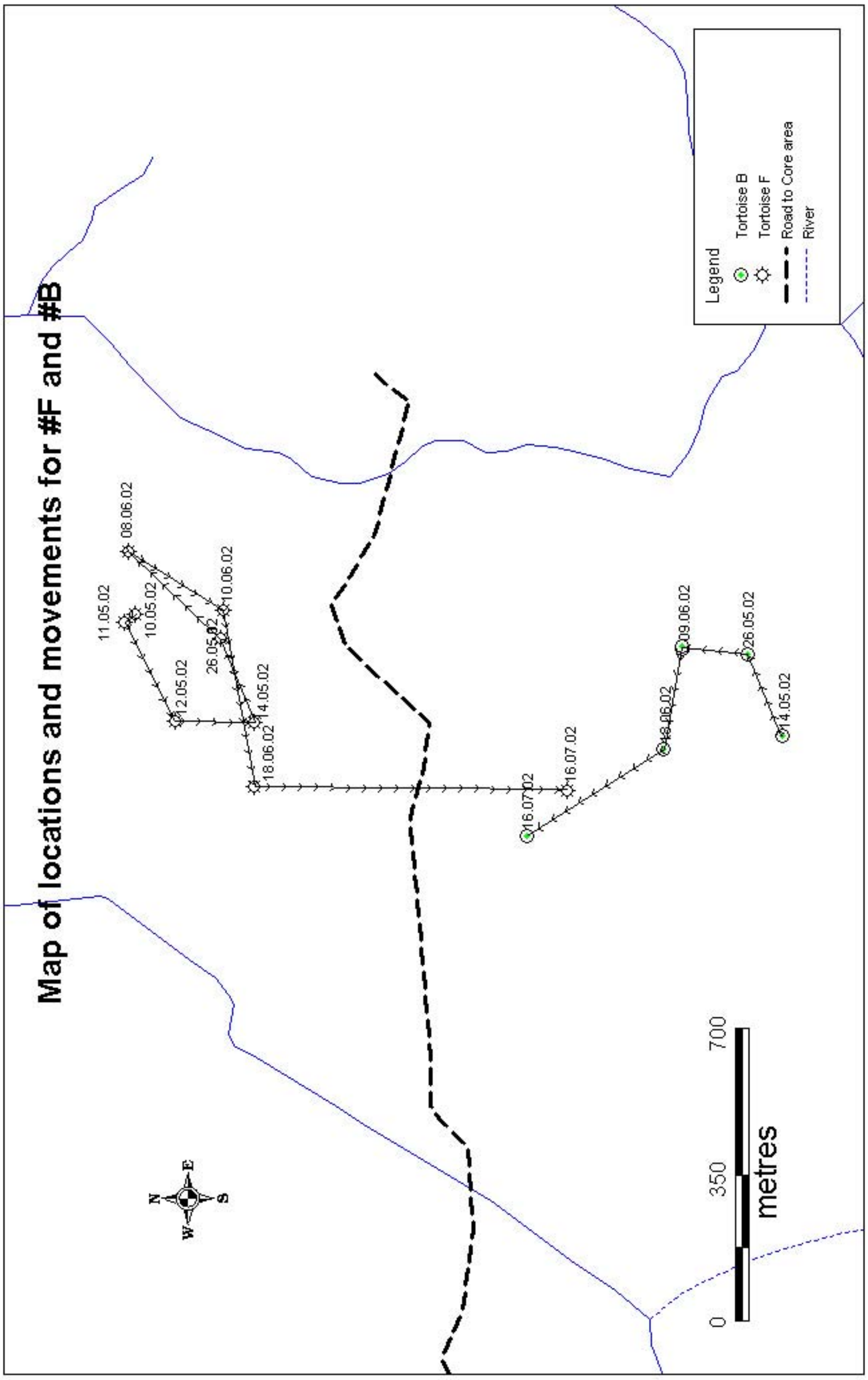
Map 2. Locations for #D, #G, #H, #I and #J. Home range is not estimated for #G, #D and #I as they were only relocated a few times due to radio transmitter failure. Note the nest site used by #J.



Map 3. Locations recorded for #C. Lines between points are direct beelines. The tortoise probably followed the dried out streambed between 29.06.02-07.07.02.



Map 4. Locations recorded for #E. Some time between 11.06.02 and 15.07.02, during a dry spell, it crossed the river. Between the road crossing and beeline crossing (line with arrowheads) the river was very low and the bottom consisted of flat sand banks



Map 5. Locations for #B and #F. During the two months of observations #F was found in the dry parts of the forest, circling round a hilltop covered with secondary growth. #B was found in a small pool of water on the 9th of June.

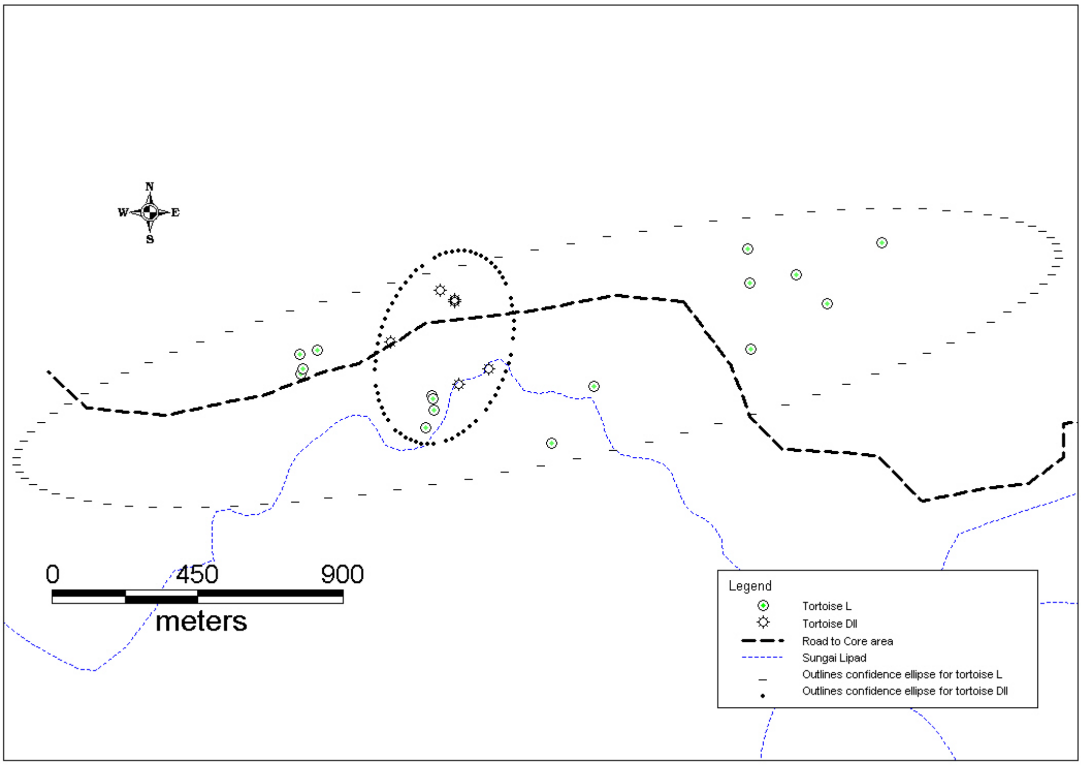


Figure 3.3.2. Location map for #L and #DII with the confidence ellipses, road and river (Sungai Lipad) plotted. The ellipses were generated from the formulas given by Batschelet (1981). The home range estimates (areas enclosed by ellipses) vary greatly between the two individuals. #L was tracked for 37 days (home range estimate = 1.81 km^2) and #DII for 31 days (home range estimate = 0.24 km^2) during February and March 2003. Even though the home range of #DII is almost encircled by that of #L the two tortoises were never closer than 80 meters to one another. Note: the stretching of the ellipse for #L in the latitudinal direction. This is a consequence of non-normal distribution of relocation coordinates in that direction. This leads to an overestimation of the home range (Ackerman et al., 1990).

3.4 Activity

During the first field trip observations on activity was accomplished manually. Whenever a tortoise was tracked, its activity was noted. On several occasions, observations were continued for longer periods (up to five hours) in order to establish an ethogram for quantification of activity. This method proved to be very laborious and no results were collected. There were various reasons for that. Primarily, tortoises showed no activity when encountered on the majority of encounters. In most cases, they would be hiding under debris or in dense vegetation. Secondarily, any tortoise exhibiting activity would become immobile, when an observers presence was detected. This behaviour continued for the rest of the observation period. Only two of the study animals (#L, #J) would perform any activity in the presence of an observer and did so only on a few occasions. In light of these circumstances, the methodology required alteration or enhancement in order to achieve any activity results.

Two study animals were fitted with ActiTrac devices for sampling of activity data. The sampling epoch was set at 2 minutes and highest sensitivity (×8). Results are graphically presented in figures 3.4.1 and 3.4.2. From the ActiTrac scoring reports (table 3.4.1) for the two data sets it is seen that #L had an active/inactive ratio of 15.4%, while #DII had a ratio of 2.3%. Differences in average activity duration are negligible, whereas the difference in average inactivity duration is more than five fold. In figures 3.4.1 and 3.4.2 it is seen that #DII tended to have short active periods followed by relatively long inactive periods when compared to #L. The longest inactive period for # DII was 9816 minutes but in fact the animal did not move (no displacement recorded based on trailer thread) between February 12th 13:50 and February 25th 9:34 when it moved 20 metres away and ate an *Alocasia*. This activity lasted 44 minutes after which the tortoise went back to hiding only two metres from its previous hide. It remained inactive in that position until March 1st 13:45. The active period just before noon on February 18th is due to handling of the animal while downloading data from the ActiTrac. Thus, this individual remained stationary for 17 days except for a 44 minutes walking and foraging bout.

Nocturnal activity was only recorded for #DII. On the evening of February 5th between 18:52 and 21:32, the tortoise moved to a new hide 130 metres southwest of the location of first encounter. Again, on February 11th a short active period starting at 22:00 was recorded, lasting six minutes. No displacement occurred during this period. #E was observed twice during night time and was both times found to be inactive.

Individual	**#DII**	**#L**
Duration of scoring	40080 minutes	48780 minutes
Total inactive time	39168 minutes	42286 minutes
Total active time	912 minutes	6494 minutes
Active/Inactive ratio	2.3%	15.4%
Longest active period	76 minutes	268 minutes
Shortest active duration	4 minutes	2 minutes
Average active duration	16 minutes	20 minutes
Longest inactive period	9816 minutes	2502 minutes
Shortest inactive duration	2 minutes	2 minutes
Average inactive duration	687 minutes	129 minutes

Table 3.4.1. Summary table for the ActiTrac scoring reports.

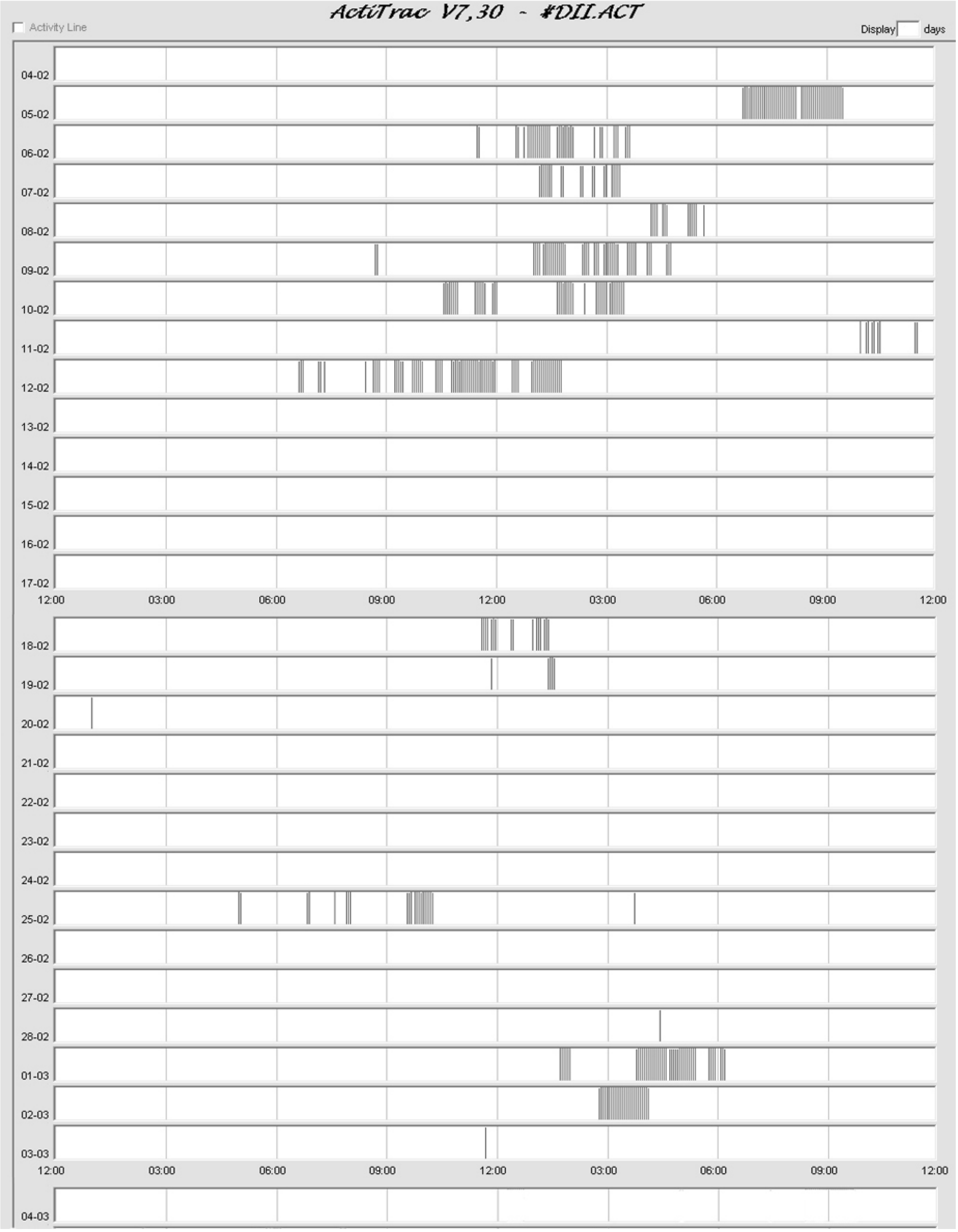


Figure 3.4.1. Bar chart of the ActiTrac recordings for #DII. Bars represent activity. Center of chart (12:00) is midday. Number to the left of each horizontal white bar is the date of recording.

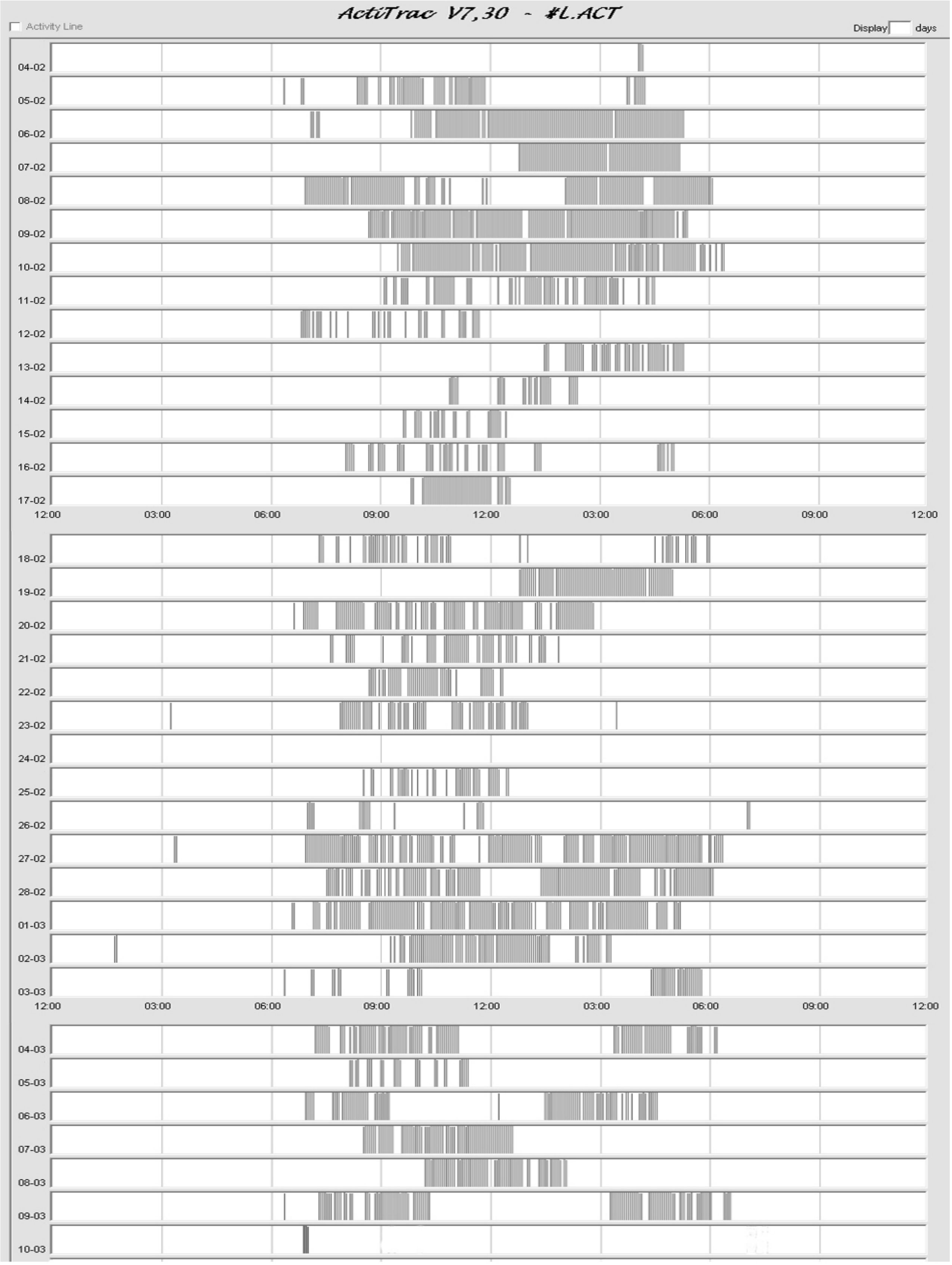
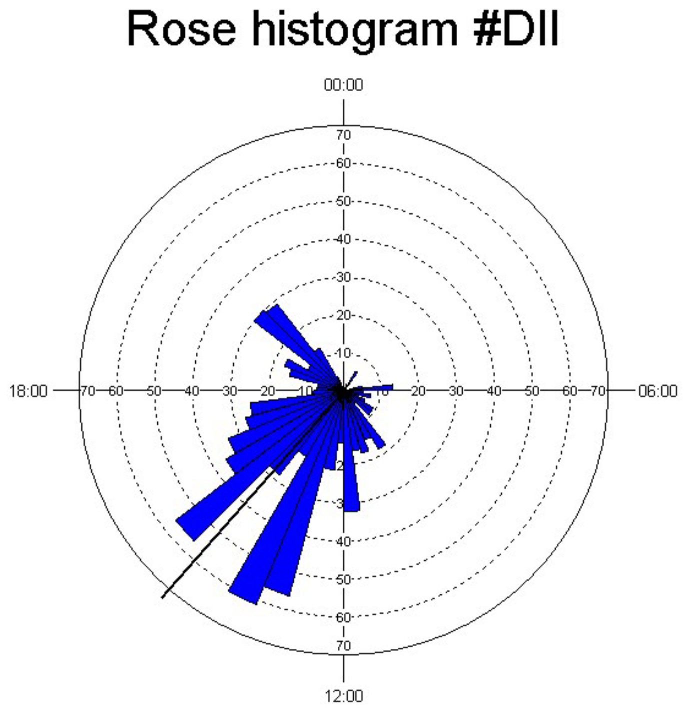


Figure 3.4.2. Bar chart of the ActiTrac recordings for #L. Bars represent activity. Center of chart (12:00) is midday. Number to the left of each horizontal white bar is the date of recording.

The results from the ActiTrac monitors were then used to test for directedness in the two sets of data. Results are shown in table 3.4.1. Rao's Spacing test showed distributions significantly different from the uniform distribution. Thus, there exists some sort of directedness (i.e. preference for time of day) in the two data sets. This is also apparent when looking at the rose histograms (figure 3.4.3). Mean vectors (m) for the two data sets were also calculated in order to determine the time of day at which the acrophase (the time of day when an individual is typically at its greatest arousal or energy level) for the individuals was centred. For #DII the acrophase was clustered around 14:45 and for #L around 12:32. The mean vector length (r) is an expression of how the data is distributed around the circle. In a unimodal distribution the mean vector length serves as a measure of concentration. For $r = 0$ the sample data has no concentration and is thus evenly distributed around the clock. As r gets closer to one the concentration increases around a single point (the mean vector). The values of r for #DII and #L respectively are 0.556 and 0.716.

Test performed	#DII (n=691)	#L (n=3567)
Mean vector (m)	14:45	12:32
Length of mean vector (r)	0.556	0.716
Rao's Spacing Test	U = 162.43 ($p < 0.01$)	U = 321.65 ($p < 0.01$)

Table 3.4.1. Summary table of test results for uniform distribution around the 24 hour circle.



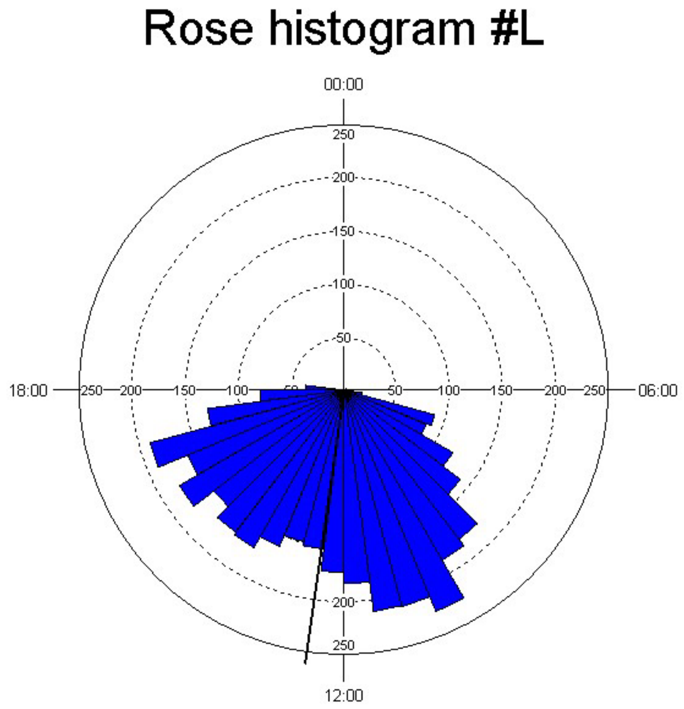


Figure 3.4.3 The Rose histograms show the accumulated number of epochs in which activity occurred during the sampling periods (29 days for #DII and 32 days for #L). Axis denotes number of epochs. Note that the axis scales of the two histograms are different. The data has been grouped in 30 minutes intervals (blue bars). The black line indicates the mean vector (m) of the ungrouped data. For #DII m = 14:45 and for #L m = 12:32.

3.5 Habitat

In this section, a qualitative rather than quantitative description of the preferred habitat types and features will be presented. As described in sections 2.7.8 and 2.7.9 different variables were measured and recorded every time a study animal was tracked (appendix III). From the site descriptions, trends and preferences for the different variables are qualitatively described.

3.5.1 Forest type

From the forest type classification data (table 3.5.1), it is seen that the study animals occurred in both primary and secondary forest types. As most of the tortoises were initially encountered along the main logging road, in what is generally considered to be secondary forest, it is not surprising that most encounters (71%) occurred in secondary forest. This introduces bias in the data collected that could lead to the conclusion that *M. e. emys* prefers the secondary forest.

N = 87	**Forest type**		**Canopy cover**		
	Primary	Secondary	Open	Semi	Full
Number of observations	25	62	10	20	57
Percentage of total obs.	29	71	11	23	66

Table 3.5.1. Summary of habitat classifications. After every animal encounter (N=87), the surrounding habitat was classified into the different qualitative groups specified in section 2.7.9.

Study animals were generally found inside the forest as opposed to gap phases and old logging roads. From table 3.5.1 it is seen that the study animals preferred places with full cover canopy in 66% of the observations. Finding the tortoises in open sites (canopy lacking) was associated with foraging on *Alocasia*s in seven out of ten cases. Only once a tortoise was found positioned directly in the sunlight, in a way that could be interpreted as basking. However, a recently eaten *Alocasia* stood a few meters next to the animal in the same gap phase, which makes it more likely that the animal had just eaten and was on its way towards the dense vegetation.

3.5.2 Temperature and microclimate

From the measurements of temperature and relative humidity taken next to study animals when relocated, the preferred microclimatic conditions were found. The overall mean microclimatic temperature (T_M) was 26.4°C ± 1.5 (n = 88). Figure 7.5.1 shows the means ± SD of both T_A and T_M measurements, grouped into two-hour intervals. The ambient temperature (T_A) was measured during February and March 2003, one kilometre from Tabin Station.

The microclimate temperatures were collected over the whole study period. The two-hour groups 18:00-20:00 and 22:00 hours until 06:00 hours are left out, as no encounters happened during those intervals.

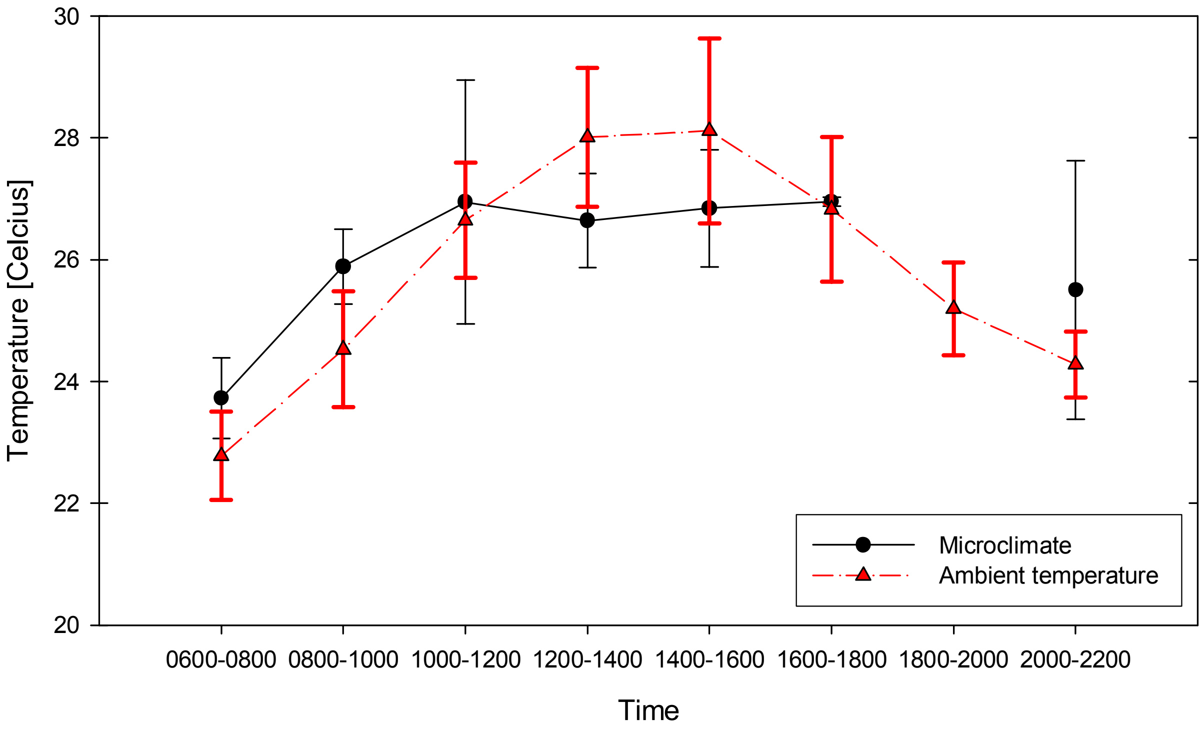


Figure 3.5.1. Temperature readings from tortoise encounters. Mean ±SD. Note the lower mean temperatures preferred during midday observations compared to the ambient temperature measurements. Overall mean temperature for microclimate is 26.4°C ± 1.5. Note: Statistics were performed on the medians (not shown here). However, the differences between the medians and means are negligible.

The median T_A of each group is tested against the median T_M using the Mann Whitney Rank Sum test. The statistics are summarized in table 3.5.1. From sunrise until midday, tortoises tend to choose microclimates with higher temperatures than the ambient. In the afternoon when ambient temperatures rise the tendency is reversed. From sunset (around 18:00 hours) and onwards the morning tendency seems to be repeated. The overall mean ambient temperature during daylight hours was 26.2°C ± 2.2 and for the dark hours 23.7°C ± 1.0.

Time	MedianT_M	Median T_A	U	*p*
06:00-08:00	23.9(5)	22.7 (170)	745.5	0.006
08:00-10:00	26.0 (9)	24.5 (137)	1156	<0.001
10:00-12:00	26.2 (27)	26.6 (140)	1876.5	0.089 (ns)
12:00-14:00	26.4 (17)	28.1 (140)	532	<0.001
14:00-16:00	26.8 (20)	28.1 (140)	857.5	<0.001
16:00-18:00	27.0 (4)	26.6 (140)	289.5	>0.9 (ns)
18:00-20:00	-	-	-	-
20:00-22:00	25.5 (2)	24.5 (136)	167	0.624 (ns)

Table 3.5.1. Summarized two tailed Mann-Whitney statistics for T_M vs. T_A . Temperatures are medians (n).

Temperatures were measured, in ten minute intervals for three days, at the site of the twelve days inactive period recorded for #DII (figure 3.4.3). The overall mean temperature in the hide was 24.6°C ± 0.9. It is seen from the graph that the daily variations are less than for the measurements recorded at breast height (T_A, figure 3.5.2). Thus, the hides provide a stable microclimate for resting individuals without imposing stressors such as overheating. This enables the animal to stay in the same place for prolonged periods and consequently conserve energy.

Relative humidity was above 90% except in four cases when tortoises were found uncovered in gap phases. The preferred hiding places were under fallen logs or under piles of rotting debris. Two things seemed to be essential in choosing hide, darkness and high humidity.

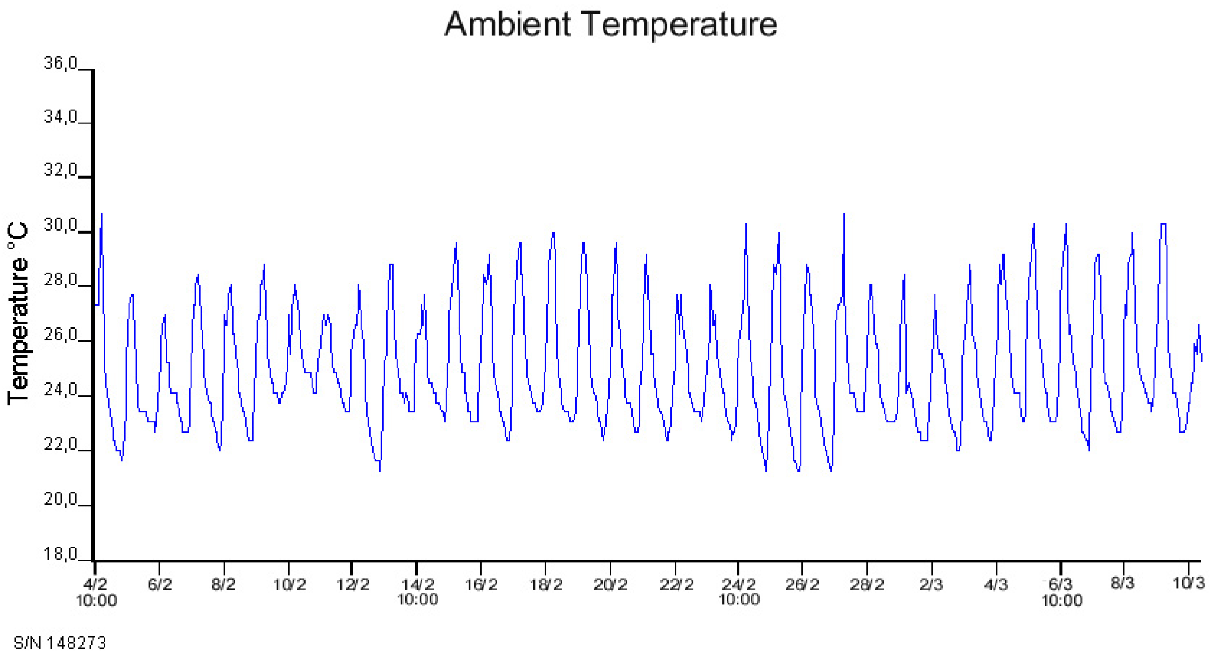


Figure 3.5.2. The ambient temperature (T_A) measured at breast height. Temperatures were measured every half hour. The site had full canopy cover. Minimum reading = 21.3°C, Maximum reading = 31.4°C, Mean = 25.0°C ± 2.1

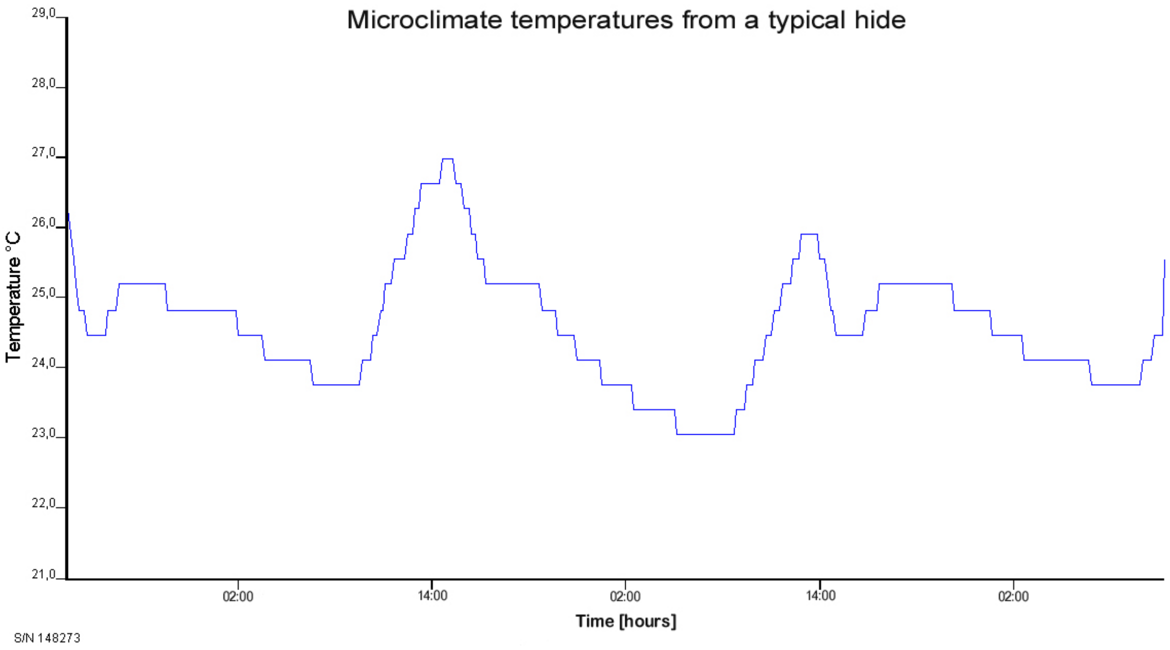


Figure 3.5.3 Temperature measurements in the hide used by #DII for twelve days. Duration of temperature measurements is three days, measuring every 10 minutes. Minimum reading = 23.0°C, Maximum reading = 27.0°C, Mean = 24.6°C ± 0.9. Note the minimum and maximum temperatures and smaller daily fluctuations comparison to the measurements of ambient temperature (figure 3.5.2.).

Temperature and relative humidity was also recorded in the surrounding oil palm plantations during four random searches for tortoises. Temperatures tended to be a few degrees above (29.3°C ± 0.8) the measurements in both the disturbed and undisturbed parts of the forest. Relative humidity ranged between 73% and 86%, (n=9).

3.5.3 Water

Distance to the nearest water body was measured in order to shed light on the diverging opinions about the preferences for still or flowing water, shown by *M. emys*.

On six occasions, study animals were found in water, of which three were recorded within 15 hours on the same individual (#E). Two occurred while #C followed a small streambed for several of days, one of which was associated with foraging on *Alocasia*, and the last was recorded for #B. This accounts for 7% of all tortoise encounters during this research. Study animals were recorded to be 50 metres or more away from nearest water source in 73% of all encounters and less than 50 metres distance in 20%.

From 17.00 hours on the 10th of June 2002 until 06.00 hours on 11th of June #E stayed submerged, only leaving the head above the surface, in a pool of water underneath two fallen logs (figure 3.5.4). If this was an attempt to thermo regulate is uncertain, as water temperature was not measured. The microclimate temperature was 28.6°C when measured two hours earlier that day, as the tortoise was radio tagged. The tortoise was also submerged in a pool of water when first encountered, though not as deep as the latter. However, in both cases the soft body parts was fully submerged.

Figure 3.5.4. #E submerged in a pool of water. Large ring encloses the head of the tortoise. Small ring encloses the radio transmitter (submerged). The pool was totally covered by two logs left from old logging activity. Photo Klaus Høybye-Mortensen

When first encountered it was noted that #E had a load of approx. ten hard ticks (Ixodidae) on the soft parts of all four extremities. An attempt to get rid of the ticks might be one explanation for the submersion.

River crossings occurred at least three times. During a dry spell (June and July 2002) #E crossed Sungai Tabin which is one of the major rivers in the reserve. At that time, the water level had dropped quiet significantly and depth was in many places below 30 cm leaving a number of opportunities for crossing. #L crossed Sungai Lipad and one of its tributaries in February 2003, again water level was low. This indicates that the major river systems do not constitute migration barriers, which could lead to isolation and subsequent development of subpopulations in the reserve.

3.6 Nesting behaviour - a case story

On July 2nd, 2002, a nesting female was found. While searching for an individual on the west side of a small hill, I observed a tortoise exhibiting highly unusual behaviour. On approach, the tortoise stood up on all four limbs with fully stretched neck as if trying to look bigger. This was the first and only time any individual showed this, somewhat aggressive/defensive behaviour towards me. After half a minute of displaying in this position, the tortoise turned round and went for a small mound two meters behind it. It then laid flat on top of the mound with the four limbs fully stretched out. At this point, I surmised that this was a female building a nest (nest site is marked in Map 2, p. 38). This was confirmed when the female was lifted off the mound and the, at this time, few centimetres thick layer of withered leaves and twigs was gently swept aside. Underneath was a shallow egg chamber dug out in the debris already collected. Oviposition had already taken place. The eggs were pale white and slightly oval shaped and approximately 6-7 cm long and 4-5 cm wide. In order to avoid disturbance and to prevent the female from rejecting completion of the nest, it was quickly reassembled and she was replaced in her original position . Thus, no measurements were taken and the exact number of eggs was not recorded.

Figure 3.6.1. Female *Manouria e. emys* on her nest. The nest site was covered by a withering bush shading out sunlight. Nest material consisted of twigs and withered leaves. Diameter of nest was 110 cm and height was 25 cm. Photo Klaus Høybye-Mortensen

After this initial observation, I sat down five meters away from the nest and waited for the female to act. After a few minutes, she started back sweeping twigs and leaves on to the mound. From this moment, she didn't seem to notice my presence any longer. The following days when arriving at the scene the female would stop scraping only for a few minutes until I had settled to start observations, and then continue back sweeping. On all other close encounters with tortoises during this study, tortoises always stopped their present behaviour and withdrew head and limbs.

The site of the nest was 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. This location was most likely chosen to ensure that the nest was protected against flooding and water running through after heavy rainfalls. The canopy was very dense and the site was always shaded from direct sunlight. On the steep slope edge of the mound was a withered bush leaning over the mound in such a way that it made a roof in the same manner as an open shed (figure 3.6.1). Thus, the selected site was very well protected against heavy rains as well as direct sunlight.

The following two days I returned to the nest site to do *ad libitum* observations. The following is notes taken during one hour of observations on July 3rd, 2002:

11:58 back sweeping with one front leg while the other holds position on the nest. Changes between the front legs after 3-4 back sweep motions. After each change of leg, the tortoise rotates slightly on the nest such that the back sweeping takes place in a new place.
12:00 Collecting new material next to the nest. Back sweeping while backing towards the nest.
12:06 Resting on top of the nest. Sniffing the top of the nest.
12:08 Sniffing and then starting back sweeping again.
12:11 Collecting new materials (always by back sweeping). Choosing another direction as the one used at 12:00.
12.17 Back sweeping on the nest. Same movement pattern as described for 11:58.
12.19 Using hind legs to stamp the material on top of the nest.
12:22 Sniffing while turning around on top of the nest.
12:26 Back sweeping on the nest.
12:28 Collecting new materials. Again in a new direction from the nest.
12:32 Returning to the nest with the new materials. Starts back sweeping on the nest.
12:35 Resting on top of the nest. The tortoise only rests on top of the nest.
12:36 Sniffing at different parts of the nest.
12:37 Starts back sweeping on the nest.
12:41 Using hind legs to stamp materials on top of the nest.
12:44 Back sweeping on the nest.
12:46 Rests on top of the nest. This continues until the observation is ended at 12:58.

July 4th, somewhere between 11:00 and 15:45, the female left the nest and moved 40 meters east of the nest site where she rested in a pile of branches and leaves. The following days the tortoise moved further away from the nest until it was last seen on July 19th, 500 meters east of the nest site (see Map 2, p. 38).

After #J had left the nest site the nest mound was measured. Diameter of the mound was 110 cm and height was 25 cm. The mound was surprisingly hard stamped and sturdy in comparison to any other pile of debris naturally occurring in the forest. The tortoise had collected nest material up to a distance of 3.40 meters away from the nest. Nest material consisted of withered leaves and twigs from the forest floor and only very few fresh herbs. As the nest site was delimited by a dense withered bush along the edge of the slope, material was only collected within an angle of approx. 180° on the flat terrain on the other side.

When returning to the nest site on the 12th of July to count, weigh and measure the eggs, the nest had been dug up by some predator. All eggs had been eaten except for the shells. The eggshells were left on top of the nest or right beside it. No shells were found more than 2 meters from the nest even after a search in the immediate area. This suggests that the predator ate the eggs right at the nest site.

The nest was presumably predated by a Civet (Viverridae). As there were no footprints from wild boars or other larger potential mammalian predators and judging from the way the nest had been dug up this would be the most likely predator. Civets are very common in TWR and they are known to eat eggs. Three of the eggshells had teeth marks from what seemed to be small pointy canines, which further supports the civet theory. The two-banded Monitor lizard (*Varanus salvator*) is another very common and potential threat against the survival of eggs and hatchlings. In this case, a Monitor Lizard is less likely to be the predator, as it would swallow the whole egg.

Figure 3.6.2. Eggshells left behind on top of the nest by the predator. Note how the eggshells are curled up, strongly indicating that the eggs were soft-shelled. Photo Klaus Høybye-Mortensen

After examination of the predated nest, a temperature logger was placed in the egg chamber and the nest was reconstructed. Temperature was measured with 20 min. intervals for 9 days (see figure 3.6.3) In the morning of July 15th, it rained heavily for a few hours. This caused the temperature to drop in the egg chamber reaching a new level approximately two degrees below the former.

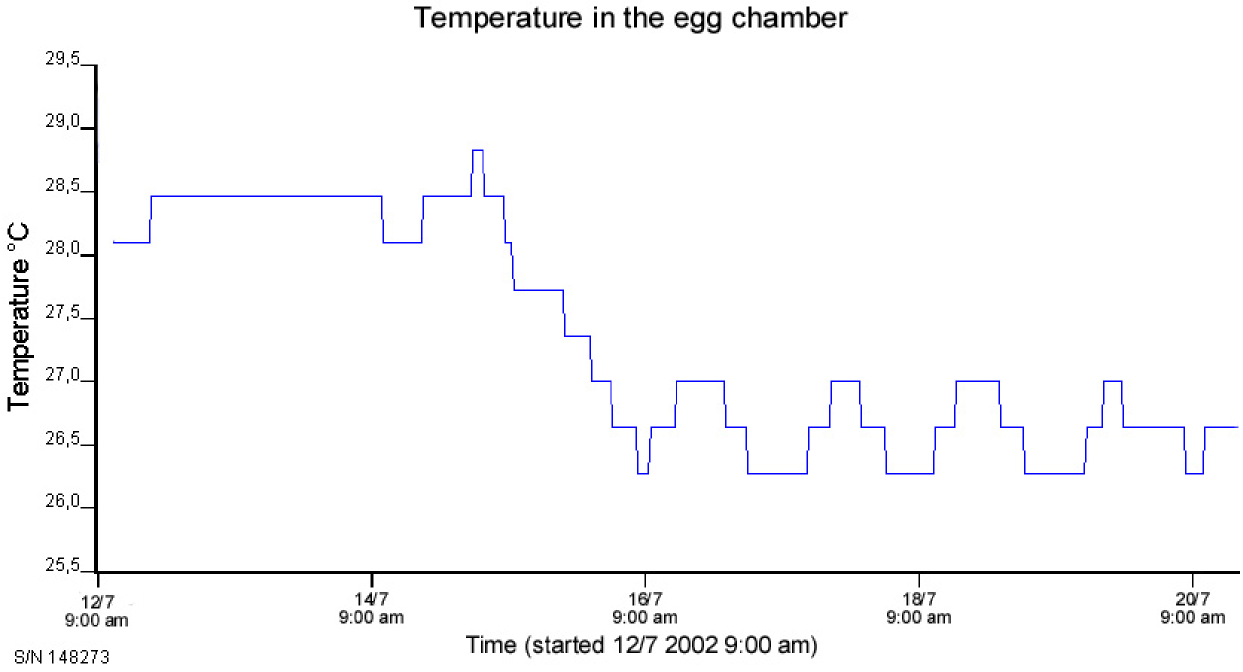


Figure 3.6.3. Temperature measurements in the egg chamber of the reconstructed nest. The sudden drop in the morning of 15th of July is a result of heavy rains.

3.7 Mating- a case story

On June 20, 2002 while walking along the main logging road, an unfamiliar sound was heard in the bushes right next to the road. The sound is best described as a loud rhythmic moaning. My first thought was that an individual of one of the larger mammals of TWR was feeling sick or perhaps dying. My second thought was that sick animals can be very aggressive and dangerous. Attempting to scare the animal away, I started slashing the bush with my parang (malay for machete). As my scaring tactic proved unsuccessful, I moved forward to further investigate. Surprisingly what met my eye were two tortoises mating.

The male (#G, transmitter attached after mating) was already positioned with its front legs on top of the female (#H, transmitter also attached after mating), neck fully extended while vigorously head bobbing vertically. The mouth was wide open while the mating vocalization was emitted. Instantly at my approach #G stopped vocalizing but continued head bobbing. This lasted for a little less than a minute until #H started moving which consequently finished the mating. #H moved towards a pile of entangled branches, probably because of my appearance. #G followed right after while head bobbing. During the next approx. ten minutes #G tried mounting #H several times. However, as #H was covered by branches mounting was impossible. In between the mounting attempts vertical head bobbing and sniffing along the sides of #H's carapace were the dominating behaviours. After that #G settled down about 50 cm from #H using the same hide. Microclimate temperature was measured to 26.8 and relative humidity was >90%. It was clear skies but the mating occurred under a full cover canopy.

One hour later as no further movements or mating attempts had taken place I decided to fit the tortoises with radio transmitters. At 14.50 the same day, the tortoises had moved 30 meters up hill to a gap phase caused by a fallen tree. The tortoises were positioned on either side of the tree under the entanglement of branches, caused by the tree fall. The following day no movements were recorded when returning to the site two times, observing the animals for 90 minutes at a time.

When relocating the two individuals on June 26 they had moved in opposite directions spaced by 25 meters. The following day #G had moved further away (spaced by 200 meters) to a small stream at the bottom of the hill. Unfortunately transmitter signals from #G was lost after this day.

The subsequent relocations of #H revealed no nesting behaviour until the end of the first field trip.

4 Discussion

4.1 Study animals and morphometry

Fourteen individuals were encountered during this study. All animals encountered belonged to the adult age class. No hatchlings or adolescents were encountered during the study. This may be due to different activity patterns and a more secretive lifestyle than that observed for adults. The younger age classes are most likely more vulnerable to predators such as the Malayan sun bear (*Helarctos malayanus*) (Wong, 2002). Hiding under debris probably reduces the pressure of predators and increases chances of survival. Furthermore, small individuals are more susceptible to rapid changes in the microclimate (e.g. moving from a hide to a sunlit place) and will consequently experience overheating at a faster rate than adult specimens (Legler, 1960).

Age estimation based on the annuli or growth rings showed that all encountered animals belonged to the adult age class (15+ years). However, the estimate could not be done for all animals, as scutes were smooth and thus not revealing the annuli. This is often seen in old individuals (Graham, 1979; Legler, 1960; Wilson et al., 2003). Once the tortoise discontinues growth, no new annuli are formed and thus the method becomes invalid.

The use of annuli in age estimation is highly questionable for a number of reasons. First, in order to make any reliable estimates the individuals in concern should be young or adolescent. Once growth stops, the one to one relationship between age and number of annuli becomes invalid. Second, the seasonality of growth patterns needs to be known for the species in concern. Not all tortoise species have one growth season per year and some continue to grow all year round (Wilson et al., 2003). The latter is often the case for species living in the tropics where seasonality (e.g. summer, winter) is less pronounced than in the temperate regions. Thus, hibernating species are more likely to form annuli in a one to one relationship, as growth stops during hibernation (Graham, 1979; Wilson et al., 2003). The growth pattern of *M. e. emys* is not known and thus the use of a one to one relationship should be considered with great caution. *M. e. emys* does not hibernate in the wild and could potentially have several growth seasons per year.

As all animals encountered during this study had between 16 and 28 annuli, it is only reasonable to say that they belong in the adult age class. However, as most tortoises have around 20 annuli this might indicate that growth stops approx. at this age. There is no doubt in my mind that a few of the individuals were much older than some of the others, judging from the wear and tear of their carapace, even though they had the approx. same number of annuli. Longevity in *M. e. emys* is believed to be in excess of 100 years (Wirot, 1979).

Morphometry data (table 3.1.1) revealed little about the gender of the animals. I can only give my full support to those authors who have previously stated that sexual dimorphism is not pronounced in *M. e. emys*. Had I known about the results obtained by Aranyavalai (1996) before the start of this study more emphasis would have been put in the morphometry variables. Even though pictures were taken of all encountered specimens, a replication based on those of the aforementioned study would not be precise enough for comparison.

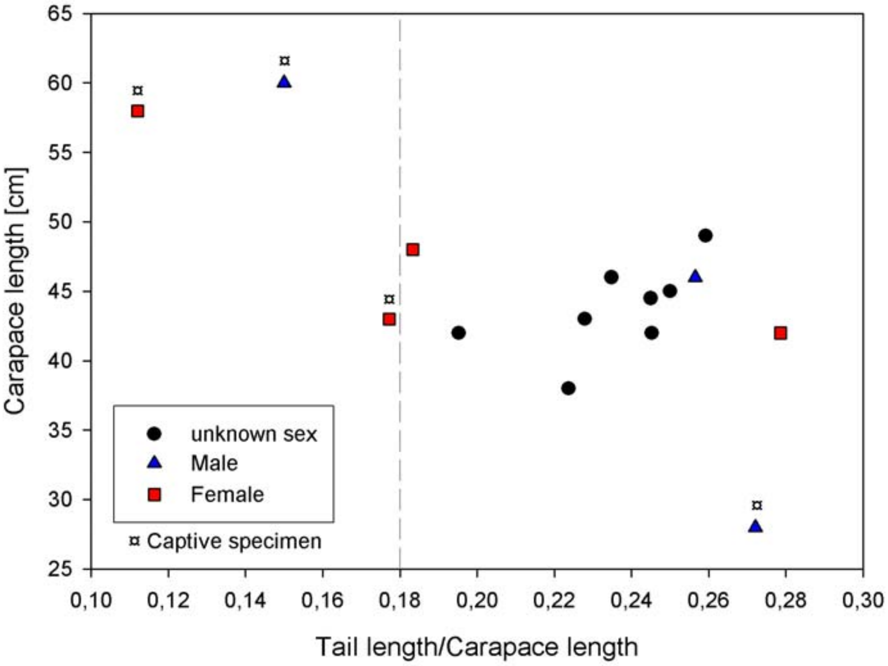


Figure 4.1.1. Graph showing the tail length/carapace length relation vs. carapace length. The genders cannot be determined according to the discriminant figure (0.18) found by Aranyavalai (1996). The measurements of the individuals marked as captive specimens comes from Honolulu Zoo and a private collection (Gomez, pers. comm.; Meier, pers. comm.)

The TL/CL discriminant figure of 0.18 found by Aranyavalai (1996) is not applicable to the measurements of this study (figure 4.1.1). First of all, the only individual with a positive sex determination in this study (#J, nesting female) shows a TL/CL value of 0.28 and should thus according to the Thai study be a male. The expected male and female, #G and #H respectively, found during a mating attempt however, fit the TL/CL prediction. Secondly, the procedure of measuring tail length might differ between this study and that of Aranyavalai. As the thesis is written in Thai only the abstract, tables and figures can be interpreted. Thus, the inconsistencies between the two data sets and methods are too large for gender evaluations of the animals in this study, based on the model proposed by Aranyavalai (1996). In addition, correlation analysis did not reveal any results usable for sex determination.

First encounter with #G and #H happened during a mounting and mating attempt by #G (described in section 3.7). The loud moaning, head bobbing and several attempts of mounting strongly suggest that #G is a male. However, a penis was not observed. From the morphometric measurements it is seen that the tail length of #G is 3.0 cm longer than that measured for #H, whereas the CL only differs 2 cm. This gives a TL/CL relation of 0.18 and 0.25 for #H and #G respectively.

To determine the gender of the study animals, blood samples would have to be drawn and analysed. Testing for testosterone levels using radioimmunoassay should be a straightforward method in Chelonians (Mao and Wang, 1999). Taking blood samples was planned for the second field trip. However, as the radio transmitter batteries were dead when arriving in TWR again, the procedure unfortunately had to be discarded. This was of course a major setback as differences in sexual strategy, activity, home range, diet, etc. could not be analysed.

Drawing blood samples off the two individuals tracked during the second field trip was considered to be of little biological significance as no reference measurements could be found.

4.2 Habitat

The majority of encounters with the study animals happened in the disturbed parts of the forest. This is not surprising as most of TWR consists of regenerating disturbed forest. Though disturbed forest is an acceptable habitat, shade seemed to be of essence. Only ten encounters (11%) happened in open areas or gap phases (no canopy). Of these, four were exposed to direct sunlight, with the rest covered under fallen trees or vegetation. This strongly suggests that *M. e. emys* exhibits a non-heliotherm lifestyle (heliotherm – poikilotherm that depend primarily on radiant energy for their body heat). The use of gap phases in the forest seemed to be associated with the presence of *Alocasia*. In three of the four cases when a tortoise was found in direct sunlight, foraging on *Alocasia* was involved.

As described in section 2.3 the topography of TWR varies from rugged hills divided by steep ravines to lowland swamps. Tortoises were found both in the deep gullies, on the steep sides of the ravines and near the top of the hills. Lowland swamps were not present in the area searched for tortoises.

The close relation to water bodies described by Obst (1986) and Wirot (1979) was not found in the present study. In fact, the study animals were found to be more than 50 meters away from the nearest water body in 73% of all encounters.

One study animal (#E) was observed staying submerged in water for a longer period. It was noted on first encounter that #E had a load of hard ticks on the softer parts of the neck and legs. The species of tick was probably *Amblyomma geoemydae* (pers. com. Sharma), which as the name indicates are almost exclusively found on turtles and tortoises (Sharma et al., 1999). A laboratory experiment on *Ixodes ricinus* showed that, when submerged in water at 17°C containing leaf litter, mortality was 100% within 14 days (Honzáková, 1971). It is not known how long #E stayed submerged and therefore it is hard to draw any conclusions. However, it might be an explanation to the reports of specimens staying submerged for prolonged periods.

4.3 Temperature preferences

From the T_M measured on every encounter with the study animals and the three days of measurements in a hide, formerly used by an animal, the preferred temperature and range can be estimated. The term preferred temperature used here refers to the mean of all T_M recorded during the study. This should not be confused with the preferred temperature often reported based on cloacal temperatures (Hutchison, 1979). The mean temperature of all recorded T_M (next to active and inactive animals) was 26.5°C ± 1.6. Highest and lowest T_M (only active animals included) recorded was 34.6°C and 25.8°C respectively, which can be considered a voluntary temperature range. The top end of the range should be considered with some caution as this extreme was only recorded once during the study and was associated with a bout of foraging.

In figure 3.5.1 it is seen that in early mornings the study animals preferred to stay in places where $T_M>T_A$. This was also the case in late afternoons and probably throughout the night. However, the results should be considered with caution due to the very small T_M sample sizes for some of the intervals. During nighttime T_A often drop to around 22°C, which will cause the study animals' body temperature to drop. It seems that the tortoises can avoid this by hiding under debris, tree falls or the like and use the hides as insulators in their thermoregulation. One advantage in the use of hides is the fact that the temperature stays within a narrower range over time, than out in the open (figures 3.5.2 and 3.5.3). If T_A gets higher than what will be tolerated by the animal it can seek shelter in a hide, and vice versa. It seems that the use of hides provide the optimum T_M. This is supported by the observations of several of the study animals staying inactive for long periods in hides; the extreme case being the 17 days spend in the same hide, only broken by 44 minutes of foraging (#DII). The use of hides for thermoregulation has been reported for various tropical species (e.g. *Testudo horsfeldi*) and other reptiles (*Varanus* sp.) (Legler, 1960; Traeholt, 1995).

The overall unimodal activity pattern observed in the present study suggests that the daily maximum temperatures at the forest floor do not exceed that tolerated by *M. e. emys*. However, on hot days bimodal activity seems to be preferred. The bimodal activity pattern exhibited by #L on the 6th and 9th of March 2004 were both associated with afternoon T_A exceeding 30°C (figure 3.5.2). Thus, the daily maximum temperature seems to have a determining effect on the activity pattern. In addition, #DII was not recorded moving on days where maximum T_A exceeded 30°C. The variability between the two animals however suggests that other factors apart from temperature interact. This relationship, of unimodal activity at temperatures below approx. 28°C and bimodal activity above, is also seen in other tortoise species, *Testudo gracea* (Lambert, 1981) and *Chersina angulata* (Ramsay et al., 2002).

The mean T_A during the hottest hours of the day was 28.1°C ± 1.5. In fact, it seems that the animals are most active during the hottest hours of the day when exhibiting unimodal activity and inactive during the dark hours and colder morning hours. This contradicts the observations of Schaffer and Morgan (2002), which was performed in significantly less canopy cover.

The strategy of staying out in the open where the first rays of sun will appear the next morning, described by Schaffer and Morgan (2002) as thermo experience was not observed. However, they describe this behaviour to be associated with night temperatures around 10°C, which is well below the range recorded in the present study. In all the cases where a tortoise was observed late in the afternoon and again the next morning the overnight use of a hide was always involved. In addition, if thermo experience were a general thermoregulatory behaviour in *M. e. emys*, activity should be expected to occur more frequently in the morning hours. This is not supported by the activity patterns observed in the present study. It should be noted that the authors studied juvenile specimens of *M. e. phayrei*, in enclosures with relatively open habitat compared to that of TWR (Schaffer, pers. comm.). In addition, juveniles probably have a different thermo strategy and cryptic behaviour than that of adults.

An important objective of the present study was to evaluate *M. e. emys'* tolerance towards habitat alterations. Viewed in the light of the agricultural development throughout SE Asia this is a very important subject. Changing forest habitat into monoculture plantations has an adverse effect on the water and climatic conditions. Monocultures being drier, hotter at midday and showing increased light levels (Johns, 1997).

From interviews with workers and managers in one of the oil palm plantations (*Elaeis spp.*), I concluded that the tortoises do not live there, as they had not been observed. The main explanation for that is likely related to the practices involved in the conversion of forest into plantation. Before any palms are planted, the area is clear-cut and cultivated. In this practice, most (if not all) tortoises will be killed by heavy machinery and even if they should survive this, they are left in a habitat not suitable for them. In the cleared areas, food is scarce, temperatures high and humidity low, all devastating to a non-heliotherm species. Thus, the remaining individuals will probably die very soon of heat stress and dehydration.

Once the plantation has matured, the shaded places are restored, though not to the same extent as in the forest. The canopy is not closed and a subcanopy is absent (Liow et al., 2001). Temperatures are generally higher than in the forest and often exceeding 35°C in the afternoon, exceeding the voluntary temperature range found in the present study. Humidity is low compared to the forest because of the spacing between the palms. Evaporation is considerably higher in the relatively open plantation. The plantation microclimate is in many ways comparable to the gap phases in the forest, discussed by Johns (1997). In addition, Pawar (1999) found significant differences in herpetofauna (lizards) species richness along a disturbance gradient in Mizoram, India.Teak plantations (*Tectona grandis*) support far fewer species than mature rainforest.

Thus, it seems that *M. e. emys* can tolerate anthropogenic disturbances to a certain degree. The fact that most study animals found during the present study roamed in secondary forest is of course an effect of most searches being conducted in this type of habitat. However, it also suggests that logging activities does not have detrimental effects on the presence of *M. e. emys* in these areas. In fact logging activities could even have a positive effect as understorey vegetation cover and diversity of herbs is higher in previously logged forest (Kjeldsen, 2003).

Whether any population parameters, (e.g. density or demography) are affected by logging activities is not known.

4.4 Diet

Because of the very few in situ studies, little is known about the diet of *M. e. emys.* Most references deal with the diet items eaten in captivity and probably does not reflect the animals' preferences in the wild. As most ground herbs growing in tropical rainforests are hard to find on the shelves of your local supermarket wild preferences are seldomly met in captive husbandry. However, tortoises in captivity are known to accept a wide variety of diet items when presented to them, both plant and animal matter (Schaffer and Morgan, In Press). From literature studies, it is known that *M. e. emys* is predominantly herbivorous but occasionally will eat animal matter such as snails, frogs and carrions (Jacobsen, 2003). Studies on the two forest dwelling tortoise species *Geochelone carbonaria* and *G. denticulata* in Venezuela showed a generalist herbivorous diet consisting of at least 33 different species of flowers and fruits in addition to foliage of numerous plants (Bjorndal, 1989; Moskovits and Bjorndal, 1990). As the Danum Valley study and captive records also show a vide variety, it was expected that *M. e. emys* would exhibit the same generalist feeding behaviour in the wild. In the study by Lambert & Howes (1994), a list of eleven different plant species was established. Seven different fungi species was eaten during the study, of which five was identified. One fallen fig fruit (*Ficus punctata*) was eaten and three different under storey plants. No intake of animal matter was observed.

Figure 4.4.1. *Manouria e. emys* feeding on *Alocasia*. The tortoise showed no interest in the other herbs surrounding the *Alocasia*. This indicates that *Manouria e. emys* practices some selectivity.
Photo: Klaus Høybye-Mortensen

No fruits were observed eaten by the study animals, which is most likely a reflection of seasonality and fruit tree abundance. Fruiting season normally occurs during the months April – October. Several individuals have been observed foraging under the same fruiting fig tree (*Ficus* sp.) in TWR in the past (Lamb, pers. comm.)

One striking fact about taro as a food item is that it has a high content of calcium oxalates, which forms needle shaped crystals. These crystals, also known as raphides, irritate skin and other soft tissues. In fact, some species of taro are listed as poisonous in the literature (Barnard, 1996; Paull, 1996). The meaning of the word poison is probably over emphasised when it comes to taros and merely means that these plants causes irritations when eaten. The acridity (extreme bitterness) of different Aracea species has been studied because of their importance as agricultural crops in the South Pacific region. Genua and Hillson (1985) found that of fourteen studied Aracea species (including *Alocasia*, *Colocasia* and *Philodendron*), thirteen contained raphides in the spongy mesophyll of the leaf blade. It now seems evident that it is not the crystals alone causing the acridity but a complex of crystal and protease activity in what has been named “Nature’s poisoned spear” (Bradbury and Nixon, 1998). Water contents were found to be in the range 83-86% in some edible taro leaves when analysed for nutritional values (Awasthi and A.B.Singh, 2000). This is probably important for the tortoises in keeping their water balance on the positive side. No tortoises were seen drinking from water bodies or licking dew off the vegetation, as is often the case for species in arid habitats (Mahmoud and Klocka, 1979).

It is also reported that wild living *M. e. phayrei* in Thailand feed on taro and recently captive specimens of both *M. e. emys* and *M. e. phayrei* in the United States readily consume both *Alocasia* and *Colocasia* when offered (Schaffer, pers. comm.) and in Indonesia captive *M. e. emys* feeds on *Colocasia* leaves (Iskandar, 2000), which are close relatives of the *Alocasias*. The female in the Danum Valley study was observed eating *Philodendron* sp. (Aracea) (Lambert and Howes, 1994), which also contains calcium oxalate. It must be stressed though that the species of taro eaten in TWR are mostly endemic to Borneo and thus the taros eaten in Thailand and other areas must be different species (e.g. *Colocasia esculentum* (Iskandar, 2000))

Why *M. emys* chooses to eat plants containing irritants is not known. One reasonable explanation could be that this diet component is ingested for medicinal reasons to control intestinal parasites (e.g. nematodes). Diets containing potentially toxic components has been described for at least two other testudine species, *Testudo hermanni hermanni* and *Testudo horsfieldi* (Longepierre and Grenot, 1999). In the case of *T. h. hermanni* a shift from the toxic plants was demonstrated when animals were treated with an antihelmintic solution, suggesting that the properties of the toxicants could have some influence on the intestinal nematodes (Lagarde et al., 2003; Longepierre and Grenot, 1999). However, this is pure speculation. As scat examinations and dissections of intestines was not part of the present study it is not known if intestinal parasites were present in the study animals. In addition, research on the properties of calcium oxalate when entering the digestive tract is needed to draw any conclusions concerning the matter. In mammals, the calcium oxalate can cause swelling of the throat to such an extent that there is a risk of suffocation. How this is avoided by *M. emys* is not known. No swellings or breathing problems were noted during the study.

Despite the toxic properties of *Alocasia*, it seemed evident that tortoises selectively foraged for these plants. In places with a wide variety of different herb species growing side-by-side (both listed and potential diet items), the *Alocasia* species were always selected if present. In areas with a sparse distribution of *Alocasia* the study animals would still find the few specimens even in thick vegetation (figure 4.4.1). This indicates that they must rely on senses other than eyesight alone. *Alocasias* are odourless compared to their close relatives the *Colocasias*, probably as an adaptation to their respective plant pollinator systems (Hay, 1998). *Alocasias* are pollinated by birds and *Colocasias* by mammals. Even so, the ability to move in an almost direct path towards an *Alocasia* without any visible contact, observed during the present study, can most likely be ascribed to the detection of chemical signals.

On two occasions, fungi were observed eaten by one study animal (#L). In one case, the fungus was covered by leaves and not visible to the tortoise. It walked straight in the direction of the fungus turned over the covering leaves and ate it. In this case, the tortoise relied totally on its sense of smell in finding the fungus. As the fungus was eaten and no others were found in the area, it could not be identified. The other fungus eaten could not be identified either. Only two accounts of fungi as diet items seems little compared to the seven different species reported in the Danum Valley study.

As the Danum Valley study lasted from 23 february until 16 April 1990 differences in seasonality does not seem to be the case. Another explanation could be the difference in abundance of *Alocasia* between Danum Valley and the secondary forested parts of TWR. Due to the differences in species ecology, TWR is expected to have a higher density of some species of *Alocasia* associated with disturbances (e.g. *A. robusta* and *A. sarawakensis*) and an overall higher abundance because of the extensive disturbance of the forest in TWR (Hay, 1998). Kjeldsen (2003) showed that the relative number of individuals did not differ much between logged and undisturbed forest, whereas the relative cover was three times larger for the logged forest compared to undisturbed. Thus, the individual plants in the logged forest are larger than in the undisturbed one. This probably means that in Danum Valley the *M. e. emys* population must rely on a different diet composition than in TWR. Though not mentioned by Lambert and Howes

(1994), this does not mean that they do not eat *Alocasias* in Danum Valley, but merely rely on other species associated with dense forest, e.g. *Alocasia scabriuscula*.

A third explanation for the differences in diet composition between this and the Danum Valley study are the differences in methodology. While this study relied partly on tracking back the tortoises path in search of foraging signs and partly on focal observations, the Danum Valley study only relied on focal observations. This means that in the Danum Valley study, *Alocasias* would not be reported eaten unless actually observed. During the present study, five of the fifteen *Alocasias* were found by following the trailer thread. Thus, the fact that no *Alocasias* were seen eaten and seven different fungi were collected during the Danum Valley study is probably a matter of chance. This is also the case for the two observations of fungi consumption in this study by one study animal. The probability of finding traces of eaten fungi by following the trailer thread is probably close to zero, as the whole fungus was eaten in both cases reported here. This leaves only the focal observations as a means of detecting fungi and other small plants as diet items. This is a matter of being in the right place, at the right time.

As for the *Alocasias*, they are easily detected using both methods. Typically, less than half of the whole plant is eaten at a time and the stem is always left untouched. Distinct bite marks and footprints are left by the tortoises. The tortoises do not compete for the green leafy parts of this diet item with other animals in the forest, probably because of its toxic properties. The only signs of other animals eating the *Alocasias* are rodent like bite marks on the stems seen now and again. Thus, *Alocasias* are easily detectable diet items and was actually found to be the best indicator (based on the presence of bitemarks) of tortoises being present in an area during this study.

These differences in detectability between diet items could lead to biased results towards the easily detectable diet items, i.e. *Alocasia*. Consequently, the trailing method has major disadvantages in detecting small food items. The fact that the study animals showed no signs of habituation further emphasised the problem. Even though an animal may have been foraging on small herbs just before my arrival, it would stop such activities as soon as my presence was felt. Thus, direct observations were of very short duration and revealed only single diet items at a time.

During this study, no animal matter was observed eaten by the tortoises. It has been suggested that *M. emys* has a higher protein intake, than other herbivores such as *Geochelone pardalis* and *Geochelone sulcata,* because the availability of invertebrates and carrions is higher in their natural environment (Jacobsen, 2003; Obst, 1986). The latter two species live in arid desert habitats. However, no data from the two field studies conducted so far supports this notion. Another radio telemetric study on the tropical forest dwelling tortoise *Indotestudo travancorica* in India revealed no foraging on animal matter (Sharath, 1997). In addition, Eggenschwiler (2003) notes that her captive *M. e. phayrei* showed no interest in snails entering the enclosure.

As for carrions, a slow and shy animal like *M. e. emys* will most likely be the looser in competition with animals such as Monitor Lizards (*Varanus sp.*) and Civets (*Viverra sp.*). On one occasion during this study, a large Wild boar carrion across the river from one of our campsites was eaten by Monitor Lizards within three days. On the other hand, Moskovits and Bjorndal (1990) found that almost half of the scat examined from *Geochelone carbonaria* and *Geochelone denticulata* in a South American rainforest showed animal matter, but the intake of animal matter was only observed once during their study. Thus, the opportunistic feeding on animal matter reported primarily from observations in captivity is not supported by the findings in this study.

Overall, *M. e. emys* must be considered a generalist herbivore feeding on a variety of herbs, fruits, shoots and fungi. The list of diet items reported here does probably not reflect the true diversity of foraging habits for *M. e. emys*. This will undoubtedly be extended with more research. The high proportion of *Alocasias* recorded in this study indicates that some degree of specialization may arise if these plants are abundant. Thus, bearing in mind that the results may be biased; *Alocasias* must be considered one of the major diet items eaten by the TWR population. However, it cannot be concluded that these tortoises are strictly herbivorous based on the results obtained here. The chance of missing observations of study animals eating a slug or snail is too big to be conclusive on the subject. Scat examinations could probably have revealed whether or not animal matter is a general constituent of the *M. e. emys* diet, which is suggested elsewhere in the literature (Jacobsen, 2003; Liat and Das, 1999; Wirot, 1979).

4.5 Activity

From the data collected in the first field trip, little can be said about the activity patterns of the study animals. It was difficult to clearly distinguish between active and inactive individuals based on direct observations. The problem was that study animals stopped whatever activity they were performing when I came within observation range, a common problem in turtle and tortoise research (Lagarde et al., 2003; Legler, 1960; Ramsay et al., 2002).

The single study animals showed no obvious signs of being habituated to the presence of a human observer during the study period. The three days of almost continuous human presence at the nesting site of #J did not elicit any ignorance towards an observer. On the contrary, #J showed a higher level of tolerance to human presence during nesting compared to encounters afterwards. A similar behaviour is also described for sea turtles that, once egg laying has begun, start to show higher tolerance to external disturbances. The level of tolerance remains high during the filling and covering phases (Ehrenfeld, 1979; Miller, 1997).

The implementation of the ActiTrac sensors enabled a precise registration of activity throughout the second field trip. The two tortoises for which activity was registered showed very distinct activity patterns. One tortoise (#L) was active every day except for one during the 35 days of registration. On many days, the active period extended to more than 50% of daylight hours. The high active/inactive ratio for this individual (15.4 %) is probably an extreme. In comparison to the other animals tracked during the present study, this seems to be the case. Ramsay et al. (2002) found an activity level of 4.4 % on wet cooler summer days (temperature range resembling that of the present study) in their study on *Chersina angulata*. However, their method was based on a study plot search, recording the activity of encountered animals. Thus, the comparison should be considered with caution.

By first look, it is apparent that the two study animals differed considerably when looking at hours of activity throughout the study period (table 3.4.1). This individual variability was also recorded for *Gopherus polyphemus* by Auffenberg and Iverson (1979). Moskovits and Kiester (1987) found statistical differences between male and female activities during mating season. More males were found walking during mating season, probably to increase their mating success, i.e. number of matings. However, as determination of sexes failed in the present study the differences in activity can only be speculation in this context.

The acrophase of #L was concentrated around 12:32 ± 3:07 h (SD) midday and for #DII it was 14:45 ± 4:08 h. An overall statistical significant unimodal activity pattern was proved using Rao's Spacing Test. However, some days clearly show a bimodal activity pattern (discussed in section 4.2). This variability is also reflected in the calculated lengths of the mean vectors, which show a moderate concentration around the acrophase.

Activities recorded after dark were infrequent and when occurring of very short duration, except for one incident. This is not surprising as tortoises are almost strictly diurnal (Auffenberg and Iverson, 1979). One period lasting 148 minutes from 18:52 onwards was recorded for #DII.

With only this single incident, the conclusion is that *M. e. emys* is diurnal and not as described by Obst (1986) nocturnal.

From other studies on testudinian species, it seems evident that the daily activity periods largely depend on ambient temperature and humidity (Auffenberg and Iverson, 1979; Lambert, 1981; Ramsay et al., 2002; Schaffer and Morgan, 2002). In relation to these variables, daily activity patterns may be either uni- or bimodal. Normally a bimodal pattern will arise if midday temperatures exceed a level tolerable for the animals.

Schaffer & Morgan (2002) reports a bimodal activity pattern in juvenile *M. e. phayrei* within the temperature range of 13-32°C. Activity level also showed a positive correlation with humidity and precipitation, though no statistics are reported. Their observations indicate two activity periods: dawn and dusk. Lambert & Howes (1994) states that the female observed in Danum Valley was mostly inactive in early morning and late afternoon and tended to move in early afternoon (a unimodal activity pattern). They also, though very vaguely, indicate nocturnal inactivity. Obst (1988), on the other hand describes *M. emys* as being predominantly active in the evening and at night. Morning activity and during overcast or rainy days is reported from Honolulu Zoo (McKeown, 1999).

4.6 Home range

The results obtained during this study in relation to home range estimates were somewhat disappointing. First, the tortoises were far harder to find than was expected. Second, all individuals found had to be included in the study to get enough animals for any general conclusions. Thus, individuals as far as 21 km inside the reserve were radio tracked and were of course far harder to reach than the individuals found near Tabin Station. Third, the radio transmitter failure at my arrival in TWR for the second field trip resulted in precious data being lost. For example seasonal ranging, home range stability or instability can not be concluded due to the lack of year round recordings. In addition, sex determination based on blood hormone analysis prepared for the second field trip had to be given up because of transmitter failure. Thus, analysing sexual differences in ranging patterns also had to be discarded.

As predicted, the two methods used for home range estimates in the present study produced different results based on the same set of data. This is a consequence of the relative small sample sizes. The bias of the convex polygon method (CPM) is greater for small sample sizes (Boulanger and White, 1990; Jennrich and Turner, 1969). However, the confidence ellipse method (CEM) also has its disadvantages because of the underlying assumptions following a parametric method. In the present study, the assumption of bivariate normal distribution is violated in either one of the directions for all individuals. A consequence of small sample sizes, which can lead to an estimate being too large (Ackerman et al., 1990).

CPM was chosen, because it is one of the most commonly reported and easy to calculate methods. CEM was chosen, because it has no underlying assumptions of circular symmetry and is unbiased even for small sample sizes.

Previously the home range of only one female *M. e. emys* has been estimated and thus data on the subject is very limited. The radio tagged female in the Danum Valley study ranged within an area of 0.6 km^2 over a period of 53 days. The same specimen was spotted just outside the confines of that area six months later (Lambert and Howes, 1994). However, the method used to estimate the ranging of this animal was not reported. When comparing the map presented with the ranging estimate it seems that their estimate is incomparable with the estimates of the present study. Thus, the home range map from Danum Valley was digitized and analysed using both the confidence ellipse method and the convex polygon method, a new estimate of home range size was calculated to be 1.0 km^2 (CEM) and for the CPM the estimate is 0.3 km^2. This was done to make the data from this study and the Danum Valley study comparable.

A study of the two tortoises *Geochelone denticulata* and *G. carbonaria* inhabiting the rainforests of North-western Brazil showed almost 200 fold differences in home range (convex polygon method) sizes for 24 individuals followed between 23 and 162 days. The minimum home range area was 0.006 km^2 recorded for a male *G. carbonaria* followed for 59 days. The maximum area was recorded for a female *G. carbonaria* ranging over 1.17 km^2 within 51 days. It is worth noting that the home range size did not relate to the number of observation days (Moskovits and Kiester, 1987).

This variability was also seen in the present study. For example #DII and #L was followed during the second field trip for 31 and 37 days respectively and ranged in the same area. Home range estimates are 0.24 km^2 and 1.81 km^2 for #DII and #L respectively (CEM). The longest distance recorded between them was 1.2 km during the period of monitoring. As they ranged in the same area, the variability can probably not be ascribed to differences in forest type, food abundance, topography, climate or seasonality. Tests for simple correlation between home range estimates (CPM, CEM) and body mass, period monitored (days), number of relocations (loci) respectively, showed no correlations except for CPM vs. loci. Thus, the variability is probably explained by variables/factors other than those reported here.

Sexual strategy could be one explanation for the high variability between the individual estimates but as sex determination of the study animals was not possible, this can only be assigned to speculation. From a number of other studies, male tortoises are recorded to maintain larger home ranges than females, especially during breeding season (Diemer, 1992). By increasing their home range, males have a greater chance of several matings in one season.

The smallest home range estimate in the present study was 0.01 km^2 (#E), based on nine loci spread over a period of 36 days. However, the nine loci were recorded during two shorter periods with 30 days of no records in between. In addition, the last five records were from the same location as the tortoise rested, probably after feeding on an *A. sarawakensis.* As there are no records of movements between the two shorter periods, the home range estimate for this specimen is considered with caution.

The home range estimates found during this study are based on short term monitoring. The longest period being 67 days for #L. Whether this reflects the long term ranging is very hard to say. Well-defined long-term home ranges have been established for burrowing tortoise species (e.g. *Gopherus*). The term burrowing in this context means that the tortoise makes use of the same hide over a longer period, returning night after night. In a study reported by Auffenberg and Iverson (1979) a marked tortoise was found within 150 meters of the original point of capture 17 and 35 years later. However, the non-burrowing tortoise *Geochelone berlandieri* in Texas move randomly throughout its activity season in a nomadic fashion. Often remaining in the same place for several days, after foraging on its preferred diet (*Opuntia* fruit) (Auffenberg and Iverson, 1979). This is the same pattern observed for the study animals in the present study and the Danum Valley animal. Tortoises using the same hide on consecutive nights was not observed if activity was recorded during the day. The tortoises always moved to another hide after a bout of activity. In addition, no centre of activity seemed to be present from which daily excursions took place, as seen in the burrowing species. Thus, the movement pattern of the study animals resembles a nomadic life style. This questions the maintenance of a well-defined long-term home range for *M. e. emys*. However, long term studies lasting several years are needed to draw conclusions.

The presence of rivers did not limit the ranging of the tortoises during the dry season. However, in the rainy season the perennial rivers will most likely obstruct the free movements of the animals due to high water levels and strong currents.

4.7 Nesting

As nesting activities were only observed once during the present study, the following discussion should be considered with this in mind.

The nest site was situated on a small hill in the secondary part of the forest. The area was shaded by the dense subcanopy and the nest site itself was partly roofed by a withered bush. Lambert and Howes (1994) notes that their study animal was observed digging between the buttresses of a huge tree and afterwards pushing herself backwards possibly in preparation of oviposition. A site like that would also provide shelter from the various weather conditions as the huge trees normally have dense canopies. However, they produced no evidence of this being nesting behaviour and thus no general conclusions can be drawn. Observations in captivity also suggest that the nest site is chosen based on shelter (Eggenschwiler, 2003; Morgan and Schaffer, 2001). This maternal nest site selective behaviour is also documented for other chelonian species, e.g. *Chrysemys picta* (Janzen, 1994; Orenstein, 2001; Spencer and Thompson, 2003)

On first encounter, the tortoise showed aggressive behaviour by moving towards me and standing up, lifting its body from the ground. After about a minute it turned round and returned to the nest mound where it laid flat on top of the mound. This is a defensive behaviour also described in captive animals (McKeown et al. 1994, Louwman 1982). Minutes later it took up nest construction again. From that moment on the tortoise was oblivious to my presence.
Most possibly the nesting drive is a lot stronger than other daily survival drives such as foraging and the oblivion towards external disturbances is common among chelonians (Ehrenfeld, 1979). This is also a well-known phenomenon in nesting sea turtles (i.e. *Dermochelyidae* and *Cheloniidae*) (Miller, 1997).

The actual oviposition was not observed as it had already taken place before my arrival. However, the mound building was observed through five one-hour observation periods between July 2nd and July 4th. The behavioural elements associated with mound construction (e.g. back sweeping and sniffing) reported from captive animals (Eggenschwiler, 2003; Fife, 1989; Glasgow Zoopark, 2003; Louwman, 1982; McKeown, 1990; McKeown et al., 1991; McKeown, 1999; McKeown, 2001; Mähn, 2001; Schaffer and Morgan, In Press) were also observed in the field.

The nest defending behaviour lasting up to 6 weeks after oviposition (Eggenschwiler, 2003) was not observed. In fact, the female left the nest after finishing it and moved eastwards until it was last relocated 500 meters away from the site on July 19th. The prolonged nest defending behaviour, seen in captive animals, could be an effect of small enclosures. Here the female is forced to stay close to the nest, which could elicit the prolonged maternal behaviour. On the other hand, the female observed in the wild might just be the exception proving the rule.

Defending the nest might just have been beneficial in securing the females investment involved in nesting. On July 12th, when returning to the nest site to secure it from predators (fencing it with chicken wire) the nest had already been subject to predation. From the collected shell pieces, it was estimated that the nest contained between 10 and 12 eggs. All shell pieces were curled up indicating that they were soft-shelled. Contradicting descriptions of the eggshell properties of *M. emys* are confusing the picture. Some report soft-shelled eggs as the ones from this study (Schaffer, pers. comm.; Eggenschwiler, 2003; Glasgow Zoopark, 2003) while others report eggs to be hard as chicken eggs but only after a few hours or days in contact with air (Gomez, pers. comm.). The hardening of the eggs is probably not a natural occurring event as they are covered right after oviposition (Mitchell, 2003). Thus, judging from this single observation, it seems evident that *M. emys* eggs are soft-shelled under natural conditions. Curiously, testudine species predominantly lay hard-shelled – brittle eggs (Ewert, 1979).

From captivity, it is known that incubating temperatures ranging from 23-29 results in successful hatching and those temperatures above and below results in almost 100% hatching failure (Fife, 1989; Louwman, 1982; McKeown et al., 1991). At Wassenaar Zoo the artificial incubation temperature was set at 28°C and the relative humidity at 90%. This gave a fertility rate of 21% over a period of three years (n=121) (Louwman, 1982). At Forth Worth Zoo, a 23°C artificial incubation temperature resulted in a fertility rate of 75% (n=32) in 1983 (McKeown et al., 1991). In a private collection, Phoenix Arizona, artificial incubation temperatures between 29-33°C resulted in no hatchlings at all (n=30) (Fife, 1989; McKeown et al., 1991). Another private collection in Germany resulted in a 70% hatching success incubated at 29 ± 0.5°C (n=34) (Mähn, 2001). Average temperatures inside nests of Testudininae are normally in the range 26-32°C (Packard and Packard, 1988).

Why *M. emys* builds these nest mounds is still a puzzle. As mentioned earlier the use of nest mounds is not documented for any other testudine species. Some suggests that the mound facilitates heating from fermentation (Schaffer, 2003). When looking at the temperature data from this study (figure 7.6.3) and the fact that artificial incubation temperatures above 29°C leads to hatching failure it seems unlikely that raising the nest chamber temperature by fermentation processes would be beneficial for the hatching success. The nest mounds of *M. emys* have been compared to those build by birds of the Megapodiidae family (McKeown et al., 1991). Temperature data from the fermentation nests of megapods living in the same region/climate shows that the temperature is kept at about 33 ± 1°C and may rise to about 50°C and even higher if not tended properly (Diamond, 1983). If this were the case for the nest mounds of *M. emys*, hatching success would probably be close to zero. Megapods constantly have to monitor the temperature in their nests to prevent overheating. Although concluded by McKeown et al. (1991), there is no valid documentation of nest alterations as a mean of temperature regulation from this or other studies. In fact, some females stop tending the nest right after finishing it, as in this case, while others spend days or weeks doing so. In order to prevent overheating one would expect the female to stay close to the nest right until hatching if the purpose of mound building was to actively regulate the temperature. At this point nest tending behaviour beyond the point of finishing the nest mound has only been documented for captive animals.

A probable cause for the nest construction of *M. emys* could be keeping the eggs moist during development. Soft-shelled eggs are more likely to loose water than hard shelled. From studies of soft-shelled sea turtle eggs (*Caretta caretta*), it was found that the water vapour conductance of these and other flexible-shelled reptile eggs was in the order of three times larger than for a similar sized hard-shelled bird eggs (Ackerman, 1997; Booth, 2002). This means that a soft-shelled egg left out in open air or only thinly covered would loose its water three times faster than a hard-shelled. Long dry spells often occur during the nesting months of *M. e. emys* and thus the eggs would face this problem without the protection of a nest mound. In addition, as seen in figure 3.6.3, the daily temperature fluctuations in the nest mound are kept at a little more than one degree, whereas the ambient temperature normally fluctuates at least 6-7 degrees (figure 3.5.2). This provides a stable incubation environment, which is very important for the development of the embryos (Ewert, 1979).

A moist nest mound could also serve in means of keeping the eggs from overheating with the evaporation of water taking excess heat away.

Protection from predators is of course another feature of the mound. As seen from this study, eggs are indeed predated upon when found. Burrowing the eggs makes it harder for potential predators locating them and may in turn increase hatching success. As suggested by McKeown et al. (1991) rain could be a crucial factor in the hatching success. Rain will most likely wash away the smell of eggs and leave the mound to smell and appear as any other mound in the forest. From the day the female left the nest until the day of my return (12th of July) no rain was recorded. This fact might have contributed to the predators discovery of the nest. It must be stressed that this is pure speculation and no data was or has previously been collected in this context. As noted above the nest was partly roofed by a bush, but by no means enough to keep the nest dry during spells of heavy rain.

4.8 Mating

Only one mating attempt was observed during this study on June 20th. In TWR, matings also occur during the months of December, January and February according to the SOS Rhino rangers and in Danum Valley during March, April and May (Lambert and Howes, 1994). Mating has been recorded throughout the year in captivity (Eggenschwiler, 2003). This may be an effect of the absence of a rainy season. However, with general observations in the wild only extending from January to August, year round matings in the wild cannot be excluded.

Observations from the present study, however of short duration, involved head bobbing and male vocalizations as in captive specimens (McKeown et al., 1991). No nesting behaviour was observed for the female after the mating.

5 Conclusion

The present study has significantly increased our knowledge about the natural habits of *M. e. emys*. Although not successful in all aspects, the questions set by the objectives of the study have been largely answered. Prior to these observations, only one published study had been conducted in the wild and thus most knowledge was based either on anecdotal material or on observations on captive specimens.

Some subjects, which cannot be studied in captivity (e.g. home range, natural diet, preferred habitat etc.), are crucial for future recommendations for the management of wild populations. Data from this study has already contributed to one effort of this type (Schaffer et al., 2003; Schaffer et al., 2004). It is my hope that I, with this study, have contributed to the future survival of this endangered species. However, as was also seen in this study, some subjects are not easily studied in the wild, over a relatively short period. For example, observations on the behavioural aspects proved very difficult in the field.

Overall, the present study provides a short glimpse of the life history of *M. e. emys* and should be considered as such. However, this will hopefully help in raising new questions and awaken the curiosity of other researchers.

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6.2 Personal communications

Bosi, E.J., Wildlife Vetenarian. Program officer - SOS Rhino Borneo and Research Fellow at Institute of Tropical Biodiversity and Conservation (ITBC), University Malaysia Sabah (UMS)

Gomez, Y.M., Yvonne Gomez holds a private collection of both *Manouria emys* subspecies in Fresno, California.

Lamb, A. Anthony Lamb is a world-renowned botanist, residing in Sabah since the 1960's. Mr. Lamb has many years of field experience in the region. Currently working on "Orchids of Borneo"

Meier, D., Duane Meier is reptile curator at Honolulu Zoo. Coauthor of "The Management and Breeding of the Asian Forest Tortoise (*Manouria emys*) in Captivity." (see McKeown, 1991)

Poulsen A.D., Field of expertise: Wild gingers (Zingiberacea) of SE Asia. http://www.dalbergpoulsen.com/ginger_poster.html

Schaffer, C. Chuck Schaffer holds a private collection in Jacksonville, California. In addition, he has authored several articles about *Manouria emys*.

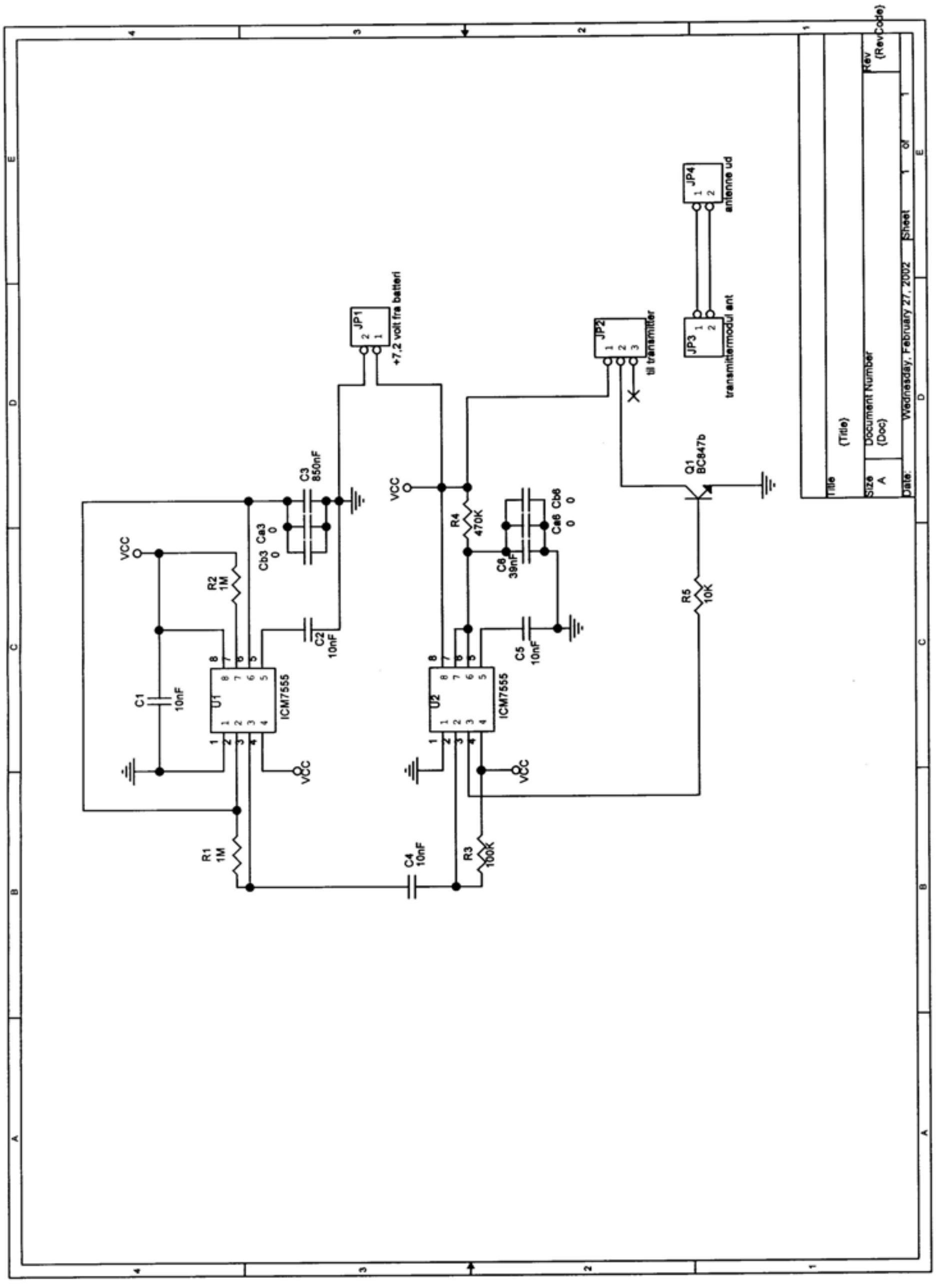
Sharma, R.S.K., Field of expertise: Veterinary Parasitology. http://www.vet.upm.edu.my/english/reuben.html

7 Appendices

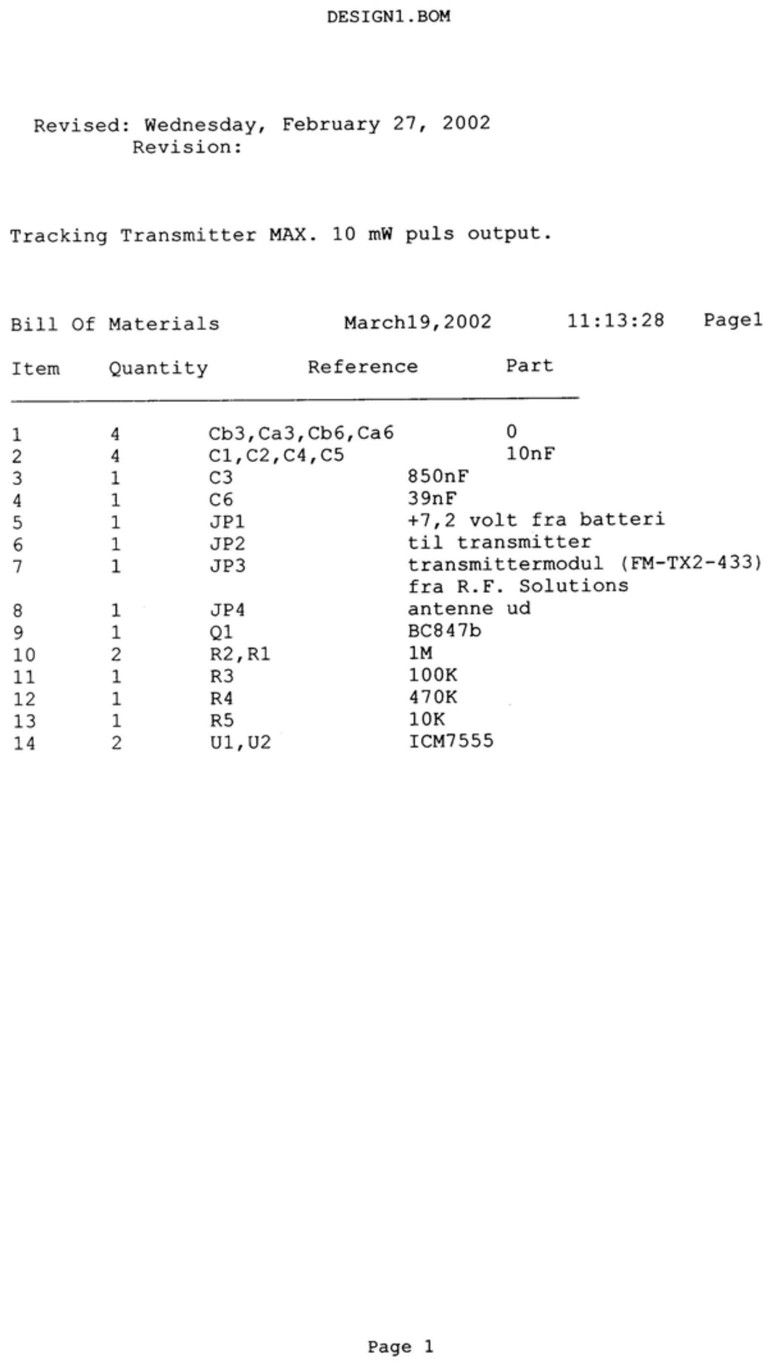
7.1 Appendix I

Diagram of radiotransmitter components.

Designed by Frank B. Mortensen, Institute of Biology, University of Southern Denmark



List of components.



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                         DESIGN1.BOM


    Revised: Wednesday, February 27, 2002
            Revision:


  Tracking Transmitter MAX. 10 mW puls output.


  Bill Of Materials          March19,2002      11:13:28    Page1

  Item    Quantity        Reference        Part
  ______________________________________________

  1       4       Cb3,Ca3,Cb6,Ca6          0
  2       4       C1,C2,C4,C5              10nF
  3       1       C3              850nF
  4       1       C6              39nF
  5       1       JP1             +7,2 volt fra batteri
  6       1       JP2             til transmitter
  7       1       JP3             transmittermodul (FM-TX2-433)
                                  fra R.F. Solutions
  8       1       JP4             antenne ud
  9       1       Q1              BC847b
  10      2       R2,R1           1M
  11      1       R3              100K
  12      1       R4              470K
  13      1       R5              10K
  14      2       U1,U2           ICM7555



                          Page 1
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7.2 Appendix II

Contingency tables and test statistics from the evaluation trials of ActiTrac at Vissenbjerg Terrarium. In all three tests (χ^2 test for independence between the two samples), a statistical significance ($p<0.0001$) shows that the samples are not independent. The correlation (Φ) is high (≥ 0.8) between the two observation methods, in all three trials.

Summary Table for ActiTrac test 1, Observer test 1

Num. Missing	0
DF	1
Chi Square	76,725
Chi Square P-Value	<,0001
G-Squared	88,129
G-Squared P-Value	<,0001
Contingency Coef.	,625
Phi	,800
Cty. Cor. Chi Square	73,545
Cty. Cor. P-Value	<,0001
Fisher's Exact P-Value	<,0001

Summary Table for ActiTrac test 2, Observer test 2

Num. Missing	0
DF	1
Chi Square	97,194
Chi Square P-Value	<,0001
G-Squared	118,680
G-Squared P-Value	<,0001
Contingency Coef.	,669
Phi	,900
Cty. Cor. Chi Square	93,626
Cty. Cor. P-Value	<,0001
Fisher's Exact P-Value	<,0001

Observed Frequencies for ActiTrac test 1, Observer test 1

	0	1	Totals
0	58	5	63
1	7	50	57
Totals	65	55	120

Observed Frequencies for ActiTrac test 2, Observer test 2

	0	1	Totals
0	58	3	61
1	3	56	59
Totals	61	59	120

Summary Table for ActiTrac test 3, Observer test 3

Num. Missing	0
DF	1
Chi Square	89,231
Chi Square P-Value	<,0001
G-Squared	•
G-Squared P-Value	•
Contingency Coef.	,653
Phi	,862
Cty. Cor. Chi Square	84,889
Cty. Cor. P-Value	<,0001
Fisher's Exact P-Value	<,0001

Observed Frequencies for ActiTrac test 3, Observer test 3

	0	1	Totals
0	84	0	84
1	7	29	36
Totals	91	29	120

7.3 Appendix III

#	Date	Time	X coord.	Y coord.	Weather	Activity	In/Out of water	Temperature [°C]	Humidity [%]	Canopy cover	Distance to nearest water source [m]	Cover	Forest type
*	12-07-02		682594	578857									
*	14-02-03	13:00	676869	573734	R	Active	O			open	>50	N	S
A	18-07-02	09:45	678681	575317	S	Active	O	25,8	>90	semi	>50	N	S
B	14-05-02	14:00	682644	574370	S	Inactive	O	27,3	>90	full	>50	C	S
B	08-06-02	12:10	682851	574609	S	Inactive	I	26,2	>90	full	0	N	S
B	09-06-02	10:45	682856	574609	S	Inactive	O	25,9	>90	full	10	C	S
B	09-06-02	15:15	682856	574609	S	Inactive	O	27,3	>90	full	10	C	S
B	16-07-02	14:30	682403	574979	S	Inactive	O	27,2	>90	semi	>50	C	P
B	26-05-02	12:40	682839	574451	S	Inactive	O	26,2	>90	full	>50	C	P
B	18-06-02	10:30	682610	574653	S	Active	O	27,0	>90	full	>50	N	P
C	27-06-02	14:50	671821	574576	LO	Active	O	26,0	>90	full	40	N	P
C	29-06-02	14:20	671752	574531	LO	Inactive	I	26,6	>90	full	0	N	P
C	07-07-02	12:50	671566	574259	S	Active	I	27,0	>90	semi	0	N	P
C	08-07-02	13:15	671569	574254	LO	Inactive	O	26,3	>90	full	4	N	P
C	21-06-02	06:50	671608	574573	S	Active	O			open	>50	N	S
D	11-06-02	09:50	669099	573976	S	Inactive	O	25,3	>90	full	>50	C	S
DII	02-02-03	11:40	667722	574510	O	Inactive	O	26,3	>90	full	>50	C	S
DII	03-02-03	10:50	667764	574481	R	Inactive	O	27,2	>90	semi	>50	C	S
DII	04-02-03	12:10	667764	574481	LO	Inactive	O	28,6	>90	semi	>50	C	S
DII	05-02-03	14:30	667767	574476	S	Inactive	O	25,4	>90	semi	>50	C	S
DII	12-02-03	12:30	667872	574267	S	Inactive	O	25,7	>90	full	>50	C	S
DII	18-02-03	11:50	667777	574219	S	Inactive	O	26,1	>90	semi	>50	C	S
DII	20-02-03	11:15	667777	574219	O	Inactive	O	25,6	>90	semi	>50	C	S
DII	27-02-03	12:00	667777	574219	O	Inactive	O	25,9	>90	semi	>50	C	S
DII	02-03-03	12:40	667568	574350	O	Inactive	O	26,4	>90	semi	>50	C	S
DII	04-03-03	11:30	667568	574350	S	Active	O	26,3	>90	semi	>50	C	S
E	11-06-02	06:00	679279	575258	S	Inactive	I	23,6	>90	semi	0	C	S

E	10-06-02	15:00	679259	575261	S	Inactive	I	28,6	>90	open	0	N	S
E	11-06-02	20:30	679279	575258	S	Inactive	I	27,0	>90	full	0	C	S
E	15-07-02	17:50	679143	575162	LO	Inactive	O	26,1	>90	full	>50	N	P
E	15-07-02	22:30	679171	575191	N	Inactive	O	23,1	>90	full	8	C	P
E	16-07-02	07:30	679171	575191	N	Inactive	O	22,9	>90	full	8	C	P
E	16-07-02	21:45	679171	575191	N	Inactive	O	24,0	>90	full	8	C	P
E	17-07-02	14:30	679171	575191	N	Inactive	O	27,0	>90	full	8	C	P
E	18-07-02	07:45	679171	575191	N	Inactive	O	23,9	>90	full	8	C	P
F	10-05-02	10:30	682935	575916	S	Active	O	28,2	>90	semi	>50	N	S
F	11-05-02	11:25	682916	575940	S	Inactive	O	30,9	79	open	>50	N	S
F	12-05-02	14:20	682677	575820	S	Inactive	O	28,1	>90	open	>50	C	S
F	14-05-02	12:00	682675	575631	S	Inactive	O	26,1	>90	full	>50	C	S
F	10-06-02	10:15	682943	575705	LO	Inactive	O	25,6	>90	full	>50	C	S
F	08-06-02	15:00	683085	575931	S	Inactive	O	27,3	>90	full	>50	C	S
F	16-07-02	16:00	682512	574881	S	Inactive	O	26,7	>90	semi	>50	C	P
F	26-05-02	10:45	682876	575710	O	Inactive	O	26,1	>90	full	>50	C	S
F	18-06-02	13:15	682522	575629	O	Inactive	O	26,3	>90	full	>50	C	S
G	20-06-02	11:45	669115	573963	S	Mating	O	26,8	>90	full	>50	N	S
G	21-06-02	09:30	669131	573995	S	Inactive	O	26,0	>90	open	>50	C	S
G	26-06-02	11:00	669191	573970	LO	Inactive	O	26,5	>90	semi	>50	C	S
G	27-06-02	07:30	669039	574042	LO	Inactive	O	24,1	>90	full	8	C	S
G	27-06-02	17:20	669045	574022	S	Inactive	O	27,0	>90	semi	35	C	S
H	20-06-02	11:45	669115	573963	S	Mating	O	26,8	>90	full	>50	N	S
H	21-06-02	09:30	669133	573998	S	Inactive	O	26,1	>90	open	>50	C	S
H	26-06-02	10:20	669218	573957	LO	Inactive	O	25,5	>90	full	>50	C	S
H	27-06-02	09:25	669218	573957	LO	Inactive	O	25,0	>90	full	>50	C	P
H	27-06-02	17:00	669218	573960	S	Active	O	26,9	>90	full	>50	C	S
H	29-06-02	16:00	669218	573957	LO	Inactive	O	26,3	>90	full	>50	C	S
H	04-07-02	08:00	669185	573925	S	Inactive	O	24,5	>90	full	>50	C	P
H	04-07-02	15:25	669190	573927	S	Inactive	O	27,3	>90	full	>50	C	P
H	06-07-02	12:20	669272	573988	LO	Active	O	28,1	>90	full	>50	N	P
H	07-07-02	10:40	669297	573999	S	Inactive	O	28,4	>90	open	>50	C	P
H	12-07-02	14:30	669272	574055	S	Inactive	O	26,8	>90	semi	1	N	P
I	19-07-02	16:40	669113	573963	LO	Inactive	O	27,1	>90	full	>50	C	S
I	20-07-02	14:40	669113	573993	S	Inactive	O	27,9	>90	open	>50	C	S

J	04-07-02	15:45	669072	574161	LO	Active	O	26,2	>90	full	>50	C	S
J	06-07-02	10:20	669160	574200	LO	Inactive	O	24,8	>90	full	>50	N	S
J	07-07-02	09:40	669168	574200	S	Inactive	O	25,6	>90	full	>50	C	S
J	19-07-02	14:25	669514	574333	S	Inactive	O	26,7	>90	full	4	C	S
J	13-07-02	12:15	669423	574259	S	Inactive	O	26,9	>90	full	>50	C	S
J ▣	02-07-02	11:40	669037	574163	LO	Active	O	26,2	>90	full	>50	N	S
J ▣	03-07-02	11:20	669037	574163	LO	Active	O	26,3	>90	full	>50	N	S
J ▣	03-07-02	15:34	669037	574163	LO	Active	O	26,6	>90	full	>50	N	S
J ▣	04-07-02	09:40	669037	574163	LO	Active	O	26,3	>90	full	>50	N	S
L	02-02-03	10:40	667289	574254	O	Inactive	O	26,0	>90	full	>50	N	S
L	03-02-03	10:00	667295	574270	R	Inactive	O	26,9	>90	full	>50	C	S
L	04-02-03	13:00	667295	574270	LO	Inactive	O	26,6	>90	semi	>50	C	S
L	05-02-03	15:30	667339	574328	S	Inactive	O	26,3	>90	full	>50	N	S
L	12-02-03	15:50	667676	574086	S	Inactive	O	25,7	>90	full	>50	C	P
L	06-02-03	10:40	667287	574313	LO	Active	O	26,2	>90	full	16	N	S
L	16-02-03	14:30	667701	574143	O	Active	O	26,9	>90	full	10	N	P
L	18-02-03	13:00	667694	574185	S	Inactive	O	25,8	>90	full	20	N	P
L	19-02-03	09:50	667700	574178	S	Inactive	O	26,1	>90	full	30	N	P
L	20-02-03	14:00	668065	574040	O	Active	O	27,5	78	full	>50	N	S
L	27-02-03	10:30	668196	574215	O	Active	O	25,9	>90	full	40	N	S
L	01-03-03	14:00	668685	574331	R	Active	O	27,1	78	full	>50	N	S
L	02-03-03	11:00	668680	574534	O	Active	O	25,9	>90	full	>50	N	S
L	03-03-03	14:00	668674	574641	O	Active	O	26,1	>90	full	>50	N	S
L	04-03-03	10:40	668824	574562	S	Active	O	26,2	>90	semi	>50	N	S
L	05-03-03	11:00	668921	574472	S	Active	O	34,6	64	open	25	N	P
L	10-03-03	13:00	669089	574660	R	Inactive	O	25,9	>90	semi	>50	C	S

Notes on all tortoise encounters during the study. Individuals (#) noted with * were not radio tracked. ▣ denotes nest site. In the weather column S = Sunny, R = Rain, L= lightly overcast, O = overcast. Cover denotes wether the tortoise was covered (C) or not covered (N). Forest type: P = primary, S = secundary

7.4 Appendix IV

Home range calculation example:

GPS points of #B and the computation of home range
using the Ellipse method (Jennrich and Turner, 1969)

i	x_i	y_i	x_i^2	y_i^2	$x_i y_i$
1	682644	574370	4,66003E+11	3,29901E+11	3,92090E+11
2	682851	574609	4,66285E+11	3,30176E+11	3,92372E+11
3	682856	574609	4,66292E+11	3,30176E+11	3,92375E+11
4	682403	574979	4,65674E+11	3,30601E+11	3,92367E+11
5	682610	574653	4,65956E+11	3,30226E+11	3,92264E+11
6	682839	574451	4,66269E+11	3,29994E+11	3,92258E+11
Totals	4096203	3447671	2,79648E+12	1.98107E+12	2,35373E+12

$$s_{xx} = \frac{1}{4}\left[\frac{2{,}79648\mathrm{E}+12 - (4096203)^2}{6}\right] = 41475{,}38$$

$$s_{yy} = \frac{1}{4}\left[\frac{1{,}98107\mathrm{E}+12 - (3447671)^2}{6}\right] = 55218{,}21$$

$$s_{xy} = \frac{1}{4}\left[\frac{2{,}35373\mathrm{E}+12 - (4096203)(3447671)}{6}\right] = -30609{,}13$$

$$|S| = 41475{,}38 \times 55218{,}21 - (-30609{,}13)^2 = 1353277363$$

$$\text{Home range estimate} = \frac{6\pi |1353277363|^{½}}{1000000} = \underline{\underline{0{,}69\ \mathrm{km}^2}}$$

7.5 Appendix V

Correlation analysis of home range vs. mass of study animals, days monitored and number of loci respectively. To test for correlation a Fisher R to Z analysis (Zar, 1999) was performed using StatView 5.0 (SAS Institute inc., 1998). The only significant ($p < 0.05$) correlation was found between number of loci and home range estimates based on the convex polygon method (CPM). Critical value for $Z = t_{0.05\,(2),\infty} = 1.9660$ (Zar, 1999)

Fisher's R to Z
Hypothesized Correlation = 0

	Correlation	Count	Z-Value	P-Value
Mass, days	-,547	8	-1,372	,1701
Mass, loci	,111	8	,248	,8040
Mass, HR	-,547	8	-1,372	,1701
Mass, CPM	-,342	8	-,797	,4256
days, loci	-,022	8	-,048	,9616
days, HR	,632	8	1,666	,0958
days, CPM	,394	8	,932	,3513
loci, HR	,549	8	1,379	,1679
loci, CPM	,707	8	1,970	,0489
HR, CPM	,946	8	4,009	<,0001

Note: HR denotes the confidence ellipse method (CEM)

7.6 Appendix VI

t-test torsdag, marts 04, 2004, 00:05:13

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = <0,001)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:05:13

Data source: Data 1 in T test på ambimicro.SNB

Group	**N**	**Missing**	**Median**	**25%**	**75%**
06:00-08:00 Microcl.	5	0	23,900	23,425	24,200
06:00-08:00 Ambient	170	0	22,700	22,300	23,400

T = 745,500 n(small)= 5 n(big)= 170 (P = 0,006)

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference (P = 0,006)

t-test torsdag, marts 04, 2004, 00:06:33

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = 0,003)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:06:33

Data source: Data 1 in T test på ambimicro.SNB

Group	**N**	**Missing**	**Median**	**25%**	**75%**
08:00-10:00 Microcl.	9	0	26,000	25,525	26,150
08:00-10:00 Ambient	137	0	24,500	24,000	25,200

T = 1156,000 n(small)= 9 n(big)= 137 (P = <0,001)

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference (P = <0,001)

t-test torsdag, marts 04, 2004, 00:07:08

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = <0,001)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:07:08

Data source: Data 1 in T test på ambimicro.SNB

Group	**N**	**Missing**	**Median**	**25%**	**75%**
10:00-12:00 Microcl.	27	0	26,200	25,900	26,800
10:00-12:00 Ambient	140	0	26,600	26,300	27,400

T = 1876,500 n(small)= 27 n(big)= 140 (P = 0,089)

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0,089)

t-test torsdag, marts 04, 2004, 00:07:49

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = 0,005)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:07:49

Data source: Data 1 in T test på ambimicro.SNB

Group	N	Missing	Median	25%	75%
12:00-14:00 Microcl.	17	0	26,400	26,175	27,150
12:00-14:00 Ambient	140	0	28,100	27,400	28,800

T = 532,000 n(small)= 17 n(big)= 140 (P = <0,001)

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference (P = <0,001)

t-test torsdag, marts 04, 2004, 00:08:16

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = 0,010)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:08:16

Data source: Data 1 in T test på ambimicro.SNB

Group	N	Missing	Median	25%	75%
14:00-16:00 Microcl.	20	0	26,750	26,300	27,300
14:00-16:00 Ambient	140	0	28,100	27,000	29,200

T = 857,500 n(small)= 20 n(big)= 140 (P = <0,001)

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference (P = <0,001)

t-test torsdag, marts 04, 2004, 00:08:47

Data source: Data 1 in T test på ambimicro.SNB

Normality Test: Failed (P = 0,009)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test torsdag, marts 04, 2004, 00:08:47

Data source: Data 1 in T test på ambimicro.SNB

Group	N	Missing	Median	25%	75%

```
16:00-18:00 Microcl.          4         0       26,950          26,500          27,050
16:00-18:00 Ambient         140         0       26,600          26,100          27,700

T = 289,500  n(small)= 4  n(big)= 140  (P = 1.000)

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random
sampling variability; there is not a statistically significant difference  (P = 1.000)


t-test                                                                                                  torsdag, marts 04, 2004, 00:09:39

Data source: Data 1 in T test på ambimicro.SNB

Normality Test:               Failed       (P = <0,001)


Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test                                                                              torsdag, marts 04, 2004, 00:09:39

Data source: Data 1 in T test på ambimicro.SNB

Group                         N      Missing        Median            25%             75%
20:00-22:00 Microcl.          2         0       25,500          24,000          27,000
20:00-22:00 Ambient         136         0       24,500          24,100          24,500

T = 167,000  n(small)= 2  n(big)= 136  (P = 0,624)

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random
sampling variability; there is not a statistically significant difference  (P = 0,624)
```

7.7 Appendix VII

```
BASIC STATISTICS
Data file -
C:\Programmer\Oriana2\SampData\DII tider.ori

DII tider
Analysis begun: 1. december 2003 10:30:00


Variable       Time
Number of Observations                  691
Data Grouped?                           No
Group Width (& Number of Groups)
Mean Vector (µ)                         14:45
Length of Mean Vector (r)               0,556
Median                                  14:50
Concentration                           1.341
Circular Variance                       0,444
Circular Standard Deviation             62,093°
Standard Error of Mean                  2,525°
95% Confidence Interval (-/+) for µ     14:26
                                        15:05
99% Confidence Interval (-/+) for µ     14:19
                                        15:11
Rayleigh Test (Z)                       213,506
Rayleigh Test (p)                       0
Rao's Spacing Test (U)                  162,43
Rao's Spacing Test (p)                  < 0.01
Watson's U² Test (von Mises, U²  )      0,33
Watson's U² Test (p)                    < 0.005
Kuiper's Test (von Mises, V)            2,248
Kuiper's Test (p)                       < 0.01
```

```
BASIC STATISTICS
Data file –
C:\Programmer\Oriana2\SampData\L tider.ori

L tider
Analysis begun: 1. december 2003 10:33:39


Variable       Time
Number of Observations                  3567
Data Grouped?                           No
Group Width (& Number of Groups)
Mean Vector (µ)                         12:32
Length of Mean Vector (r)               0,716
Median                                  12:22
Concentration                           2,111
Circular Variance                       0,284
Circular Standard Deviation             46,804°
Standard Error of Mean                  0,78°
95% Confidence Interval (-/+) for µ     12:26
                                        12:38
99% Confidence Interval (-/+) for µ     12:24
                                        12:40
Rayleigh Test (Z)                       1830,187
Rayleigh Test (p)                       0
Rao's Spacing Test (U)                  321.648
Rao's Spacing Test (p)                  < 0.01
Watson's U² Test (Uniform, U²)          94,957
Watson's U² Test (p)                    < 0.005
Kuiper's Test (Uniform, V)              31.19
Kuiper's Test (p)                       < 0.01
```