Locomotor Behaviour and Ecology of Three Sympatric Lemur Species in Mantadia National Park, Madagascar

This thesis is the result of my own work. The material contained in the thesis has not been presented, nor is currently being presented, either wholly or in part for any other degree or other qualification.
The research work was carried out in Mantadia National Park, Madagascar

Thesis submitted in accordance with the requirements of the University of
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Mary L. Blanchard
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Dedicated to:

Irene Beatrice Hoare

28 June 1913 to 7 July 2006

My grandmother 'Nan', for always telling me 'go do it!' Her bewitched letters were wonderful to receive. Her strength my inspiration.

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Abstract

This study compares the locomotor behaviour of three sympatric species of folivorous (leaf-eating) lemur; *Indri indri* (indri), *Propithecus diadema* (diademed simpona) and *Hapalemur griseus griseus* (eastern lesser bamboo lemur). *I. indri* and *P. diadema* are large bodied 'vertical clingers and leapers'. *H. g. griseus* is small bodied, combining 'vertical clinging and leaping' with quadrupedal walking. The three species were studied in Mantadia National Park, Madagascar.

One social group each of *I. indri* (n=4) and *P. diadema* (n=7) and two groups of *H. g. griseus* (n=6 and n=4) were followed during an eleven month period. Data was collected ad-hoc for locomotor mode and support use preferences, and by the method of 'focal animal sampling' for activity, diet, ranging and vertical spatial usage.

In terms of activity, *I. indri* and *P. diadema* were found to be diurnal, while *H. g. griseus* was crepuscular (activity at dawn and dusk). The active period for *I. indri* and *P. diadema* mirrored sunrise and sunset, a pattern not observed in *H. g. griseus.* Length of feeding period did not seasonally alter in *I. indri*, while rest and travel periods decreased in the austral (southern hemisphere) winter. Rest and travel periods of *P. diadema* decreased in winter while feeding time increased. Feeding time did not alter seasonally in *H. g. griseus*, while rest and travel increased slightly during the austral winter.

There was considerable dietary overlap between *I. indri* and *P. diadema*, up to 53%, but *P. diadema* maintained a more diverse diet. *I. indri* had longer, but fewer, daily feeding bouts compared to *P. diadema*. All three study species displayed marked seasonality in diet.

P. diadema had the largest home range (27ha), followed by *I. indri* (13ha), while *H. g .griseus* had the smallest home ranges (3.5ha and 5.4ha). *P. diadema* had significantly longer daily path lengths (902m) compared to *I. indri* (482m). The daily path length in *I. indri* and *P. diadema* positively correlated with hours of daylight; decreasing daylight in the austral winter led to shorter path lengths.

H. g. griseus were found at a mean height of 7.8m, lower than that of both *I. indri* (12.6m) and *P. diadema* (10.6m). The difference all three species is significant.

I. indri were observed to display a greater preference for non-vertical supports and *P. diadema* a greater preference for vertical supports. Contrary to expectation, although both species used supports with diameters sized 5.1 to 10cm most frequently, in comparison *I. indri* showed a preference for supports sized over 10.1cm and *P. diadema* for those smaller than 10cm. As expected, *I. indri* and *P. diadema* utilised leaping more frequently during travel and all other modes less frequently, while during feeding leaping was used less frequently and all other modes more frequently.

In summary a relationship was found to exist between support use, locomotion and stratum, and between stratum, dietary preference and predation risk for all three species. Contrary to prediction, seasonality was found to exert, at most, only a weak effect on the ecology of *H. g. griseus*. However, marked seasonality (yearly patterns of behaviour) was found in activity, diet and ranging for *I. indri* and *P. diadema*.

Chapter 1 Introduction

This chapter includes an overview and the rationale of the study as a whole. It includes background information on the geography and climate of Madagascar, followed by a description of the biogeography and origin of lemurs. To aid the reader a complete list of Latin and English vernacular name of all species referred to in this thesis can be found in Appendix A.

1.1 Background and Overview of the Study

This study investigates the behavioural ecology of three sympatric species of lemur, *Indri indri* (indri), *Propithecus diadema* (diademed simpona) and *Hapalemur griseus griseus* (eastern lesser bamboo lemur) in Mantadia National Park, Madagascar. When different species, especially those that are closely related, live sympatrically, differences may reasonably be presumed to exist within their ecology. Studies on sympatric species have been made for many primate groups and the reasons for tolerance of co-existence vary. For example, Harcourt and Nash (1986) found that niche separation for *Galagoides zanzibaricus* (Zanzibar bushbaby [140g]) and *Otolemur garnettii* (Garnett's greater bushbaby [800g]) was based upon diet and height, diameter and orientation of supports. These differences were attributed to size difference. The larger *G. garnettii* ate more fruit (50% of its diet) while the smaller *G. zanzibaricus* was found to be more insectivorous (70% of its diet was composed of invertebrates). On the other hand locomotor repertoire differentiated the quadrupedal *Cebus apella* (tufted capuchin) from the more saltatory *Saimiri sciureus* (squirrel monkey [Fleagle *et al.*, 1981]).

The results presented here are from a study commencing in October 2004 and continuing to October 2005. Year-long studies are important as there can be significant changes in behaviour from season to season. For example it has been found that *Pan troglodytes verus* (West African chimpanzee) in Guinea spend more time in the trees during the rainy season rather than the dry season (Takemoto, 2004). It is particularly important to encompass seasonal variation in any study of Malagasy fauna since Madagascar experiences more pronounced seasonality than most tropical countries (Scholz & Kappeler, 2004).

Chapter 1 continues with an overview of the climate and geography of Madagascar, and includes a brief review of lemur biogeography and origins. **Chapter 2** presents information on the study site, while background information to the three study species is given in **Chapter 3**. General field observations of the lemurs are reported in **Chapter 4**, while the daily and seasonal activity rhythms of the three species are discussed in **Chapter 5**. Feeding behaviour is discussed in **Chapter 6**, followed by ranging behaviour in **Chapter 7**. The spatial utilisation of the canopy is covered in **Chapter 8**, while locomotor behaviour is examined in **Chapter 9**. **Chapter 10** includes a review of predation in lemurs as well as summarising cases of predation observed or inferred during the field study. This chapter is particularly important since predation, and thus predator-avoidance tactics, plays a large part in the adaptation of most species, exerting influences across various aspects of a species' ecology.

1.2. Madagascar: Geography and Climate

Figure 1.1. Map of Madagascar, from www.intute.ac.uk/.../html/947_map.html. ●Approximate position of field site.

Madagascar (Figure 1.1) is the world's fourth largest island, following Greenland, New Guinea and Borneo in area (Tattersall & Sussman, 1975; Jenkins, 1987; Ganzhorn *et al.*, 1999). It is 1600km at its longest and 580km at its widest, covering an area of 590,000km^2 (Koechlin, 1972; Tattersall & Sussman, 1975; Jenkins, 1987). Madagascar lies between S11°57' and S25°32' and E43°14' and E50°27', all but the southern tip lying within the Tropic of Capricorn (Donique, 1972; Koechlin, 1972; Tattersall & Sussman, 1975; Jenkins, 1987). Madagascar is orientated NNE/ SSW, and is separated from Mozambique on the African mainland by the Mozambique Channel, which varies in width from 350 to 1200km (Tattersall & Sussman, 1975).

Madagascar is considered to have a relatively harsh seasonal environment, with low plant productivity, variable food availability, low plant species diversity, few seasonal food sources, drought and cyclones (Pochron & Wright, 2003). This seasonality is reflected in lemur biology by highly seasonal birth patterns and features of testicular size, testosterone function, hair growth, food intake, metabolically-active hormones, and adipose-tissue mass (Pochron & Wright, 2003).

1.2.1. Topography

Madagascar is a geomorphologically asymmetrical island, an east-of-central plateau being surrounded by coastal lowlands, which are narrow on the east but wider on the west (Tattersall & Sussman, 1975). This crystalline-rock plateau, 1500 to 3000m in elevation, contains the three highest peaks (Tattersall & Sussman, 1975). It runs the length of the island, separating a steep escarpment and narrow coastal strip to the east, from a gently sloping western plain (Tattersall & Sussman, 1975; Pollock, 1979a). Malagasy environmental conditions are dominated by the presence of a central plateau, which climatologically splits the country in two halves (Tattersall & Sussman, 1975).

1.2.2. Climate

Due to its size, Madagascar has the climatic features of a small continent, and there is considerable regional variation (Tattersall & Sussman, 1975). The two seasons are the austral, southern hemisphere, summer (November to April) and austral winter (May to October [Tattersall & Sussman, 1975]). There is considerable risk from cyclones throughout the summer, 70% of the yearly total precipitation occurring from January to March (Donique, 1972). Cyclones are capable of depositing between 600 and 700mm of rain in the four or five days they take fully to pass (Donique, 1972). This can cause widespread flooding and destruction of forest (Jenkins, 1987).

There are a number of climatic zones. The extreme southern tip is hot and semi-arid, often experiencing drought, having a distinct rainy season (Tattersall & Sussman, 1975). The western lowlands are seasonal, rainfall and temperature decrease with increasing latitude (Tattersall & Sussman, 1975). The central plateau is temperate, although climate varies with altitude (Tattersall & Sussman, 1975). The eastern strip is hot and humid, and experiences rain all year (Tattersall & Sussman, 1975).

1.2.2.1. Temperature

In general terms, at any given latitude, the east coast of Madagascar is a few degrees cooler than the west coast, and the north is usually a few degrees warmer than the south (Donique, 1972; Tattersall & Sussman, 1975; Pollock, 1979a). Inland temperatures are largely dependent on altitude (Tattersall & Sussman, 1975). Minimum temperatures are found in July and August throughout Madagascar, although maximum temperatures do not follow such a simple pattern (Tattersall & Sussman, 1975). On the central highlands, the maximum temperature is in November; while in the south-west it is in January and March, and on the east coast around January and February (Tattersall & Sussman, 1975). The extreme northeast experiences double maxima in April and December, and the northwest double maxima in March to April and October to December (Tattersall & Sussman, 1975).

1.2.2.2. Rainfall

Rainfall varies greatly throughout Madagascar, from a minimum of 120mm at Morombe in the south west, to 5000mm at Tamatave, in the east (Tattersall & Sussman, 1975). An east-west distinction in rainfall results from the rain-shadowing effect of the central plateau (Pollock, 1979a). There is a clearly defined rainy season in the austral summer for the western half of the country, which is present, but less pronounced, in the eastern half, where any day can have 100mm of rainfall (Tattersall & Sussman, 1975). For example, in the highlands and west 90% of the total rainfall falls between October and April, however in the east only 50% of their total rainfall falls in the same period. In the west there is also a graduation of rainfall, southern parts receiving less rain than the north (Pollock, 1979a).

1.2.3. Vegetation

There is a high degree of floristic endemism in Madagascar (Koechlin, 1972). In the western region there is 38% generic endemism, and 89% specific endemism (Koechlin, 1972). There is less endemism in the east, but it is still 22% at the generic level and 82% at the species level (Koechlin, 1972). Madagascar can be separated into two main vegetation zones, the eastern and northern wet and evergreen forest, and the western and southern dry forest (Koechlin, 1972; Tattersall & Sussman, 1975; Pollock, 1979a).

1.2.3.1. Eastern Domain

There is a variety of forest types in the east, but they are all characteristically dense evergreen rainforests (Tattersall & Sussman, 1975; Pollock, 1979a). Forest types are largely separated by altitude.

A: Low-Altitude Rainforest: 0 to 800 meters

This region extends almost the entire length of the country, but is only a few tens of kilometres wide (Koechlin, 1972). Rainforests lying at altitudes up to 800m are highly stratified: they contain an open forest floor and abundant epiphytes (Koechlin, 1972; Tattersall & Sussman, 1975). Trees reach 25 to 30m, and are mixed with lianas such as liana bamboo (Koechlin, 1972). The ground often bears only dead leaves, although areas of ferns, dwarf palms and shrubs or herbaceous plants can be found (Koechlin, 1972). Examples of lowland rainforest are the Masoala National Park, Mananara-Nord Biosphere Reserve and Nosy Mangabe Special Reserve (Garbutt, 1999).

B: Mid-Altitude Rainforest: 800 to 1,300 metres

Forest in the eastern area of the central domain is seasonal, experiencing high rainfall but a definite dry season (Koechlin, 1972; Tattersall & Sussman, 1975). Only isolated patches exist due to deforestation (Koechlin, 1972). The canopy is a single layer around 0m to 25m, below which is herbaceous or shrubby undergrowth (Koechlin, 1972; Tattersall & Sussman, 1975). At the higher altitudes the latter becomes more mossy and herbaceous (Koechlin, 1972). Analamazoatra Special Reserve, Mantadia National Park, Ranomafana National Park and Montagne d'Ambre National Park are all examples of mid-altitude rainforest (Garbutt, 1999).

C: High-Altitude 'Lichen Forest': 1,300 to 2,000 metres

Forest is sclerophyllous, characterised by small, hard leaves and twisting trunks, and trees which reach a height of only 10 to 12m (Koechlin, 1972). Epiphytes, such as ferns and orchids, are abundant, hanging in long strands from moss or found on the thick layer of moss covering the forest floor (Koechlin, 1972). Only small patches of such forest remain, the rest having been destroyed by humans (Koechlin, 1972).

D: High Mountains: over 2,000 metres

There are four high mountain domains above 2000m: Tsaratanana (2,886m) and Marojejy (2,137m) in the north, Ankaratra (2,643m) in the centre and Andringitra (2,659m) in the southeast (Koechlin, 1972). Climatic conditions are harsh and there is a large range of temperature, humidity and sunshine (Koechlin, 1972). There are frosts in the winter and the lowest temperature in Madagascar was recorded on the Andringitra Massif, -15°C in June (Koechlin, 1972). Microclimates allow lichen or moss forest to extend above 2,000m, but generally only bushy and herbaceous plants survive (Koechlin, 1972; Tattersall & Sussman, 1975). Mountain prairie can also be found, which can resemble a peat bog in the wetter areas (Koechlin, 1972).

1.2.3.2. Western Domain

The western region has seasonal rainfall and temperatures decrease north to south. The western region can be divided into two domains, the south, and the west (Tattersall & Sussman, 1975; Pollock, 1979a).

A: Western

The distribution of vegetation in the westerly western region is largely dependent on soil characteristics: siliceous, calcareous or rocky (Koechlin, 1972; Tattersall & Sussman, 1975; Pollock, 1979a). Deciduous forests are found on silicaeous soils, usually by river valleys (Tattersall & Sussman, 1975). These forests are dominated by *Tamarindus indica* (kijy trees) which reach 50m, and the forest floor is usually very open (Tattersall & Sussman, 1975). Xerophytic vegetation, which can survive with little water, is found on poorer-quality and drier calcareous soils (Tattersall & Sussman, 1975). There is a dense understorey and the canopy height is lower (Tattersall & Sussman, 1975). Dry soils lead to xerophytic thickets, which have fewer species than those found in the southern western domain (Tattersall & Sussman, 1975). Overall due to decreasing rainfall north to south, more deciduous forest is found in the northern parts, but zones do merge into one another (Tattersall & Sussman, 1975). Examples of this type of forest are Ankarafantsika Nature Reserve, Kirindy Forest, Ankarana Special Reserve and Analamera Special Reserve (Garbutt, 1999).

B: South

The southern tip of Madagascar is extremely arid and often experiences drought. This area contains rich thickets or forests of endemic, bushy, xerophytic vegetation; Didiereaceae (*Didierea* spp. and *Alluaudia* spp.) and Euphorbiaceae (*Euphorbia* spp.) are predominant (Tattersall & Sussman, 1975; Pollock, 1979a). To conserve moisture, trees have thick trunks and small leaves, usually reaching no more than 15m in height (Pollock, 1979a). The deciduous forests typical of the west can also be found, as gallery-forest primarily along rivers (Pollock, 1979a; Tattersall & Sussman, 1975). Examples are Beza-Mahafaly Special Reserve and Berenty Reserve (Garbutt, 1999).

1.3. Biogeography and Lemur Origins

Madagascar has a high diversity of mammals at low taxonomic levels, combined with a low diversity of major taxa (Ganzhorn *et al.*, 1999; Tattersall, 2006). The low diversity of major taxa is considered to result from the inherent difficulties for terrestrial mammals in dispersing across substantial water barriers (Tattersall, 2006). There is a great diversity of lemurs: 15 genera and 90 species (Rylands, 2007), ranging from 30g to 7kg (Ganzhorn *et al.*, 1999). Mittermeier *et al.* (1994) placed Madagascar third on a list of high-primate-diversity countries. Lemurs have a range of dietary categories from omnivorous to folivorous and include some of the world's most specialised primates, such as *Hapalemur griseus alaotrensis*

(Alaotran bamboo lemur) and *Daubentonia madagascariensis* (aye-aye [Ganzhorn *et al.*, 1999]). Until the arrival of humans, 2,000 years ago there were also a number of large (up to gorilla-sized) lemurs (Ganzhorn *et al.*, 1999).

There has been much debate as to the origins of Malagasy vertebrates. Although Madagascar has been an island for 83 million years, its entire extant vertebrate fauna share ancestors with non-Malagasy vertebrates more recently than this (Stankiewicz *et al.*, 2006). Of the few Mesozoic mammals known from the Malagasy fossil record, none are closely related to extant fauna (Tattersall, 2006). The issue is further complicated as radiations of different taxa occurred at different times (Stankiewicz *et al.*, 2006). For example, while it is thought that lemuroids diverged from the Afro-Asian lorisoids around 60 million years ago, with the basal Malagasy divergence about 55 million years (Masters *et al.*, 2006), all Malagasy *carnivores* share a common ancestor around 24 million years ago (Yoder *et al.*, 2003).

The process leading from the super-continent of Gondwana to the southern continents of today occurred between 170 and 30 million years ago (Masters *et al.*, 2006). Gondwana first began to fragment 170 to 150 million years ago, beginning the separation of Africa and Madagascar (Masters *et al.*, 2006). This event left South America and Africa attached in the west, while Madagascar, India, Antarctica and Australia lay on the eastern side of the basin (Masters *et al.*, 2006). This process was completed 138 million years ago; Madagascar settled into its present position, 430km from the Mozambique coast, 120 million years ago. Prior to this Madagascar was displaced south along the Davie Fracture Zone, passing close to Africa 140 million years ago. Madagascar completely separated from India between 83 and 89 million year ago, at which point India began to rapidly move north to collide with Asia (Masters *et al.*, 2006).

The traditional theory of how animals reached Madagascar is they rafted across from Africa on large mats of vegetation (Kappeler, 2000a; Masters *et al.*, 2006; Tattersall, 2006). This process has been observed for *Iguana iguana* (green iguana) in the Caribbean (Censky *et al.*, 1998): a minimum of 15 male and female individuals rafted between islands on a mat of logs and uprooted trees up to 30m long (Censky *et al.*, 1998). This event was probably triggered by a hurricane, progress of the raft(s) occurring in the direction of prevailing currents: based on the initiation of the hurricane, it took 29 to 30 days (Censky *et al.*, 1998). Recolonisation of Caribbean islands by *Anolis* lizards on rafts following local extinction by hurricanes has been shown to occur (Calsbeek & Smith, 2003).

These cases involve dispersal along paths of the prevailing surface current and to some extent the winds (Masters *et al.*, 2006; Stankiewicz *et al.*, 2006). Present day (extending back at least to the Late Eocene, around 40 million years ago) currents and winds in the Mozambique Channel are however not conducive for rafting to occur from Africa to Madagascar, although they would allow the reverse (Stankiewicz *et al.*, 2006). Stankiewicz *et al.* (2006) concluded that rafting from Africa to Madagascar is unlikely in the relevant time period.

A further complication to the rafting theory for the origin of Malagasy vertebrates is the likelihood of individuals surviving a crossing. The known cases of dispersal by rafting previously mentioned involve reptiles. Unlike mammals, reptiles do not need to maintain a constant body temperature (Stankiewicz *et al.*, 2006). Martin (1972) was the first to propose that the ability of some lemurs (*Microcebus* spp. [mouse lemurs] and *Cheirogaleus* spp. [dwarf lemurs]) to hibernate for extended periods would have made it more possible for the ancestral lemur to raft while hibernating (Kappeler, 2000a: Yoder *et al.*, 2003). Torpor has also been observed in a non-Malagasy strepsirrhine, the Asian *Loris tardigradus* (slender loris [Mzilikazi *et al.*, 2006]). Kappeler (2000a) suggests that a group of lemur ancestors, hibernating together in a tree, could have been washed across the Mozambique Channel. However it has been suggested that ancestral lemurs would have weighed in the order of 2kg and would therefore have been too large to exhibit hypometabolism (Stankiewicz *et al.*, 2006; Masters *et al.*, 2007). In addition one of the closest extant relatives of lemurs living in Africa, *Galago moholi* (southern lesser galago), does not exhibit torpor or hibernation, even in stressful environments (Mzilikazi *et al.*, 2006; Stankiewicz *et al.*, 2006). Studies have yet to examine torpor in other galagos (Mzilikazi *et al.*, 2006). Of course it is entirely possible that the ancestor of both lemurs and galagos exhibited torpor and that this trait has been lost in extant galago and some lemur species (Mzilikazi *et al.*, 2006). The alternate hypothesis is that torpor has evolved independently in cheirogaleids and loris (Mzilikazi *et al.*, 2006).

These complications have led Stankiewicz *et al.* (2006) to suggest that either the ancestral lemur did not originate in Africa; or that inter-channel islands along the Davie Fracture Zone (DFZ), at the end of the Mesozoic and early Cainozoic, aided dispersal, a theory further discussed by Tattersall (2006). Studies of the floor of the

Mozambique Channel have indicated areas of potential subaerial exposure and erosion (Tattersall, 2006). Core samples have suggested the presence of topographic highs along the DFZ resulting in subaerial sediment deposition (Tattersall, 2006). The time period for the possible existence of such 'islands' is between 45 and 26 million years ago, which falls within the time bands of colonisation of Madagascar by its extant mammalian fauna (Tattersall, 2006). This theory is endorsed by Godinot (2006).

The biogeography debate is further complicated by the fossil record outside of Madagascar and by recent genetic phylogenies. The sub-order Strepsirrhini contains not only lemurs but African galagos (Galagidae), and Afro-Asian pottos and lorises (Lorisidae [Tattersall, 2006]). All extant strepsirrhines are linked, among other things, by the possession of a procumbent tooth-comb in the lower jaw (Tattersall, 2006). Until recently fossil evidence of strepsirrhines was limited to the African Miocene, after divergence of the lemurs (Tattersall, 2006). Yoder *et al.* (1996) believe that the molecular and fossil record suggests an African birthplace of the primates, including the strepsirrhines. Following an examination of the fossil record however, Martin (2003), suggested that strepsirrhines evolved in Indo-Madagascar and not in Africa. In this scenario lemurs became isolated in Madagascar when it split from India and lorises migrated to Africa (Martin, 2003). There is also some suggestion that the primate clade may have evolved in Asia and rafted to Madagascar (Martin, 2000; Marivaux *et al.*, 2001; Masters *et al.*, 2006).

Recent discoveries from the Late-Middle Eocene Jebel Qatrani Formation of Egypt have given us the earliest known definite tooth-combed strepsirrhine fossil (Seiffert *et al.*, 2003; Godinot, 2006; Stevens & Heesy, 2006; Tattersall, 2006). This 40 million year old fossil, *Karanisia clarki*, is possibly a lorisid, from a sister taxon to the extant West African genus *Arctocebus* (Seiffert *et al.*, 2003; Stevens & Heesy, 2006; Tattersall, 2006). The same stratigraphic sediments have elicited possible galagid molars in the form of *Saharagalago misrensis* (Stevens & Heesy, 2006; Tattersall, 2006). This suggests that the two non-Malagasy strepsirrhines had diverged prior to the Late Eocene (Stevens & Heesy, 2006; Tattersall, 2006).

A recent discovery of a strepsirrhine fossil with a strong resemblance to cheirogaleid lemurs, in Pakistan, suggests a non-African birth of the strepsirrhines if not the entire primate clade (Marivaux *et al.*, 2001). This fossil, named *Bugtilemur mathesoni*, is from the Oligocene and suggests an Asian origin for the loris-lemur clade (Marivaux *et al.*, 2001). The situation is further complicated because genetic studies by DelPero *et al.* (2006) have suggested that cheirogaleids are centrally located in the lemuroid radiation and therefore are not a suitable proxy for the ancestral lemur. The potential similarity between *B. mathesoni* and cheirogaleids could either be due to homoplasy or to a second radiation originating from Madagascar (Tattersall, 2006). Godinot (2006) further, disagrees with Marivaux *et al.* (2001) classification of *B. mathesoni*, considering it an adapiform.

Molecular studies tend to support the monophyly of the lemurs (Yoder *et al.*, 1996; DelPero *et al.*, 2006; Tattersall, 2006). It would appear from these studies that the basal split was between lorisoids and lemuroids, Daubentoniidae being an outlier among lemuroids (Tattersall, 2006).

Genetic studies by DelPero *et al.* (2006) found that the first group to diverge was *Daubentonia*. There is discussion over which group emerged next. Similarities between the teeth and skulls of daubentoniids and indriids have led to the suggestion that they are sister taxa: indriids would therefore be the second taxa to emerge (DelPero *et al.*, 2006). However this similarity may be homoplastic, where it evolved separately in different phylogenetic lineages, and there is indication that Megaladapidae was the second lineage to emerge (DelPero *et al.*, 2006). DelPero *et al.* (2006) concluded that the cheirogaleids were either the sister taxon to Megaladapidae or the third lineage to emerge. The differences between investigators' interpretation of lemuroid phylogenies stems from the lack of data points between the ancient divergences (DelPero *et al.*, 2006). DelPero *et al.* (2006) give two possible explanations: either that the early divergence was very rapid; or that there is too much 'noise' in the samples. Godinot (2006) suggests that the early divergence of the daubentoniids could indicate that they had already diverged from the other lemur families before arrival on Madagascar.

1.4. Summary

Madagascar is a large island with an almost complete range of climatic and biogeographic zones: rainfall ranges from 120 to 5,000mm; temperatures plummet below 0°C and rise to 50°C. There is over 80% endemism at the species level for flora and 90% endemism in mammalian species. The origin of the extant mammalian fauna is under debate as Madagascar became an island prior to the divergence of their lineages from those in mainland Africa and Asia; no doubt debates over rafting and alternative sites of divergence will long continue. What is not under dispute is that the few mammalian species that managed to reach Madagascar have undergone a high degree of speciation and evolved to fill niches not observed in their ancestors or present-day related species in Africa and elsewhere.

This study sets out to examine the behavioural ecology of three sympatric species; *I. indri*, *P. diadema* and *H. g. griseus*. Niche separation will presumably exist between sympatric species, and mechanisms for this range from differences in diet through to locomotion. It would therefore be expected to find ecological differences between sympatric *I. indri*, *P. diadema* and *H. g. griseus*. Temporal effects are important throughout primate species, especially so in Madagascar where there is a high degree of seasonality.

Stratum is a key factor in niche separation between sympatric primates (Chapter 8). Fleagle (1980) found no association between diet, locomotor behaviour and stratum in platyrrhines. However Crompton (1984) noted associations for gumnivores and insectivores. Therefore it is expected for the study of folivores that **Key Hypothesis 1.1: that in all three sympatric species a relationship exists between support use, locomotion and stratum on the one hand and between stratum and dietary preference and predation risk on the other.** As has been previously discussed Madagascar is a strongly seasonal environment and this is reflected in lemur biology (Pochron and Wright, 2003). Further small mammals have the greatest metabolic response to temperature change (Hart, 1956). Thus it is expected **Key Hypothesis 1.2: in all three sympatric species seasonality will be apparent in activity, feeding and ranging and that it will be especially marked in the small-bodied *H. g. griseus*.**

Chapter 2 Study Site

The environment in the study location, Mantadia National Park is described in this chapter, including local climatic information, forest structure, fauna, and usage of the forest by local people. The aim of this chapter is to describe climatic and structural conditions within the study site so that behaviour of the study species can be examined within the ecological setting in which it occurs.

2.1. Mantadia National Park

Mantadia National Park is a mid-altitude (800 to 1,260m) montane rain forest in east-central Madagascar (Garbutt, 1999; Powzyk & Mowry, 2003). Mantadia is located at S18°46 to S18°56 and E48°28 to E48°32; lying 26km north of Andasibe and the Analamazoatra Special Reserve (Garbutt, 1999; Powzyk & Mowry, 2003). The Analamazoatra Special Reserve was created on 21 June 1970, protecting 810ha (Jenkins, 1987); whereas Mantadia became a national park in 1989 and originally covered 10,000ha (Powzyk, 1997 [Figure 2.1]). The protected area in Mantadia was increased in 2003 and now covers 15,500ha. The two areas were combined to create the Parc National Andasibe-Mantadia (PNAM), under the control of the Association Nationale pour la Gestion des Aires Protégées (ANGAP; ANGAP is a non-governmental organisation [NGO], created in 1990 which has the purpose of managing and protecting Malagasy national parks).

Forest around Perinet is high and relatively cold (Pollock, 1979a). This area contains bamboo and there is widespread epiphytic parasitism by tree ferns, mosses and orchids (Pollock, 1979a). The montane nature of this area leads to variability between valleys and ridge tops: trees in the (wetter) valleys are usually buttressed, tall (45m), with slim, straight trunks and wide horizontal canopies, while exposed ridges carry shorter, twisted, epiphyte-infested trees, which have an intermingled network of superficial root systems (Pollock, 1979a).

The study site was situated approximately 16km north of Andasibe along a miners' road (Figure 2.1), between S18°48.5 and S18°49 and E48°25.5 and E48°26.5 (Figure 2.2 and Figure 2.3). The road acted as the western limit of the study site: no study group crossed it. Four main trails were cut during the study, each heading up and over ridges, these were called: 'Props trail', 'Hapa trail', 'Joseph trail' and 'Indri trail' (Figure 2.2).

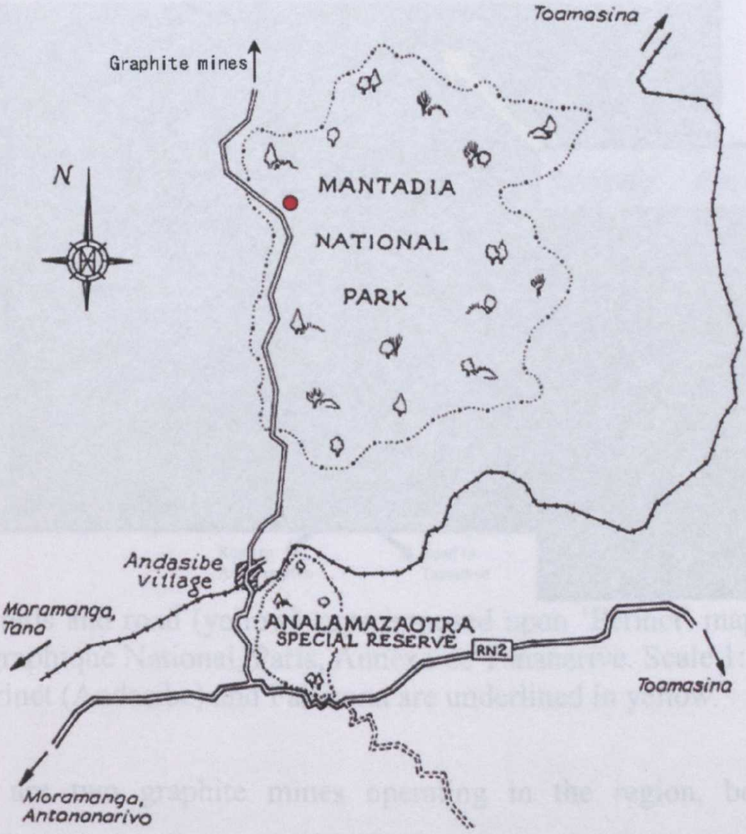


Figure 2.1. Mantadia National Park and Analamazoatra Special Reserve, adapted from Bradt (1997), where ● is approximate position of field site.

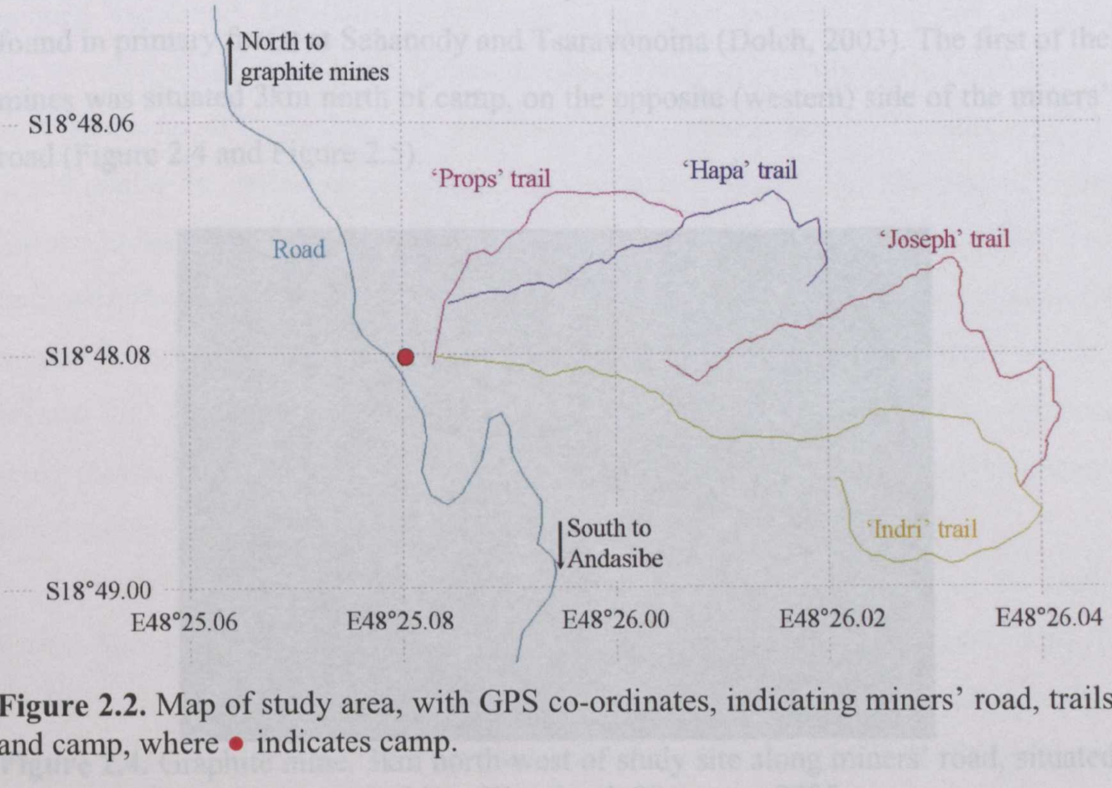


Figure 2.2. Map of study area, with GPS co-ordinates, indicating miners' road, trails and camp, where ● indicates camp.

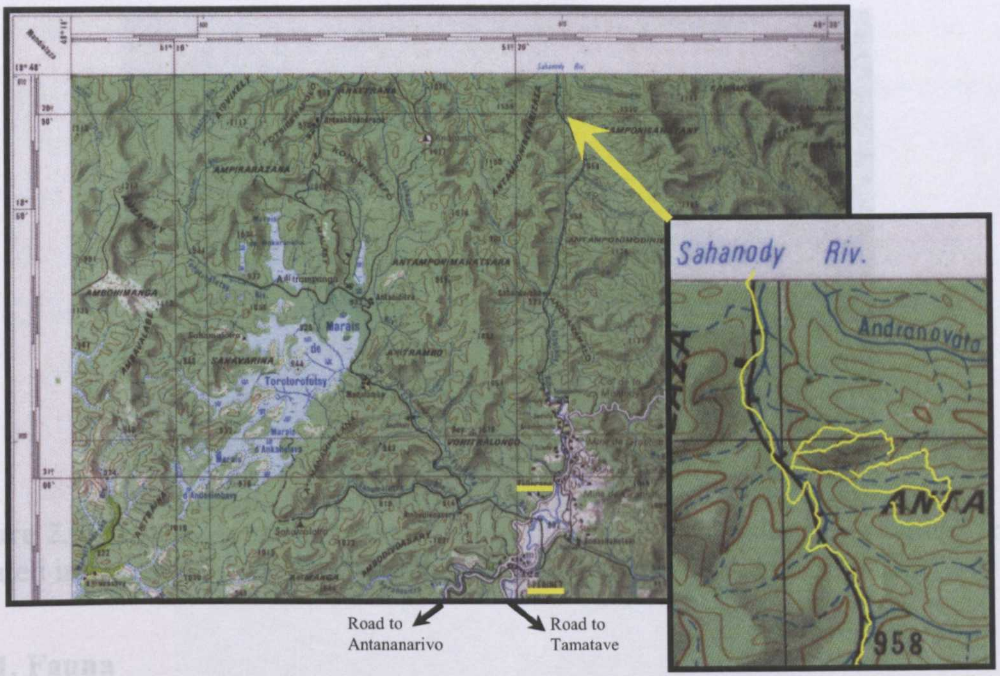


Figure 2.3. Trails and road (yellow) superimposed upon 'Perinet' map (S-47) from Institute Géographique National, Paris, Annexe de Tananarive. Scale 1: 100,000. The villages of Périnet (Andasibe) and Falierana are underlined in yellow.

There are two graphite mines operating in the region, both providing employment for the local community. However they are not beneficial to the environment: the processing of graphite by the Izouard mines near Falierana spills waste water into local rivers (Dolch, 2003; personal observation). Graphite mines are found in primary forest at Sahanody and Tsaravonoina (Dolch, 2003). The first of the mines was situated 3km north of camp, on the opposite (western) side of the miners' road (Figure 2.4 and Figure 2.5).

Figure 2.4. Graphite mine, 3km north-west of study site along miners' road, situated in primary forest. Photograph: Mary Blanchard, 08 August 2005.

Figure 2.5. Disused graphite mine, 3km north-west of study site along miners' road, situated in primary forest. Photograph: Mary Blanchard, 08 August 2005.

2.1.1. Fauna

The association 'ANGAP' has recorded seventy-three mammal species in Mantadia: five carnivores, 21 bats, 20 insectivores, 14 rodents and 12 primates. The twelve lemur species are: *Propithecus diadema* (diademed simpona), *Indri indri* (indri), *Avahi laniger* (eastern woolly lemur), *Varecia variegata editorum* (southern black-and-white ruffed lemur), *Eulemur fulvus* (common brown lemur), *Eulemur rubriventer* (red-bellied lemur), *Hapalemur griseus griseus* (eastern lesser bamboo lemur), *Lepilemur microdon* (small-toothed sportive lemur), *Allocebus trichotis* (hairy eared dwarf lemur), *Cheirogaleus major* (greater dwarf lemur), *Daubentonia madagascariensis* (aye-aye) and *Microcebus* sp. (mouse lemur [Garbutt, 1999]). Traditionally the *Microcebus* recorded at Mantadia is referred to *Microcebus rufus* (brown mouse lemur [Garbutt, 1999]). However, a new species of *Microcebus* has been identified from Andasibe and Mantadia, *Microcebus lehilahytsara* (Goodman's mouse lemur [Kappeler *et al.*, 2005; Ashokan, 2006]). The five carnivore species present are: *Fossa fossana* (fanaloka), *Eupleres goudotii* (falanouc), *Cryptoprocta ferox* (fossa), *Galidictis fasciata* (broad-striped mongoose), *Galidia elegans* (ring-tailed mongoose [Garbutt, 1999]).

Eight of the twelve lemur species were observed or heard during the study period, those neither heard nor observed were all nocturnal (i.e. *L. microdon*, *A. trichotis*, *C. major* and *D. madagascariensis*). A group of *V. v. editorum* was frequently heard in forest on the opposite side of the miners' road at the beginning of the study. Towards the end of the study this group was no longer heard; reasons for this are unknown. Full details of sightings of non-study lemur species can be found in Appendix B1. A pair of *A. laniger* (Figure 2.6) was observed 13 December 2004 (S18°48.853, E48°26.309 [Figure 2.9]), presumably including the adult male that was later found predated (Chapter 10). At least one group of *E. rubriventer* (Figure 2.7) was observed throughout the study area. *E. fulvus* (Figure 2.8) were observed close to camp and seen crossing the miners' road.

Figure 2.6. *Avahi laniger* (eastern woolly lemur) in Mantadia National Park. Photograph: Mary Blanchard, 13 December 2004.

Figure 2.7. *Eulemur rubriventer* (red-bellied lemur), Mantadia National Park. Photograph: Mary Blanchard, 29 September 2005.

Figure 2.8. *Eulemur fulvus* (common brown lemur), Mantadia National Park. Photograph: Mary Blanchard, 05 October 2005.

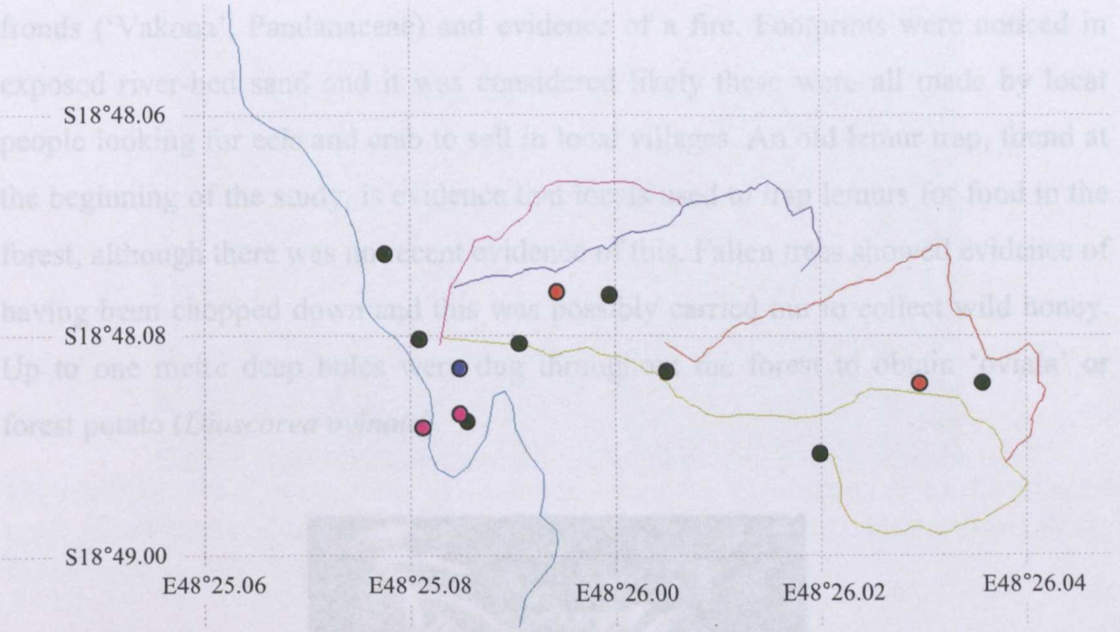


Figure 2.9. Map of location of observation of other lemur species seen during the study, where ●*E. rubriventer*, ●*E. fulvus*, ●*Microcebus* sp. and ●*A. laniger*.

2.1.2. Forest Usage

ANGAP had erected signs along the miners' road informing local residence what practises were not allowed in the protected area (Figure 2.10): no hunting, firewood collection or grazing of zebu (*Bos primigenius indicus*). Unfortunately these signs were ignored by local people.

Figure 2.10. ANGAP signs positioned along miners' road in Mantadia, informing locals that hunting, collecting fire wood and grazing of zebu is forbidden. Photographs: Mary Blanchard, 10 January 2005.

At the beginning of the study in November 2004, a camp was found next to a small river (Figure 2.11), consisting of a shelter made of branches and *Pandanus* fronds ('Vakona', Pandanaceae) and evidence of a fire. Footprints were noticed in exposed river-bed sand and it was considered likely these were all made by local people looking for eels and crab to sell in local villages. An old lemur trap, found at the beginning of the study, is evidence that locals used to trap lemurs for food in the forest, although there was no recent evidence of this. Fallen trees showed evidence of having been chopped down and this was possibly carried out to collect wild honey. Up to one metre deep holes were dug throughout the forest to obtain 'oviala' or forest potato (*Dioscorea ovinala*).

Figure 2.11. Photograph of a camp, presumably used to search for eels. Photograph: Mary Blanchard, November 2004.

2.1.3. Summary and Discussion

Small groups of zebu were frequently seen on the road, sometimes herded by young boys, and would enter the forest edges to feed. Zebu wandered into camp, and were seen while following both *H. g. griseus* groups. ANGAP officials were alerted to this, and guides, (alongside police, dispatched to talk to zebu owners. Unfortunately owners (like their zebu) were stubborn and often repeat offenders. Zebu caused considerable damage to the forest, trampling down undergrowth and eating many plants, including young leaves of giant bamboo.

Locals living on the edges of the park practised 'tavy', Malagasy slash-and-burn farming (Figure 2.12). During the study period the tavy area extended further into the National Park; ANGAP were informed but appeared powerless to stop it.

Figure 2.12. South-west limit of Mantadia National Park adjacent to the miners' road, showing evidence of 'tavy', slash-and-burn farming. Photograph: Mary Blanchard, 27 July 2004.

Illegal and destructive usage of the National Park was common and local officials appeared powerless to stop this despite national law. Locals were eager to know when the present study would finish; presumably to know when they could start using the forest without risk of being caught. This indicates the importance of long term field sites, not simply for the data they collect, but also for the effect of their presence in the local community. The continual presence of researchers and guides acts as a deterrent towards locals using the forest illegally. It also indicates that national laws are not enough to protect national parks; local populations must believe that the forest is worth protecting and be able to see a benefit in doing so.

2.2. Climate

Powzyk (1997) recorded mean monthly minima, varying from 10.1°C to 17.3°C and mean monthly maxima varying from 17.2°C to 30.1°C. In 1993 and 1994 the hottest month was November, the coldest months being July and August (Powzyk, 1997). Although average rainfall for Mantadia is quoted as between 1,500 and 2,000mm per year (Garbutt, 1999), Powzyk (1997) recorded 3,721mm in 1994. Indeed during the 22 month study the total rainfall was 5,920mm; however, in 1994 two cyclones had hit, on 13 February 1994 and 04 February 1994. Powzyk (1997) designated the west season as January to August and the dry season as September to December.

2.2.1. Methods

Weather readings were recorded daily at camp (S18°48.802, E48°25.829), in the late afternoon, as close to 17:30 as possible, by Mary Blanchard or Joseph Rasolofoniaina. Minimum and maximum readings were recorded using a Tenax UK Ltd. maximum-minimum thermometer with magnetic reset hung 1.6m high from a tree in a shady location (Figure 2.13 A). A humidity gauge (Tenax UK Ltd.) was attached beneath the thermometer, 1.3m from the ground (Figure 2.13 A). A rain gauge (Bosmere Products Ltd.) was placed in a cut-off bamboo 1.5m from the ground in as clear an area as possible (Figure 2.13 B). It was placed above the ground as dogs were known to frequent the area and may have displaced a lower gauge. During periods of heavy rain, the gauge was emptied multiple times during the day and night as necessary.

Figure 2.13. A: Maximum-minimum thermometer and humidity gauge at camp. **B:** Rain gauge at camp. Photographs: Mary Blanchard, 29 September 2004.

2.2.2 Recorded Climate

Climatic variables were recorded daily at camp between November 2004 and October 2005 (Appendix B2). To examine correlations between the quantitative climatic variables and hours of daylight, Spearman's rank correlation coefficient (ρ) was used. This was chosen in preference to the Pearson correlation co-efficient in view of lack of normality in rainfall and daylight data. Normality was investigated using skewness as a measure of the asymmetry of a distribution; in normal distributions skewness is zero (Kinnear & Gray, 2004). Values over 1 indicate a strongly skewed distribution and values between 0.5 and 1 indicate a moderately skewed distribution (Kinnear & Gray, 2004). Kurtosis measures the clustering of the points and in normal distributions the value is zero (Kinnear & Gray, 2004).

The minimum recorded temperature was 5°C (July 2005) and the maximum 34°C (January 2005). December and January were the hottest months, July and August the coldest (Figure 2.14 and Table 2.1). Total recorded rainfall for the eleven month study (329 days) was 2183.6mm; April was the driest month (57.2mm) and December the wettest (371.3mm). April was the month with the greatest proportion of dry days: it rained on only 30% of days. Humidity remained high for the entire study period, never falling below 73% (24 April 2005) and largely remaining at 100%. During periods of sunny weather, the humidity could decrease considerably during the day, but would always increase at sundown when readings were taken.

Table 2.1. Monthly minimum and maximum temperatures (°C), average humidity (%), total rainfall (mm) and percentage of rainy days, for full months only, measured at camp in Mantadia National Park (S18°48.802, E48°25.829).

Month	Maximum (°C)	Minimum (°C)	Humidity	Rainfall (mm)	% of rainy days
December	31	9	94	371.3	84
January	34	13	92	273.6	71
February	28	14	94	216.89	89
March	30	10	95	259.4	71
April	25	12	92	57.2	30
May	23	12	99	189.8	90
June	20	9	100	179.2	90
July	19	5	99	210	71
August	21	8	97	189.6	74
September	22	9	96	200.7	83

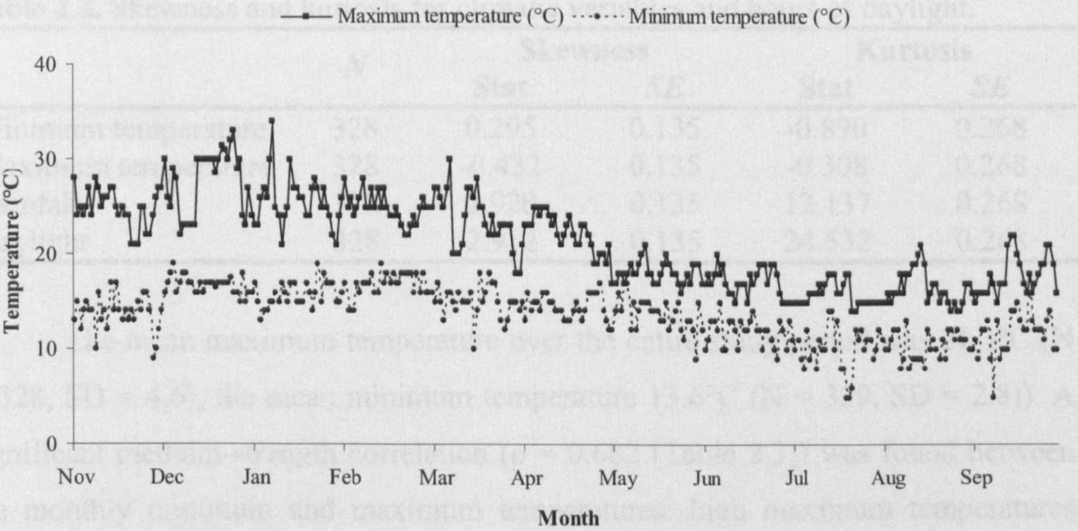


Figure 2.14. Daily maximum and minimum temperature (°C) at camp, Mantadia National Park (12 November 2004 to 05 October 2005).

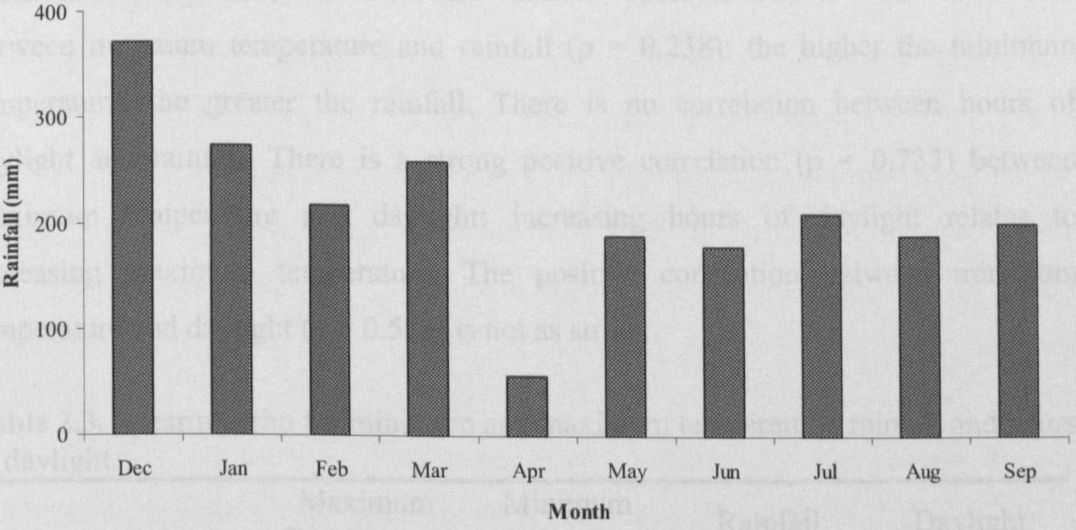


Figure 2.15. Total monthly rainfall (mm) at camp, Mantadia National Park (December 2004 to September 2005, full months only).

Climate measurements and hours of daylight were checked for normality. Neither maximum nor minimum temperatures were found to deviate very greatly from a normally distributed population (Table 2.2). However rainfall and hours of daylight differed strongly from normal distribution.

Table 2.2. Skewness and kurtosis for climatic variables and hours of daylight.

	N	Skewness		Kurtosis	
		Stat	***SE***	**Stat**	***SE***
Minimum temperature	328	0.295	0.135	-0.890	0.268
Maximum temperature	328	-0.432	0.135	-0.308	0.268
Rainfall	328	2.920	0.135	12.137	0.268
Daylight	328	2.912	0.135	24.532	0.268

The mean maximum temperature over the entire study period was 21.3°C (N = 328, SD = 4.6), the mean minimum temperature 13.6°C (N = 329, SD = 2.8)). A significant medium-strength correlation (ρ = 0.682 [Table 2.3]) was found between the monthly minimum and maximum temperatures: high maximum temperatures correlating with high minimum temperatures (Figure 2.14). There is a weak negative correlation (ρ = -0.253) between maximum temperature and rainfall: the higher the maximum temperature, the lower the rainfall. There is also a weak correlation between minimum temperature and rainfall (ρ = 0.238): the higher the minimum temperature, the greater the rainfall. There is no correlation between hours of daylight and rainfall. There is a strong positive correlation (ρ = 0.733) between maximum temperature and daylight: increasing hours of daylight relates to increasing maximum temperature. The positive correlation between minimum temperature and daylight (ρ = 0.559) is not as strong.

Table 2.3. Spearman rho for minimum and maximum temperature, rainfall and hours of daylight.

		Maximum Temperature	Minimum temperature	Rainfall	Daylight
Maximum temperature	ρ		0.682**	-0.253**	0.733**
	p		0.000	0.000	0.000
	N		328	328	328
Minimum temperature	ρ	0.682**		0.238**	0.559**
	p	0.000		0.000	0.000
	N	328		328	328
Rainfall	ρ	-0.253**	0.238**		-0.008
	p	0.000	0.000		0.887
	N	328	328		328
Daylight	ρ	0.733**	0.559**	-0.008	
	p	0.000	0.000	0.887	
	N	328	328	328	

** Significant at the 0.01 level (two-tailed).

2.2.3. Summary and Discussion

The total recorded rainfall for the eleven month study (2183.6mm) is higher than the annual total quoted for the park (1,500 to 2,000mm), Powzyk (1997) recorded 5,920mm over 22 months, but this period included two cyclones. The absence of a cyclone during the study period indicates that this was a wetter than average period. Climatic correlations show that maximum, and to a lesser extent minimum temperature, alter seasonally with the hours of daylight: shorter winter days are colder than longer summer days. Rainfall showed no correlation with hours of daylight or minimum temperature and had only a weak negative correlation with maximum temperature. This indicates there is no seasonal change in rainfall, but a tendency for increasing rain with decreasing temperature.

2.3. Habitat Structure Analysis

To enable ecological data to be interrelated correctly, a survey was carried out of the forest structure. Scaled photographs were taken throughout the ranges of the four study groups to be representative of habitat type. An attempt was made to classify the forest based on support availability by giving the scaled photographs to two naïve people, told to group them based on support type. These groups predominantly fell into 'ridge', 'slope', 'valley' and 'secondary forest' as discussed in the summary.

Further, a number of transects were taken to show a cross-section of support availability. Transects have been represented graphically to scale (Figure 2.16) to indicate support size (<5cm, 5 to 10cm, 10.1 to 15cm and >15.1cm) and orientation (vertical, angle, oblique and horizontal). Categories are the same as those used for locomotor support analysis (Chapter 9).

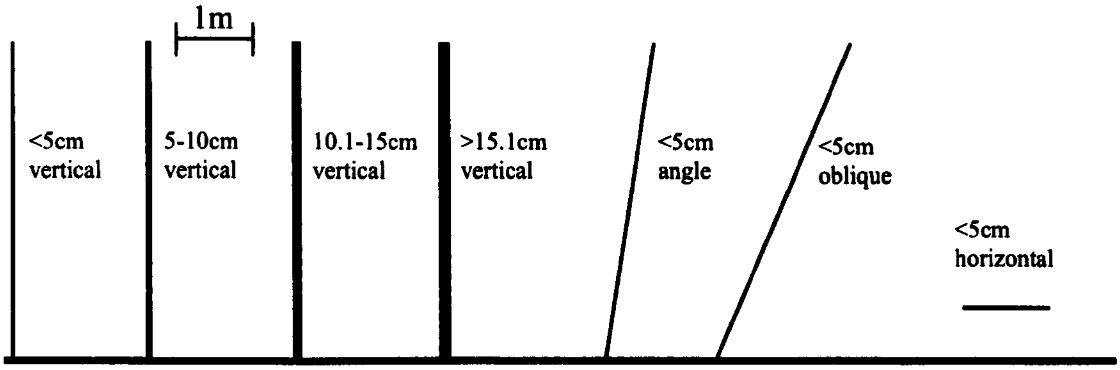


Figure 2.16. Graphical representation of size, orientation and distribution of supports in *P. diadema* and *H. g. griseus* transects.

2.3.1. Methods

Locations were taken at random, in areas that were used by study groups. Photographs were taken using a Canon EOS 1000FN body and Canon Ultrasonic Wide-angle 22 to 55mm lens (f4 to 5.6). The lens was set to 28mm for all photographs and was held orthogonal to the photographer. Branches used for scale had silver tape placed on them to marking a one-metre distance, the inside edges of the tape demarcating the metre distance. Further tape was placed at the 50cm mark, the tape being placed astride the 50cm mark, centred as far as possible on the mark. Transects were measured along a tape measure, with trees recorded at 1.5m from the ground, approximately at the recognised 'breast height'. Support orientations used to describe photographs are the same as used in the locomotor behavioural study (Figure 2.17).

Figure 2.17. Definitions of support orientation in this study.

Name	Definition
Horizontal	-10° to 10°
Oblique	11° to 45° and -11° to -45°
Angle	46° to 80° and -46° to -80°
Vertical	81° to 90° and -81° to -90°

2.3.2. Results

2.3.2.1. *Indri indri* Home Range

Eleven locations were chosen to describe the territory of *I. indri* (Figure 2.18). Due to time constraints these were located on or close to a ridge and actually exemplify ridge forest structure throughout the range of both *I. indri* and *P. diadema.*

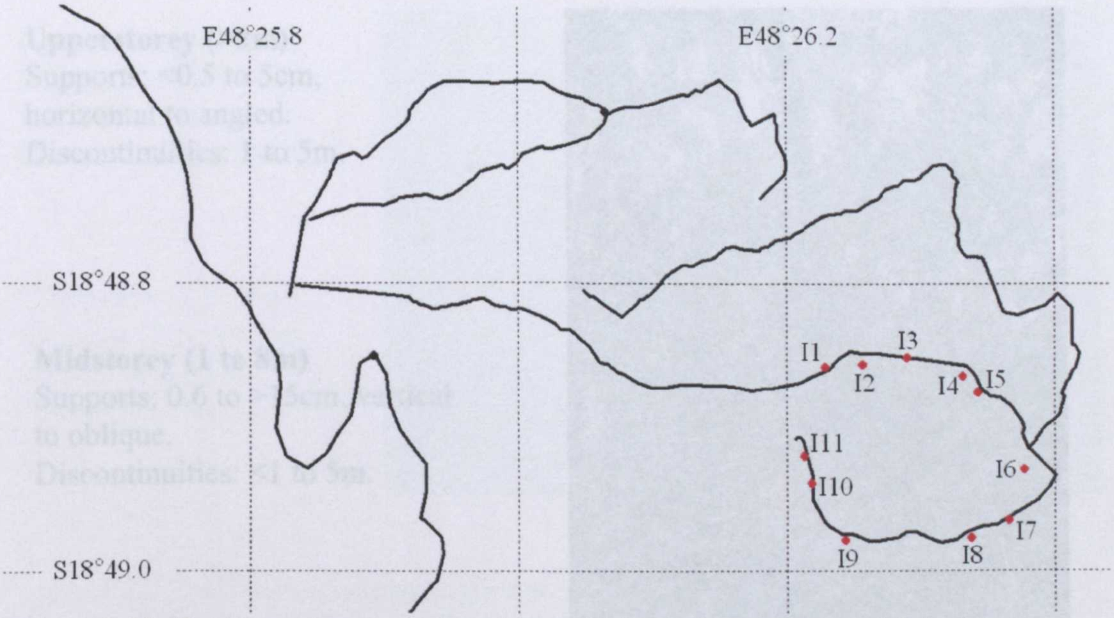


Figure 2.18. Position of transect locations within the home range of *I. indri*.

Upperstorey (>8m)
Supports: <0.5 to 10cm, angled to horizontal.
Discontinuities: <1m.

Midstorey (1 to 8m)
Supports: <0.5 to 15cm, vertical to oblique.
Discontinuities: <1 to >4m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.19. Predominant support types at Location I1: S18°48.858, E48°26.229. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>8m)
Supports: <0.5 to 5cm, horizontal to angled.
Discontinuities: 1 to 5m.

Midstorey (1 to 8m)
Supports: 0.6 to >15cm, vertical to oblique.
Discontinuities: <1 to 5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.20. Predominant support types at Location I2: S18°48.856, E48°26.257. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>8m)
Supports: <0.5 to 15cm, angled to horizontal.
Discontinuities: 1 to 3m.

Midstorey (1 to 8m)
Supports: 0.6 to >15.1cm, vertical and angled.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.21. Predominant support types at Location I3: S18°48.851, E48°26.290. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>8m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: 1 to 5m.

Midstorey (1 to 8m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: <1 to >5m.

Figure 2.22. Predominant support types at Location I4: S18°48.864, E48°26.331. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>10m)
Supports: <0.5 to 10cm, angled to horizontal.
Discontinuities: 1 to 2m.

Midstorey (1 to 10m)
Supports: 0.6 to >15cm, vertical to angled.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.23. Predominant support types at Location I5: S18°48.876, E48°26.343. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>6m)
Supports: <0.5 to >15.1cm, vertical to horizontal.
Discontinuities: 1 to 3m.

Midstorey (1 to 6m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

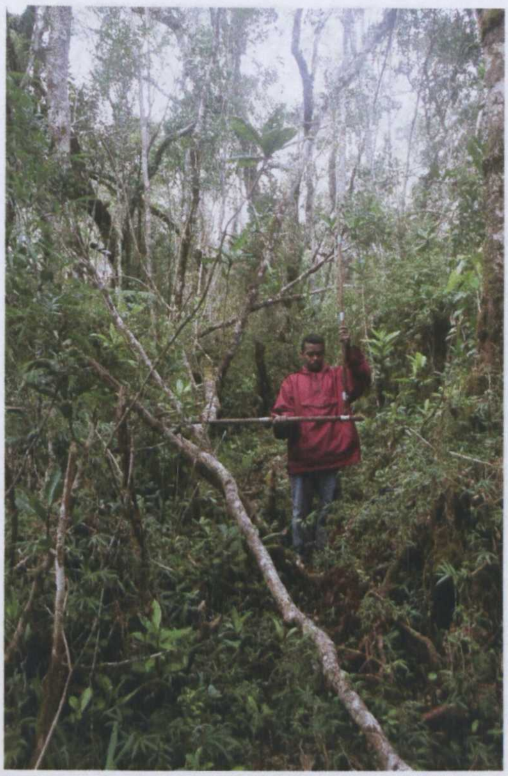


Figure 2.24. Predominant support types at Location I6: S18°48.929, E48°26.377. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>10m)
Supports: <0.5 to 15cm, angled to horizontal.
Discontinuities: 1 to 3m.

Midstorey (1 to 10m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.25. Predominant support types at Location I7: S18°48.965, E48°26.366. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>6m)
Supports: <0.5 to >15.1cm, angled to horizontal.
Discontinuities: 1m.

Midstorey (1 to 6m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to 3m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.26. Predominant support types at Location I8: S18°48.977, E48°26.338. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>8m)
Supports: <0.5 to >15.1cm, vertical to oblique.
Discontinuities: 1 to 4m.

Midstorey (1 to 8m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to 5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.27. Predominant support types at Location I9: S18°48.978, E48°26.244. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>6m)
Supports: <0.5 to >15cm, vertical to oblique.
Discontinuities: <1 to 5m.

Midstorey (1 to 6m)
Supports: 0.6 to >15cm, vertical to oblique.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.28. Predominant support types at Location I10: S18°48.939, E48°26.219. Photograph: Mary Blanchard, 12 September 2005.

Upperstorey (>5m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: <1m.

Midstorey (1 to 5m)
Supports: <0.5 to 10cm, vertical and angled.
Discontinuities: <1 to 3m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.29. Predominant support types at Location I11: S18°48.920, E48°26.213. Photograph: Mary Blanchard, 12 September 2005.

2.5.2.2. *Propithecus diadema* Home Range

Eleven transects were recorded within the home range of *P. diadema*. Transects S1 to S8 and S11 exemplify valley conditions in the study area, while S9 and S10 are characteristic ridges.

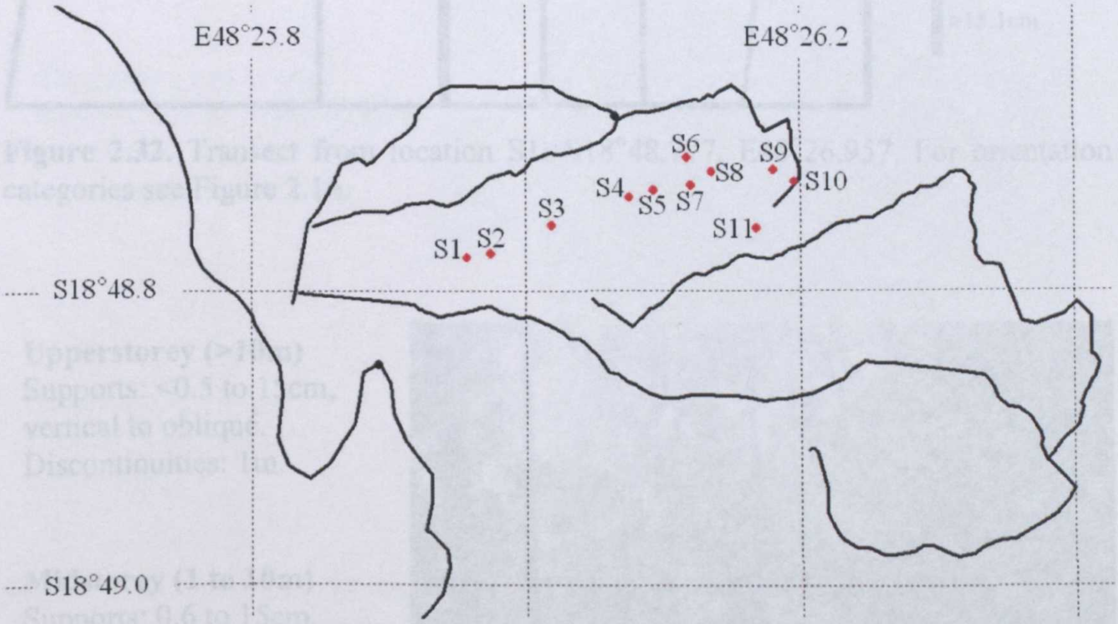


Figure 2.30. Locations of transects within the home range of *P. diadema*.

Upperstorey (>10m)
Supports: <0.5 to 15cm, vertical to oblique.
Discontinuities: 1m.

Midstorey (1 to 10m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: <1 to 3m.

Figure 2.31. Predominant support types at Location S1: S18°48.777, E48°26.957. Photograph: Mary Blanchard, 29 September 2005.

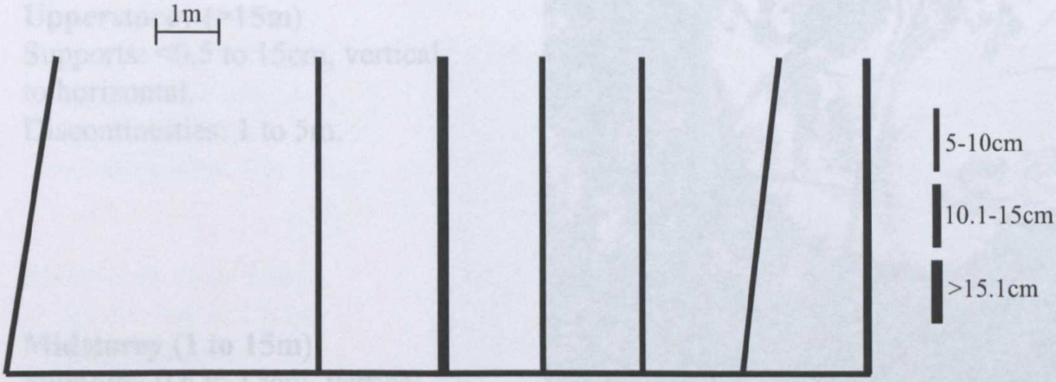


Figure 2.32. Transect from location S1: S18°48.777, E48°26.957. For orientation categories see Figure 2.16.

Upperstorey (>10m)
Supports: <0.5 to 15cm, vertical to oblique.
Discontinuities: 1m.

Midstorey (1 to 10m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: <1 to 3m.

Figure 2.33. Predominant support types at Location S2: S18°48.755, E48°26.974. Photograph: Mary Blanchard, 29 September 2005.

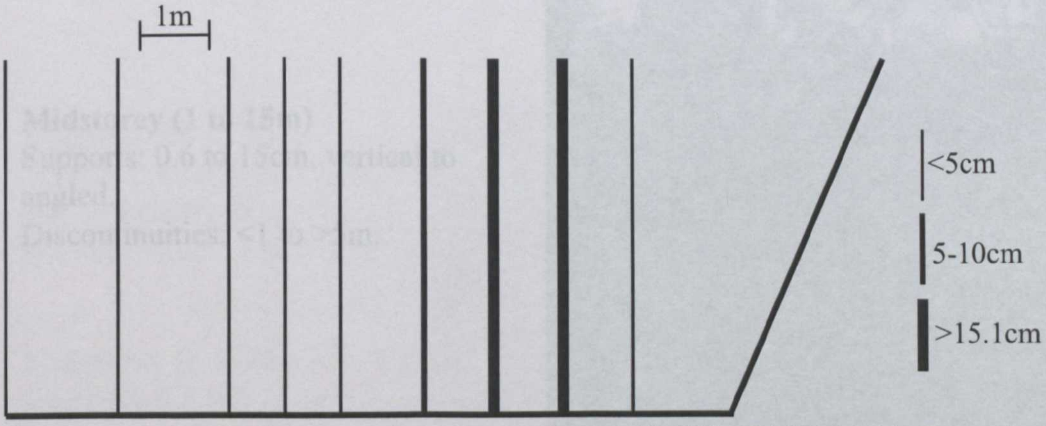


Figure 2.34. Transect from location S2: S18°48.755, E48°26.974. For orientation categories see Figure 2.16.

Upperstorey (>15m)
Supports: <0.5 to 15cm, vertical to horizontal.
Discontinuities: 1 to 5m.

Midstorey (1 to 15m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: 1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.35. Predominant support types at Location S3: S18°48.755, E48°26.018. Photograph: Mary Blanchard, 27 August 2005. Top right has been altered to show horizontal branch used for bipedal walking by *P. diadema*.

Upperstorey (>15m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: 1 to 5m.

Midstorey (1 to 15m)
Supports: 0.6 to 15cm, vertical to angled.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.36. Predominant support types at Location S4: S18°48.736, E48°26.075. Photograph: Mary Blanchard 27 August 2005.

Upperstorey (>15m)
Supports: <0.5 to 15cm,
vertical to oblique.
Discontinuities: 1 to 10m.

Midstorey (1 to 15m)
Supports: 0.6 to 15cm,
vertical to angled.
Discontinuities: <1 to >10m.

Figure 2.37. Predominant support types at Location S5: S18°48.731, E48°26.093. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>8m)
Supports: <0.5 to 15cm,
vertical to horizontal.
Discontinuities: 1 to 3m.

Midstorey (1 to 8m)
Supports: 0.6 to 15cm,
vertical to oblique.
Discontinuities: <1 to 4m.

Figure 2.38. Predominant support types at Location S6: S18°48.709, E48°26.117. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>20m)
Supports: <0.5 to >15.1cm,
angled to horizontal.
Discontinuities: 1 to >10m.

Midstorey (1 to 20m)
Supports: 0.6 to >15.1cm,
vertical to angled.
Discontinuities: 1 to >10m.

Figure 2.39. Predominant support types at Location S7: S18°48.728, E48°26.120. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>20m)
Supports: <0.5 to >15.1cm,
vertical to horizontal.
Discontinuities: 1 to >10m.

Midstorey (1 to 20m)
Supports: 0.6 to >15.1cm,
vertical to angled.
Discontinuities: 1 to >10m.

Figure 2.40. Predominant support types at Location S8: S18°48.718, E48°26.135. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>20m)
Supports: <0.5 to >15.1cm,
vertical to horizontal.
Discontinuities: 1 to >10 m.

Midstorey (1 to 20m)
Supports: 0.6 to >15.1cm,
vertical to angled.
Discontinuities: 3 to >10m.

Understorey (<1m)
Supports: <0.5cm in all
orientations.

Figure 2.41. Predominant support types at Location S9: S18°48.717, E48°26.180. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>15m)
Supports: <0.5 to >15.1cm, vertical to oblique.
Discontinuities: 1 to >5m.

Midstorey (1 to 15m)
Supports: 0.6 to >15.1cm, vertical.
Discontinuities: <1 to >10m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

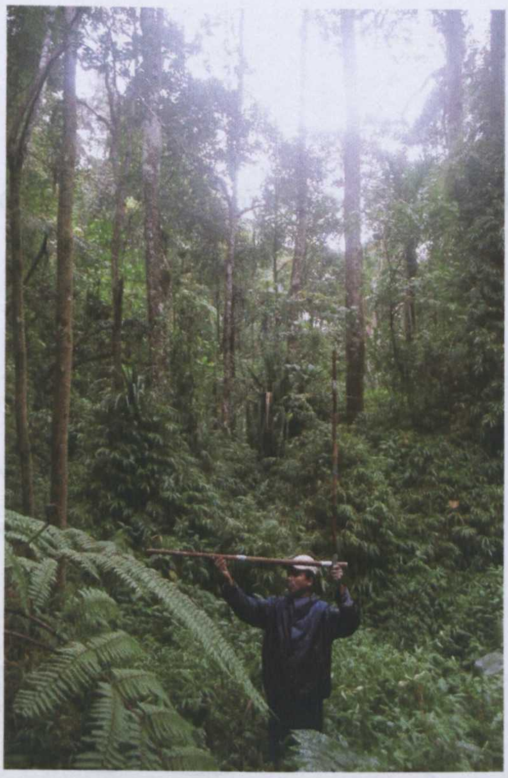


Figure 2.42. Predominant support types at Location S10: S18°48.725, E48°26.195. Photograph: Mary Blanchard, 27 August 2005.

Upperstorey (>10m)
Supports: <0.5 to >15.1cm, vertical to horizontal.
Discontinuities: 1 to 5m.

Midstorey (1 to 10m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to 3m.

Understorey (<1m)
Supports: <0.5cm in all orientations.

Figure 2.43. Predominant support types at Location S11: S18°48.757, E48°26.168. Photograph: Mary Blanchard, 27 August 2005.

2.5.2.3. *Hapalemur griseus griseus*

A: Group One

Five locations were used for transects within the home range of Group One *H. g. griseus* (Figure 2.44).

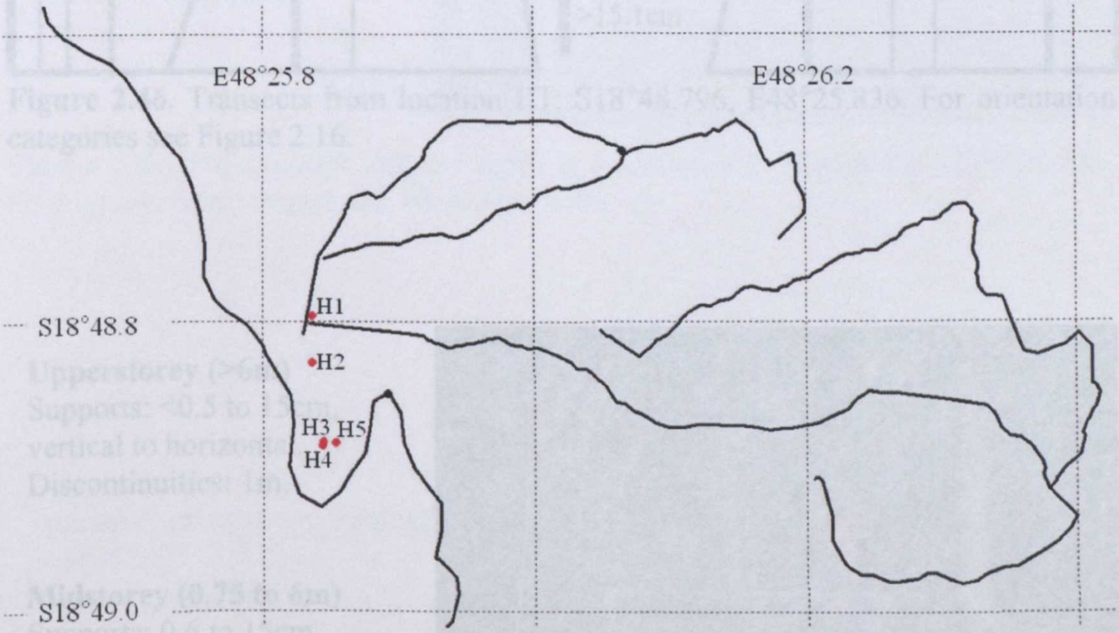


Figure 2.44. Transect locations for *H. g. griseus* Group One.

Upperstorey (>6m):
Supports: <0.5 to 10cm,
vertical to horizontal.
Discontinuities: 1 to 3m.

Midstorey (0.75 to 6m):
Supports: 0.6 to 10cm,
vertical to oblique.
Discontinuities: <1 to 3m.

Figure 2.45. Predominant support types at Location H1: S18°48.796, E48°25.836. Photograph: Mary Blanchard, 16 August 2005.

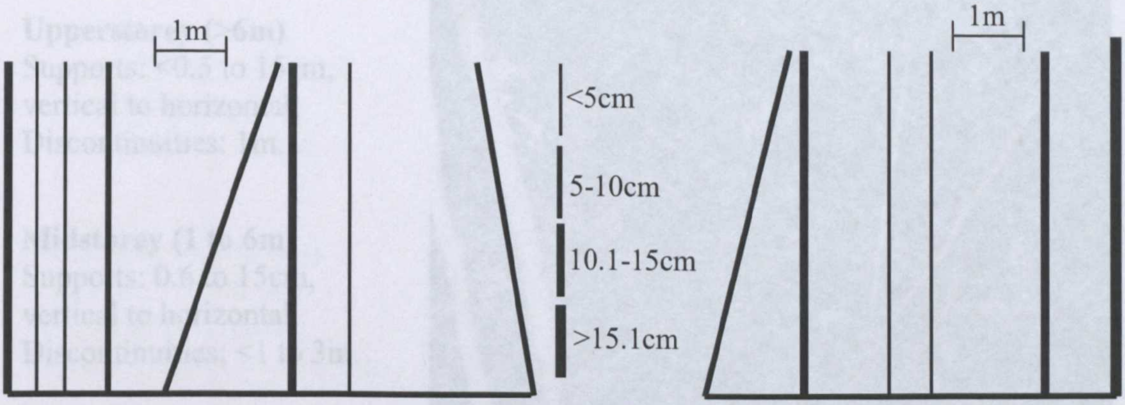


Figure 2.46. Transects from location H1: S18°48.796, E48°25.836. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 15cm,
vertical to horizontal.
Discontinuities: 1m.

Midstorey (0.75 to 6m)
Supports: 0.6 to 15cm,
vertical to oblique.
Discontinuities: <1 to 3m.

Figure 2.47. Predominant support types at Location H2: S18°48.828, E48°25.836. Photograph: Mary Blanchard, 16 August 2005.

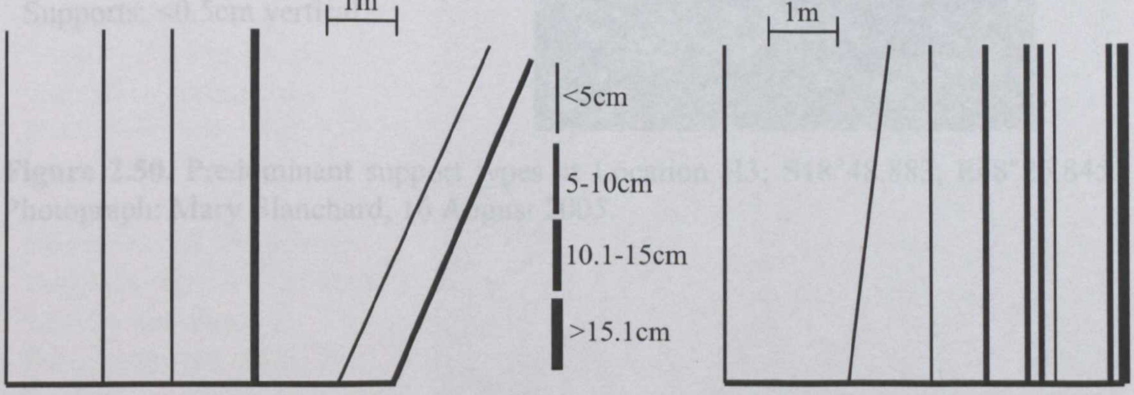


Figure 2.48. Transects from location H2: S18°48.828, E48°25.836. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 15cm, vertical to horizontal.
Discontinuities: 1m.

Midstorey (1 to 6m)
Supports: 0.6 to 15cm, vertical to horizontal.
Discontinuities: <1 to 3m.

Figure 2.49. Predominant support types at Location H2: S18°48.828, E48°25.836. Photograph: Mary Blanchard, 16 August 2005.

Upperstorey (>6m)
Supports: 0.6 to 10cm, vertical to horizontal.
Discontinuities: >5m.

Midstorey (1 to 6m)
Supports: <0.5 to 5cm, vertical to horizontal.
Discontinuities: <1 to >10m.

Understorey (<0.5m)
Supports: <0.5cm vertical.

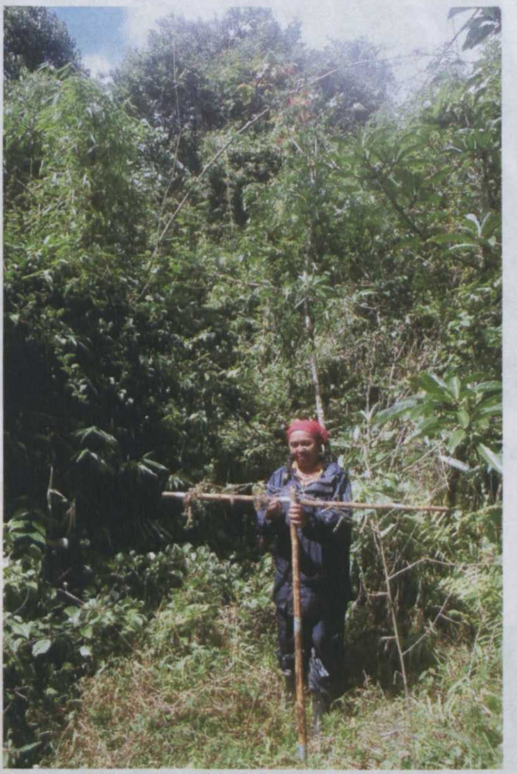


Figure 2.50. Predominant support types at Location H3: S18°48.883, E48°25.845. Photograph: Mary Blanchard, 16 August 2005.

Upperstorey (>6m)
Supports: 0.6 to 10cm,
vertical to horizontal.
Discontinuities: >5m.

Midstorey (0.5 to 6m)
Supports: <0.5 to 5cm,
vertical to horizontal.
Discontinuities: <1 to >10m.

Figure 2.51. Predominant support types at Location H3: S18°48.883, E48°25.845. Photograph: Mary Blanchard, 16 August 2005.

Upperstorey (>5m)
Supports: 0.6 to 10cm,
vertical to horizontal.
Discontinuities: <1m.

Midstorey (0.75 to 5m)
Supports: <0.5 to 10cm,
vertical to horizontal.
Discontinuities: <1 to 2m.

Figure 2.52. Predominant support types at Location H4: S18°48.886, E48°25.844. Photograph: Mary Blanchard, 16 August 2005.

Upperstorey (>5m)
Supports: 0.6 to 10cm,
vertical to horizontal.
Discontinuities: <1m.

Midstorey (0.75 to 5m)
Supports: <0.5 to >15.1cm,
vertical to oblique.
Discontinuities: <1 to 3m.

Figure 2.53. Predominant support types at Location H4: S18°48.886, E48°25.844. Photograph: Mary Blanchard, 16 August 2005.

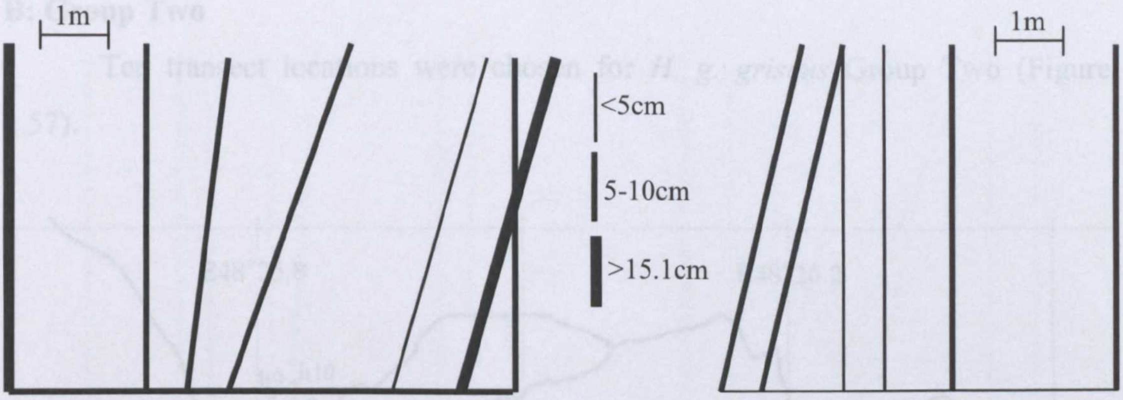


Figure 2.54. Transects from location H4: S18°48.886, E48°25.844. For orientation categories see Figure 2.16.

Upperstorey (>5m)
Supports: 0.6 to 10cm,
vertical to horizontal.
Discontinuities: <1m.

Midstorey (0.75 to 5m)
Supports: 0.6 to 10cm,
vertical to horizontal.
Discontinuities: <1 to 3m.

Figure 2.55. Predominant support types at Location H5: S18°48.884, E48°25.854. Photograph: Mary Blanchard, 16 August 2005.

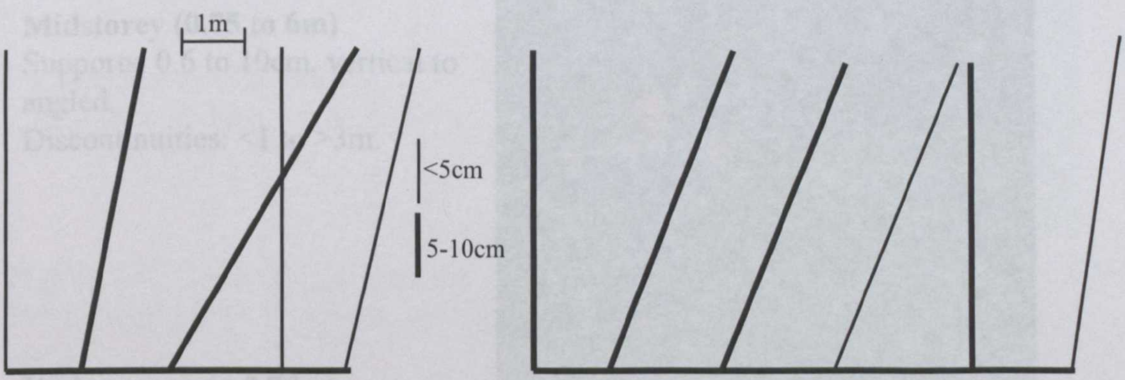


Figure 2.56. Transects from location H5: S18°48.884, E48°25.854. For orientation categories see Figure 2.16.

B: Group Two

Ten transect locations were chosen for *H. g. griseus* Group Two (Figure 2.57).

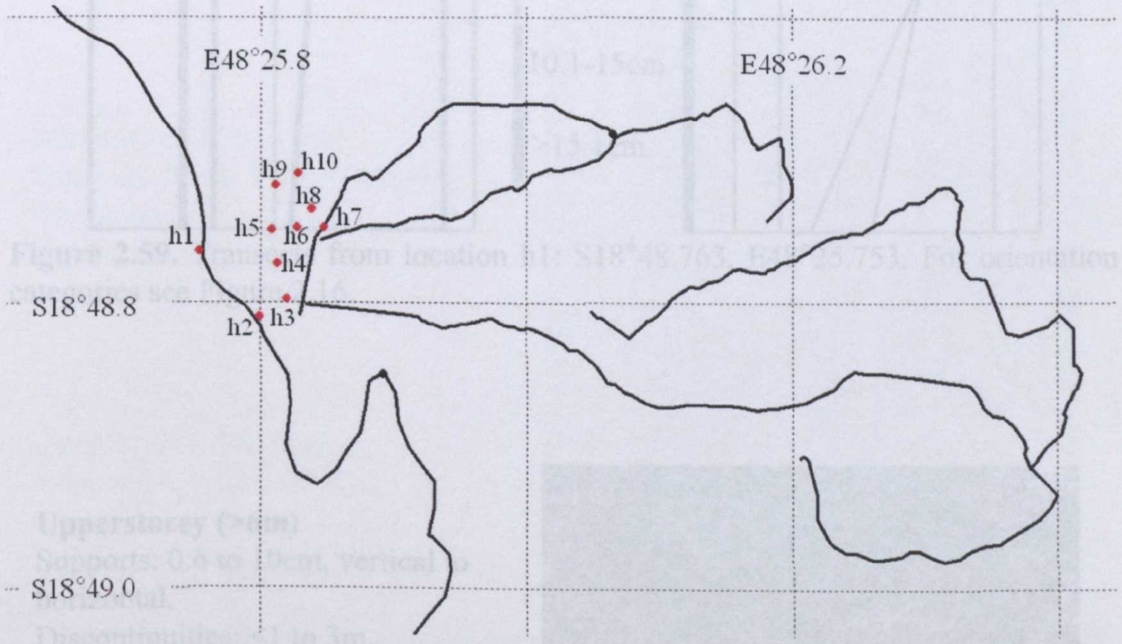


Figure 2.57. Transect locations for *H. g. griseus* Group Two.

Upperstorey (>6m)
Supports: 0.6 to 10 cm, vertical to horizontal.
Discontinuities: <1 to 3m.

Midstorey (0.75 to 6m)
Supports: 0.6 to 10cm, vertical to angled.
Discontinuities: <1 to >3m.

Understorey (< 0.75m)
Supports: <0.5cm, vertical.

Figure 2.58. Predominant support types at Location h1: S18°48.763, E48°25.753. Photograph: Mary Blanchard, 16 August 2005.

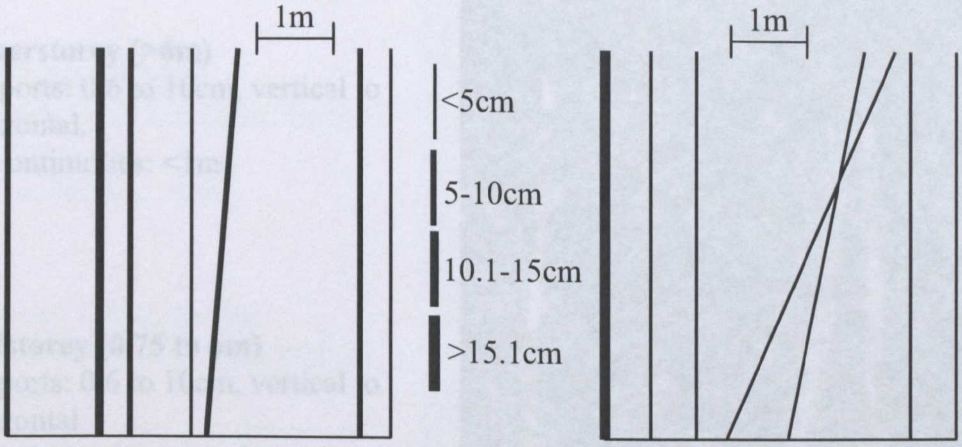


Figure 2.59. Transects from location h1: S18°48.763, E48°25.753. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: 0.6 to 10cm, vertical to horizontal.
Discontinuities: <1 to 3m.

Midstorey (0.75 to 6m)
Supports: 0.6 to 10cm, vertical to oblique.
Discontinuities: <1 to 3m.

Understorey (<0.75m)
Supports: <0.5cm, vertical.

Figure 2.60. Predominant support types at Location h2: S18°48.809, E48°25.799. Photograph: Mary Blanchard, 16 August 2005.

Upperstorey (>6m)
Supports: 0.6 to 10cm, vertical to horizontal.
Discontinuities: <1m.

Midstorey (0.75 to 6m)
Supports: 0.6 to 10cm, vertical to horizontal.
Discontinuities: <1 to 3m.

Understorey (<0.75m)
Supports: <0.5cm vertical.

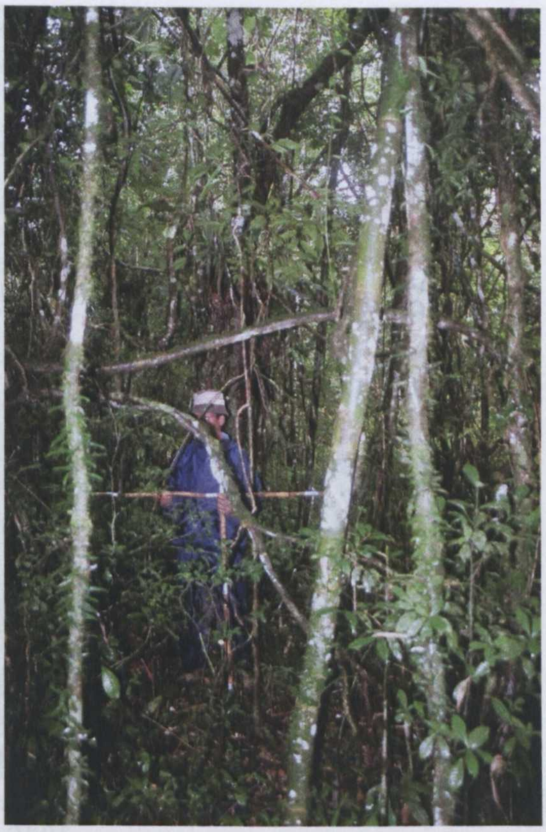


Figure 2.61. Predominant support types at Location h3: S18°48.797, E48°25.819. Photograph: Mary Blanchard, 16 August 2005.

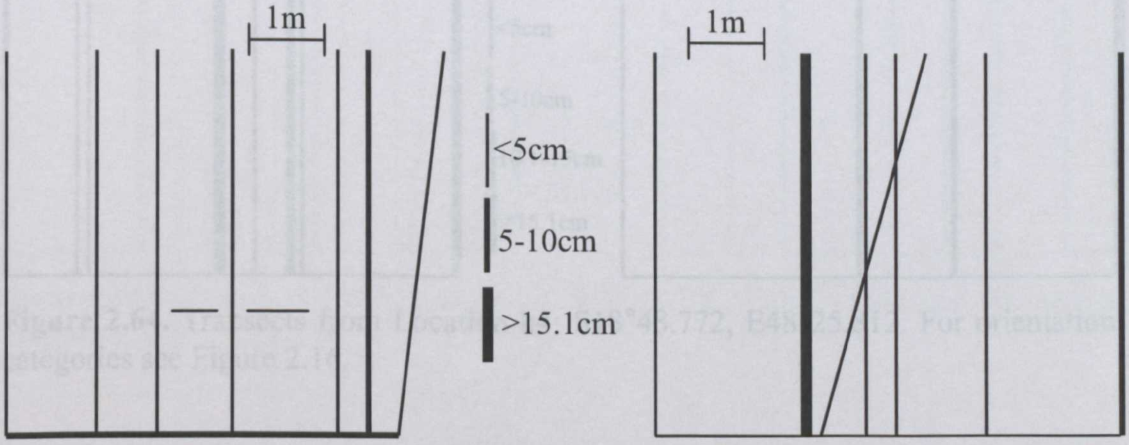


Figure 2.62. Transects from Location h3: S18°48.797, E48°25.819. For orientation categories see Figure 2.16.

Upperstorey (>8m)
Supports: <0.5 to >10cm, vertical to oblique.
Discontinuities: <1m.

Midstorey (0.75 to 8m)
Supports: 0.6 to >5.1cm, vertical to angled.
Discontinuities: <1 to 4m.

Understorey (<0.75m)
Supports: <0.5cm vertical.

Figure 2.63. Predominant support types at Location h4: S18°48.772, E48°25.812. Photograph: Mary Blanchard, 16 August 2005.

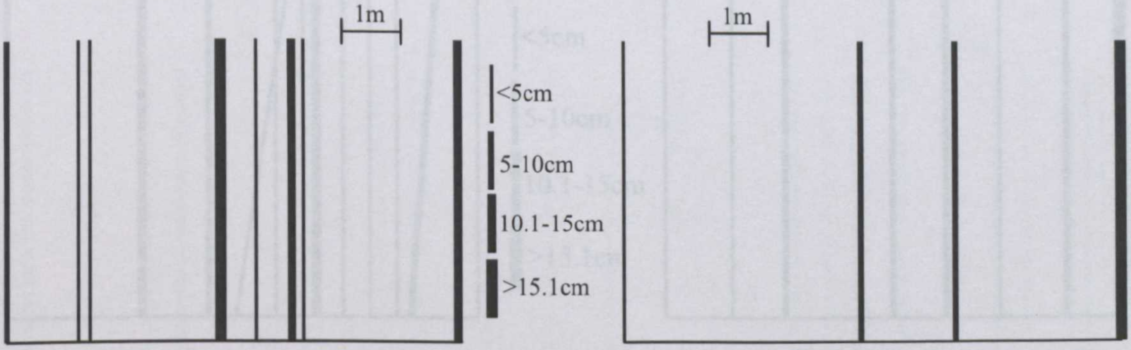


Figure 2.64. Transects from Location h4: S18°48.772, E48°25.812. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: <1m.

Midstorey (0.75 to 8m)
Supports: 0.6 to >15.1cm vertical to angled.
Discontinuities: <1 to 4m.

Understorey (<0.75m)
Supports: <0.5cm vertical.

Figure 2.65. Predominant support types at Location h5: S18°48.748, E48°25.808. Photograph: Mary Blanchard, 16 August 2005.

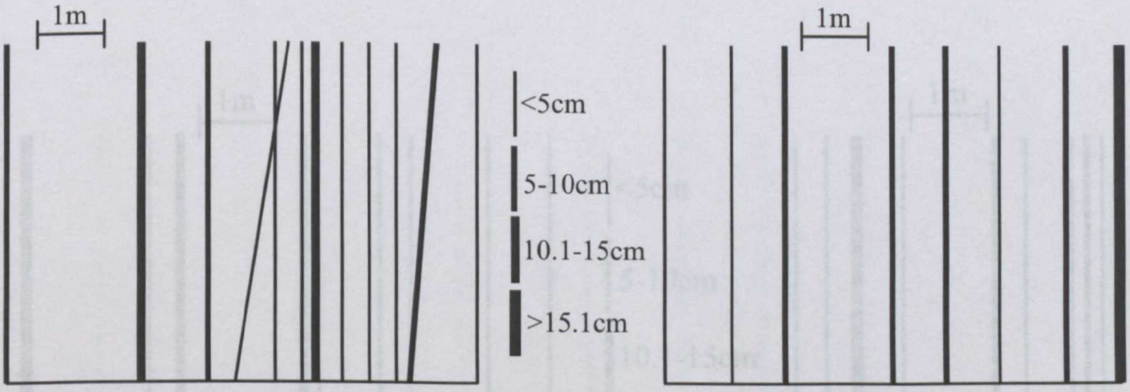


Figure 2.66. Transects from location h5: S18°48.748, E48°25.808. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: <1m.

Midstorey (0.75 to 6m)
Supports: 0.6 to >15.1cm, vertical to angled.
Discontinuities: <1 to 4m.

Understorey (< 0.75m)
Supports: < 0.5cm vertical.

Figure 2.67. Predominant support types at Location h6: S18°48.747, E48°25.827. Photograph: Mary Blanchard, 16 August 2005.

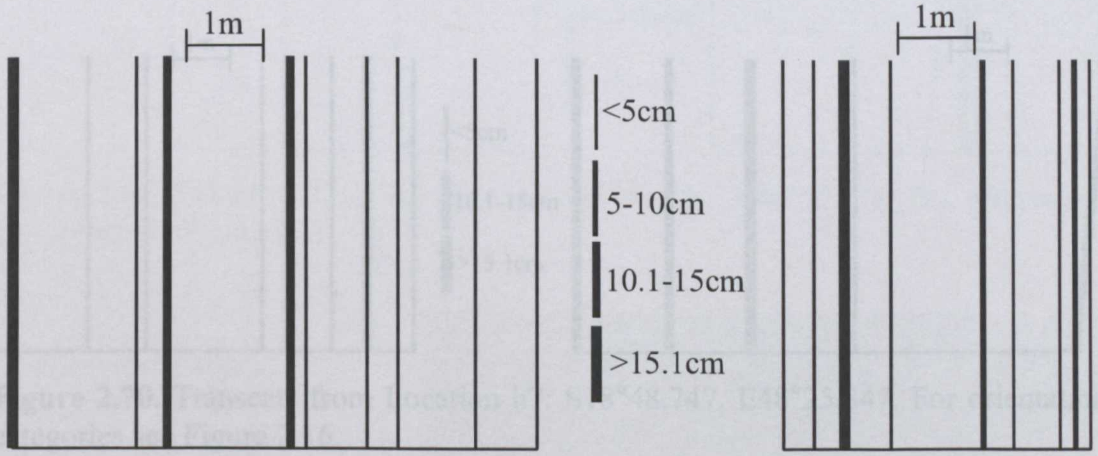


Figure 2.68. Transects from Location h6: S18°48.747, E48°25.827. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 10cm, vertical to oblique.
Discontinuities: <1m.

Midstorey (1 to 6m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to 3m.

Understorey (<1m)
Supports: <0.5cm vertical.

Figure 2.69. Predominant support types at Location h7: S18°48.747, E48°25.847. Photograph: Mary Blanchard, 16 August 2005.

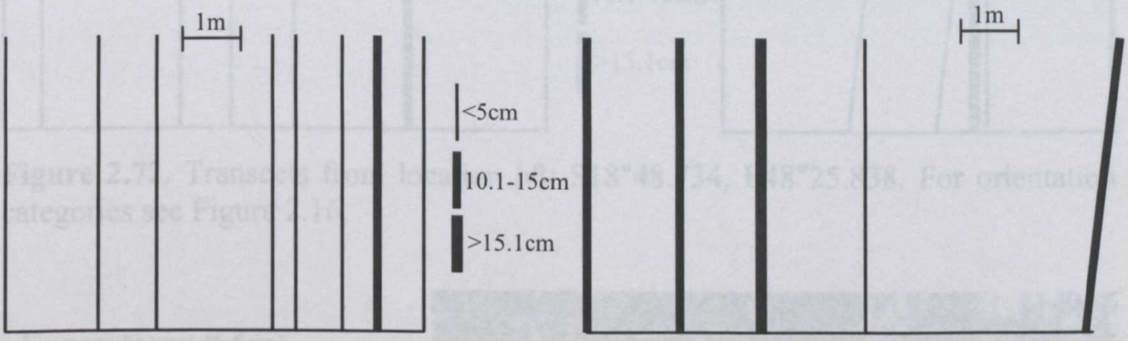


Figure 2.70. Transects from Location h7: S18°48.747, E48°25.847. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 10cm, vertical to horizontal.
Discontinuities: <1m.

Midstorey (1 to 6m)
Supports: 0.6 to >15.1cm, vertical to horizontal.
Discontinuities: <1 to >5m.

Understorey (<1m)
Supports: <0.5cm, vertical.

Figure 2.71. Predominant support types at Location h8: S18°48.734, E48°25.838. Photograph: Mary Blanchard, 16 August 2005.

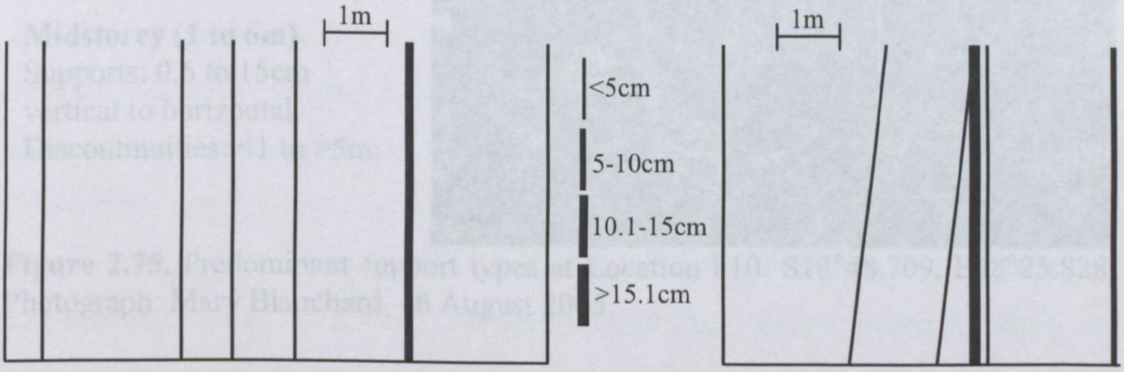


Figure 2.72. Transects from location h8: S18°48.734, E48°25.838. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 10cm, vertical to horizontal.
Discontinuities: <1m.

Midstorey (1 to 6m)
Supports: 0.6 to >15.1cm, vertical to oblique.
Discontinuities: <1 to >5m.

Figure 2.73. Predominant support types at Location h9: S18°48.717, E48°25.811. Photograph: Mary Blanchard, 16 August 2005.

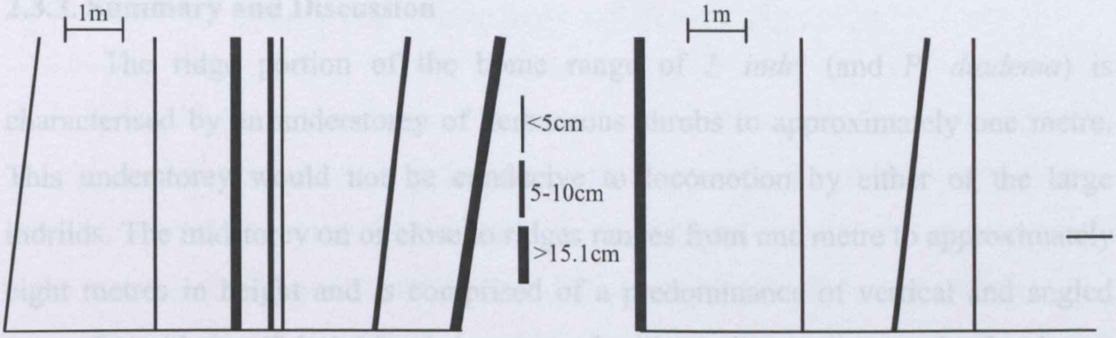


Figure 2.74. Transects from Location h9: S18°48.717, E48°25.811. For orientation categories see Figure 2.16.

Upperstorey (>6m)
Supports: <0.5 to 15cm,
vertical to horizontal.
Discontinuities: <1m.

Midstorey (1 to 6m)
Supports: 0.6 to 15cm
vertical to horizontal.
Discontinuities: <1 to >5m.

Figure 2.75. Predominant support types at Location h10: S18°48.709, E48°25.828. Photograph: Mary Blanchard, 16 August 2005.

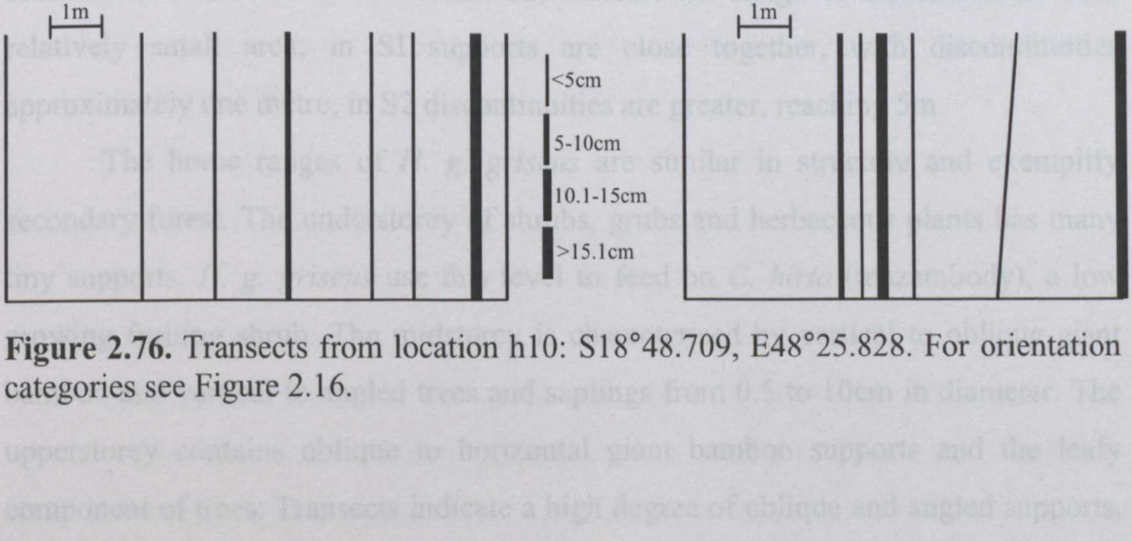


Figure 2.76. Transects from location h10: S18°48.709, E48°25.828. For orientation categories see Figure 2.16.

2.3.3. Summary and Discussion

The ridge portion of the home range of *I. indri* (and *P. diadema*) is characterised by an understorey of herbaceous shrubs to approximately one metre. This understorey would not be conducive to locomotion by either of the large indriids. The midstorey on or close to ridges ranges from one metre to approximately eight metres in height and is comprised of a predominance of vertical and angled trees of a mid-size (5.1 to 15cm), interspaced with smaller saplings and a few larger tree trunks. Discontinuities ranged from less than one metre to over five metres. This stratum included leaves of a few small samplings and liana. The upperstorey, above five to eight metres is typified by being the leafing area. Supports are predominantly smaller leafing branches of the larger trees and are likely to be angled to horizontal. Discontinuities are far less as tree branches spread into each other.

Valley transects for *P. diadema* show that there is a clear difference in tree height between valley and ridge. Trees on ridges are approximately 10m, while in the valley they can reach 50m. There is again a low understorey of low growing ferns and shrubs which would not be suitable as supports for the larger indriids. The midstorey is taller, ranging from 1m to approximately 20m. In this area there are many vertical and angled trees from small saplings (<5cm) to large tree trunks (>15.1cm). Smaller saplings ensure that there are leafy areas with many fine branches (<0.5cm). Discontinuities in this area can vary greatly, from under one metre to over 10 or 15m. The upperstorey, over 20m, is the portion in which the larger trees branch. Discontinuities tend to be smaller as branches of neighbouring trees meet. Supports range from horizontal to vertical and include small terminal branches (<5cm). Transects S1 and S2, indicate the range of discontinuities in a relatively small area; in SI supports are close together, with discontinuities approximately one metre, in S2 discontinuities are greater, reaching 5m.

The home ranges of *H. g. griseus* are similar in structure and exemplify secondary forest. The understorey of shrubs, grubs and herbaceous plants has many tiny supports. *H. g. griseus* use this level to feed on *C. hirta* (mazambody), a low growing fruiting shrub. The midstorey is characterised by vertical to oblique giant bamboo and vertical to angled trees and saplings from 0.5 to 10cm in diameter. The upperstorey contains oblique to horizontal giant bamboo supports and the leafy component of trees. Transects indicate a high degree of oblique and angled supports, with a predominance of discontinuities of less than one metre.

Chapter 3 Biology of Study Species

This chapter introduces background information on the study species: taxonomy and systematics; geographical range; size and morphology; group size, composition and dynamics. The aim is to describe known behavioural ecology of the three study species to permit integration of the new data into present knowledge.

Three species were the focus of the present study, *Indri indri*, *Propithecus diadema* and *Hapalemur griseus griseus*. *Indri* and *Propithecus* belong to Indriidae, together with *Avahi* (Mittermeier *et al.*, 1994; Groves, 2001). Genetic studies indicate that *Avahi* was the first genus to separate, a common *Indri-Propithecus* lineage continuing to evolve before divergence (Warter *et al.*, 2000; Rumpler *et al.*, 2004). *Indri* (6 to 7kg body weight) and *Propithecus* (3 to 7kg body weight) are diurnal and large bodied, *Avahi* nocturnal and small bodied (around 1kg body weight [Mittermeier *et al.*, 1994]).

There is general agreement that the genus *Hapalemur* is appropriately classified in family Lemuridae (Macedonia & Stranger, 1994; Groves, 2001; Pastorini *et al.*, 2002). This family also contains the genus *Lemur*, occupied by one species, *Lemur catta* (ring-tailed lemur), and separate from *Eulemur* spp. (true lemurs [Crovella *et al.*, 1993; Groves, 2001]). *Eulemur* species were classified as *Lemur*, until Simons and Rumpler (1988) moved all except *Lemur catta* into the *Eulemur* genus. All three, *Hapalemur*, *Lemur* and *Eulemur*, were initially classified in the same clade, but Groves and Eaglen (1988) considered that monophyly of *Hapalemur* and *Lemur* was probable, although could not be confirmed at that time. Since then DNA-sequencing studies have given support to the separation and place *Hapalemur* and *Lemur* in a single clade to the exclusion of *Eulemur* (Montagnon *et al.*, 1993; Yoder, 1997).

3.1. *Indri indri* (Gmelin, 1788)

3.1.1. Nomenclature and Systematics

Gmelin first described the genus *Indri* in 1788 (Groves, 2001). The name 'indri' comes from a mistaken interpretation of the Malagasy 'there it is'. Malagasy local to the Andasibe-Mantadia region call *I. indri* 'babakoto'. Differences in pelage colour throughout the range of *I. indri* have led some to believe there are two sub-species (Powzyk & Thalman, 2003). The second was named *Indri indri variegatus* by Gray in 1872 (Groves, 2001). This form is found from 18°S to 19°S (Figure 3.1) and type specimens originate from Tamatave, Sianaka and Andripirina (Groves, 2001). However morphometric analysis has shown no diagnostic differences between the two potential subspecies (Zaonarivelo *et al.*, 2007).

There are numerous Malagasy myths surrounding *I. indri* and the name 'babakoto' has many translations. Garbutt (1999) gives the origin of the name from the Betsimisaraka tribe, the tribe local to Andasibe, and translates it as 'ancestor of man'. However it is also translated as 'little father' or 'man of the forest' (Rowe, 1996). Another legend tells that the (almost) tailless *I. indri* (*I. indri* are the only lemur to lack a long tail [Powzyk & Thalman, 2003]) are the ancestor of man (Bradt, 1997). Yet another explains the story of a man who climbed a tree to gather wild honey and was so severely stung by bees that he fell from the tree, but was caught by an *I. indri* that carried him on his back to safety (Bradt, 1997). This myth is also given with a twist: a father named 'Koto' and his young son went to collect wild honey but never returned (Greenway, 1997). A search party could not locate the pair, instead spotting two *I. indri* in the trees. The people believed the father and son had been turned into *I. indri* and gave the *I. indri* the name 'Papa Koto' or 'Babakoto'. The Tsimihety tribe, from the north, believe that *I. indri* once gave them medicine against injuries caused by the iron weapons of invaders (Thalman *et al.*, 1993).

For these reasons, it is considered 'fady' to hunt *I. indri* (Thalman *et al.*, 1993; Bradt, 1997). A 'fady' is a belief, often localised, that an action will have a specific bad outcome (Bradt, 1997). Unfortunately although it is 'fady' for many native Malagasy to kill *I. indri*, immigrants do kill and eat them. The Moramanga region witnessed an influx of Chinese immigrants to build a Chinese-funded road and these people were accused of eating *I. indri* (Mittermeier *et al.*, 1994). Further there is an apparent erosion of beliefs among native Malagasy, leading to an increase in hunting (Mittermeier *et al.*, 2006).

3.1.2. Geographical Range

The range of *I. indri* is limited to the north by the Bemarivo River and to the south by the Mongoro River (Figure 3.1 [Goodman & Ganzhorn, 2004]). Historically its range extended further north and west (Powzyk & Thalman, 2003). *I. indri* is sympatric with *P. diadema* over 90% of their range (Powzyk, 1997).

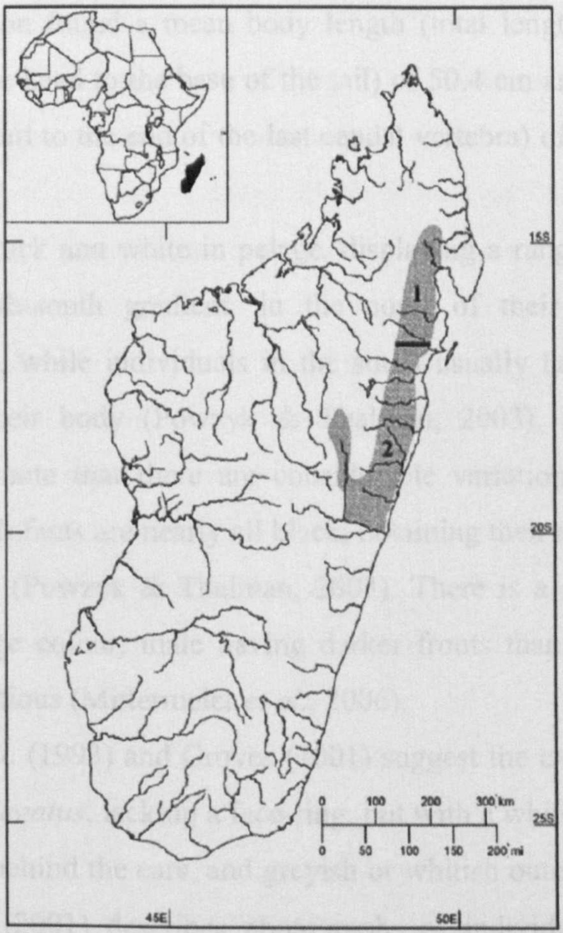


Figure 3.1. Geographic range of *I. indri*, separated into **1)** *I. indri* and **2)** *I. indri variegates*, from Quinn and Wilson (2002).

3.1.3. Weight and Morphology

Long considered the largest extant lemur species, *I. indri* has been described as weighing from 6 to 9.5kg (Mittermeier *et al*., 2006), although Pollock (1977) quotes the weight as 10 to 15kg. Powzyk (1996; 1997) weighed four adult individuals at an average weight of 6.48kg; two male and two female. The females weighed 6.75 and 7.52kg, while the males were lighter, weighing 5.75 and 5.9kg (Powzyk, 1996; 1997). Although this is a small sample, it does suggest that *I. indri* may be sexually dimorphic; females being larger than males. However Powzyk (1997) found no substantial differences in limb and cranial measurements between the sexes. This suggested to Powzyk (1997) that differences in weight reflect less skeletal size than increased fat and/or muscle on females. Powzyk (1997) suggested that female *I. indri* are the largest extant lemurs, however in Analamazoatra male *I. indri* appear larger than the female (Mittermeier *et al*, 2006). Powzyk (1997) recorded *I. indri* as having an end of tail to crown length of 54 to 68cm and a tail length of 5 to 7cm ($N = 4$), while a study of 105 individuals throughout their geographic distribution found a mean body length (total length of body from the occipital crown of the head to the base of the tail) of 50.4 cm and a tail length (total length from base of tail to the end of the last caudal vertebra) of 5.3cm (Zaonarivelo *et al.*, 2007).

I. indri are black and white in pelage, displaying a range of pelage patterns with a general north-south gradient: in the north of their range *I. indri* are predominantly black, while individuals in the south usually have white heads and white patches on their body (Powzyk & Thalman, 2003). Powzyk (1997) and Zaonarivelo (2007) note that there are considerable variations in *I. indri* pelage pattern at Mantadia. Infants are nearly all black, obtaining their adult pelage at two to three months of age (Powzyk & Thalman, 2003). There is a suggestion of sexual dimorphism in pelage colour, male having darker fronts than females, but this is unproved and contentious (Mittermeier *et al.*, 2006).

Thalman *et al.* (1993) and Groves (2001) suggest the existence of a possible sub-species: *I. i. variegatus*, lacking a face-ring, but with a white occipital cap, white collar extending up behind the ears, and greyish or whitish outer sides to the leg and lower arm. Groves (2001) describes photographs of individuals from Perinet as exemplars of this subspecies pelage pattern.

3.1.4. Life History

Thalman *et al.* (1993) states that infants are born from December and are initially carried ventrally on the mother. However, according to Mittermeier *et al.* (1994) births occur in May after a 120 to 150 day gestation.

Walker *et al.* (2006) compared age at first reproduction with longevity across primate clades, including strepsirrhines. Their research found that longevity is strongly associated with age at first reproduction: the older an individual is at first reproduction the longer they will live. This led Walker *et al.* (2006) to support the hypothesis that higher adult mortality selects for earlier reproduction. The hypothesis would appear to be sustained in the case of female individuals of *I. indri* which reach an age of seven or more before first reproduction (Mittermeier *et al.*, 1994) and have low adult mortality. *I. indri* females reproduce only every third year. The evolution of late reproduction would suggest that once attaining adulthood, *I. indri* are under low risk of mortality for many years. From this we might conclude that predation has never been significant for adult *I. indri*.

Another correlate of life history is diet. Godfrey *et al.* (1994) compared life history of folivorous indriids with frugivorous lemurids. Although *I. indri* and *Propithecus* spp. infants remain with their parental group for a long time, and take time to reach adult size, they are quickly capable of feeding on an adult diet due to early tooth development. This phenomenon results in a low maternal input to infants, but a longer reproductive life (Godfrey *et al.*, 2004). Lemurids adopt the opposite strategy: high maternal input and quick infant growth (Godfrey *et al.*, 2004). Godfrey *et al.* (2004) suggest indriids are more tolerant of moderate environmental stress, but lemurids are better at quickly rebuilding numbers after a long period of high stress.

3.1.5. Group Size, Composition and Dynamics

I. indri are monogamous, living in groups of three to five, comprised of an adult pair and dependent offspring (Pollock, 1975; 1977; 1979a; 1979b; Powzyk, 1997; Rigamonti *et al.*, 2005). Only after the death of their mate do adult *I. indri* seek out new partners (Powzyk & Thalman, 2003).

Rigamonti *et al.* (2005) followed four *I. indri* groups; two groups previously habituated for tourists and two newly habituated groups in Analamazoatra Special Reserve. The first tourist-habituated group had two adult females, one adult male and one sub-adult male (determination of sub-adult status was based on size). The second such group consisted of two adult males, one sub-adult male, one adult female and one sub-adult female. The newly-habituated groups were comprised of, in one case one adult female, one sub-adult female, one adult male and one sub-adult male; and in the other, one adult male, one adult female and two sub-adult females. Rigamonti *et al.* (2005) noted that there were two infants, but do not say which groups they were from. There is no description of how individuals were sexed, only that pelage colour and other physical differences differentiated individuals.

Powzyk (1997) obtained group size information for seven groups of *I. indri* within Mantadia. Each group contained one adult male and one adult female, and for four of the groups this was the total. Two of the remaining groups also contained one infant, while the other group contained two sub-adults and one infant.

As with many lemur species, *I. indri* display female dominance over males. (Pollock, 1977; 1979b; Mittermeier *et al.*, 1994). Females usually lead in group progressions, feeding before males and continuing to feed after males have moved (Pollock, 1977b).

3.1.6. Territorial Defence

A: Calling

I. indri defend territories by long calling or 'singing' (Pollock, 1986a). Long calls began with a communal 'roar' in 87% of cases observed by Pollock (1986a). The roar also acts as the *I. indri* aerial predator alarm call (Powzyk, 1997). Pollock (1986a) found that calls were usually initiated by males, although it was the adult female that called for the longest. Sub-adults (three to six years) sang in the first half of the duet, infants (one to three years) joining in with the roar for the first few notes (Pollock, 1986a). Calls can travel 2km (Pollock, 1975), if not further (Petter & Peyrieras, 1974).

I. indri are commonly heard singing in the early morning, although they can be heard at all times of the day (Pollock, 1975; 1979b; Oliver & O'Connor, 1980; Pollock, 1986a; Thalman *et al.*, 1993; Powzyk, 1997). The calling of one group apparently stimulates neighbouring groups to begin calling, with calls being answered from up to 3km away (Pollock, 1975; 1979b). The frequency of singing bouts is dependent on season, weather, and location of neighbouring groups (Pollock, 1975; 1977; Powzyk, 1997). Calling is more common during dry weather, and accordingly Petter and Peyriéras (1974) found calling most frequent from December to January. Powzyk (1997) found a peak in calling for two groups during the breeding season, lasting from September to February. However, two other groups displayed no seasonal bias in calling (Powzyk, 1997).

Geissmann and Mutschler (2006) compared the calling of *I. indri* with that of *Varecia variegata variegata* (black-and-white ruffed lemur) in Zahamena. They found that *I. indri* preferentially sung in the morning, and Geissmann and Mutschler (2006) concluded that their call did act as a territorial announcement. (The use of calls in territorial defence is by no means unique to *I. indri*. To give just one example, male and female *Callicebus personatus* [masked titi monkey] duet before leaving sleeping trees, apparently as territorial defence [Kinzey & Becker, 1983]).

B: Inter-group Encounters

Powzyk (1997) observed no aggressive inter-group encounters between *I. indri* in Mantadia. Two inter-group encounters were witnessed: one encounter, in a fruiting tree, involved a few 'agitation' calls; one group subsequently turned and left

(Powzyk, 1997), while on another occasion a study group rested within 50m of another group of *I. indri* (Powzyk, 1997).

Aggressive inter-group encounters have been witnessed in Analamazoatra (Young, pers. comm. to Powzyk, 1997). Pollock (1975) noted two male *I. indri* at Analamazoatra had injuries, a missing ear and eye respectively, but observed no fighting. Individuals were seen to reach out and attempt to 'grapple' with members of a neighbouring group (Young, pers. comm. to Powzyk, 1997). Powzyk (1997) suggests this difference between Mantadia and Analamazoatra is due to differences in population densities between the two sites. There are fewer individuals in Mantadia compared to Analamazoatra, which may alleviate pressure between groups at Mantadia.

3.1.7. Sleep Sites

At night group members often sleep up to 100m apart at a height of 10 to 30m; at most two individuals sleep together; young sleep with their mothers for the first year (Pollock, 1975).

3.1.8. Density

At Analamazoatra *I. indri* density was calculated to be 9 to 16 individuals per square kilometre in primary and degraded forest (Pollock, 1975; 1979a; Ganzhorn, 1992). Comparative analysis at Betampona yielded two different population densities. Census data gave densities of 1.1 individual per square kilometre, whereas home range analysis gave a density of 14 individuals per square kilometre (Glasscock & Britt, 2003). Pollock (1979b) indicated that population density of *I. indri* at Betampona was lower than at other reserves. Powzyk (1997) calculated the density of *I. indri* in Mantadia at 5.2 individuals per square kilometre, or 6.6 individuals per square kilometre when infants were included.

3.1.9. Habituation

I. indri are regarded as difficult to find and observe: Petter and Peyriéras (1974) noted that their colouration and habit of resting in forks of trees made them difficult to spot and that movement or vocalisation by the animal was required in order to locate *I. indri*. In addition they may quickly flee a long distance when disturbed (Petter & Peyriéras, 1974; Powzyk, 1997). Groups in Betampona were located by listening for their territorial call (Glessner, K. pers. comm.).

Pollock (1975) found that after a week of following *I. indri* at Perinet, alarm vocalisations and fleeing decreased. Approaches to as close as a few metres were tolerated after 3 weeks (Pollock, 1977). Pollock (1975) noted that adult females and young were easier to habituate than adult males, which stayed further away from the observer. This has consequences for *I. indri* living in areas of land disturbed by humans. They are quick to leave human-disturbed areas, leading to increased concentrations in undisturbed forest (Petter & Peyriéras, 1974).

It took three months for Powzyk (1997) to satisfactorily habituate two groups of *I. indri*. After this time the groups could be approached within 10m (Powzyk, 1997). A study of manual laterality in Analamazoatra Special Reserve habituated two wild groups of *I. indri* (Rigamonti *et al.*, 2005). These two groups lived in an area in which zoological and botanical surveys had previously been conducted. Habituation took 11 weeks, after which time the animals could be observed from a minimum distance of 5m.

3.2 *Propithecus diadema* (Bennett, 1832)

Where there is no specific information on *P. diadema*, information from other *Propithecus* species is used as a proxy in this description. *Propithecus edwardsi* (Milne-Edward's simpona) is chosen as the primary proxy as it is a similarly-sized and closely-related rainforest species of *Propithecus*.

3.2.1. Nomenclature and Systematics

Propithecus are commonly called sifaka. The name, sifaka, results from an onomatopoeic interpretation of a vocalisation given by dry forest *Propithecus verreauxi* (Verreaux's sifaka) and *Propithecus tattersalli* (Tattersall's sifaka [Powzyk, 1997]). Jolly (1966) calls 'true sifaka' those that give the 'sifaka' vocalisation. Powzyk (1997) suggests that rainforest *Propithecus* should be known as simpona. Simpona is the Malagasy name for *Propithecus diadema* in the Andasibe-Mantadia area. The term 'simpona' appears to be the most accurate for *P. diadema*. *Propithecus diadema* is commonly referred to as the 'diademed simpona'; diademed meaning crowned in this case.

The genus *Propithecus* and species *P. diadema* were first recognised in 1832 by E.T. Bennett (Tattersall, 1986; Groves, 2001). At times there have been nine sub-species recognised (Tattersall, 1986). The genus *Propithecus* has been traditionally split into three species, *Propithecus diadema*, *Propithecus verreauxi*, and the monotypic *Propithecus tattersalli* (Mittermeier *et al.*, 1994; Richard, 2003; Mayor *et al.*, 2004). The western species, *Propithecus verreauxi,* found in dry forests, is further split into four sub-species: *P. v. coquereli* (Coquerel's sifaka), *P. v. coronatus* (crowned sifaka), *P. v. deckeni* (Decken's sifaka) and *P. v. verreauxi* (Mittermeier *et al.*, 1994; Richard, 2003; Mayor *et al.*, 2004). Five subspecies of *Propithecus diadema* have been suggested: *P. d. diadema*, *P. d. candidus* (silky simpona), *P. d. edwardsi* (Milne-Edward's simpona), *P. d. holomelas* and *P. d. perrieri* (Perrier's simpona [Mittermeier *et al.*, 1994; Richard, 2003; Mayor *et al.*, 2004]). *P. d. holomelas* is now usually considered part of *P. d. edwardsi* (Tattersall, 1986; Mittermeier *et al.*, 1994; Mayor *et al.*, 2004).

Groves (2001) believes that *Propithecus* are 'over-lumped'. Following a genetic study Mayor *et al.* (2004) elevated four *Propithecus* subspecies to species level: *P. diadema perrieri* to *P. perrieri*, *P. diadema candidus* to *P. candidus*, *P. diadema edwardsi* to *P. edwardsi* and *P. verreauxi coquereli* to *P. coquereli*. This leaves *P. diadema diadema* as *P. diadema* and *P. verreauxi verreauxi* as *P. verreauxi* (Mayor *et al.*, 2004).

3.2.2. Geographical Range

As with *I. indri,* the southern limit of the range of *P. diadema* is usually held to be marked by the Mangoro River (Figure 3.2 [Goodman & Ganzhorn, 2004]). However, there is a possibility that *P. diadema* may be found at Marolambo, south of the Mangoro River, where it is possibly sympatric with *P. edwardsi* (Randriamampionona, R. pers. comm. to Mayor *et al.*, 2004). Irwin (2006c) suggests that populations between the Mangoro and Onive Rivers are morphologically different from the typical *P. diadema* and may be taxonomically different.

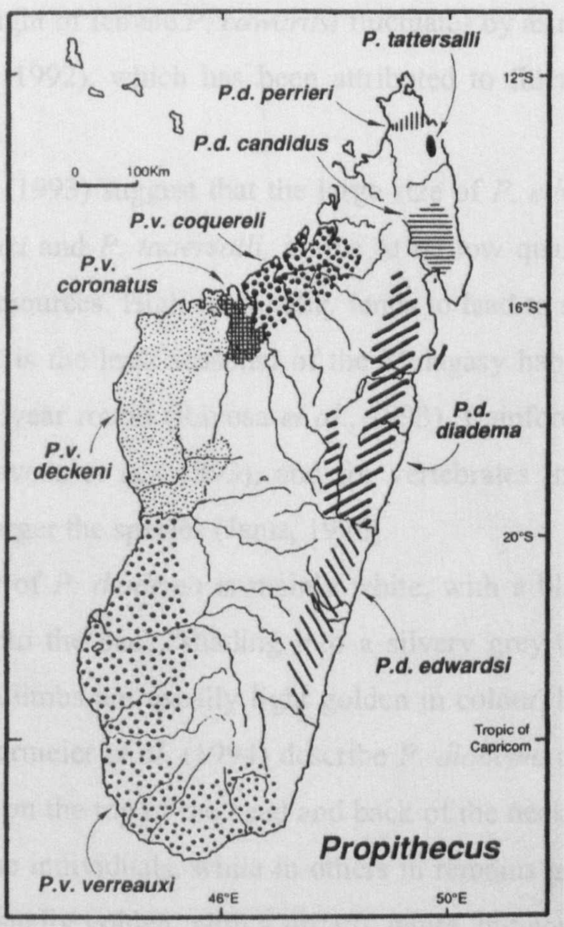


Figure 3.2. Geographic range of *Propithecus* spp., from Mittermeier *et al*. (1994).

3.2.3. Size and Morphology

P. diadema is a large lemur (end of tail to crown length of 560 to 1120mm and tail length of 290 to 580mm [*N* = 11, Powzyk, 1997]) second in size only to *I. indri* (Mittermeier *et al*., 1994), although Powzyk (1997) describes *I. indri* and *P. diadema* as the two largest lemur species. Powzyk's conclusion was drawn on the basis of an average measured weight of eleven *P. diadema* of 6.5kg compared to an average of 6.5kg for four *I. indri* (Powzyk, 1996; 1997). Mittermeier *et al*. (2006) give a range of 6 to 8.5kg. Female *P. diadema* were found to weigh more (6.5kg for six individuals) than males (6.5kg for five individuals [Powzyk, 1996; 1997]). This suggests that *P. diadema* are not sexually dimorphic.

Similarly, there is confusion as to whether or not *P. edwardsi* is sexually dimorphic: Ravosa *et al*. (1993) believe that it is, however Pochron *et al*. (2004) believe it to be monomorphic. Powzyk (1997) warns that it is difficult to infer the existence of sexual dimorphism from body weight information. Body weight has been shown to fluctuate from year to year, and possibly season to season, in re-capture studies of *Saguinus fuscicollis* (saddle-backed tamarin) by Goldizen *et al*.

(1988). The body weight of female *P. edwardsi* fluctuates by as much as 12% year to year (Glander *et al.*, 1992), which has been attributed to fluctuations in available food resources.

Ravosa *et al.* (1993) suggest that the large size of *P. edwardsi*, compared to dry-forest *P. verreauxi* and *P. tattersalli,* is due to its low quality diet and lack of seasonality in food resources. High seasonality tends to lead to smaller animals, and the eastern rainforest is the least seasonal of the Malagasy habitats, having a more constant food source year round (Ravosa *et al.*, 1993). Rainforests also have a low folivore biomass (Ravosa *et al.*, 1993), and for vertebrates in general, the lower quality the diet, the larger the species (Janis, 1976).

Pelage colour of *P. diadema* is mainly white, with a black crown and nape which can extend onto the back, shading into a silvery grey (Groves, 2001). The hindquarters and hindlimbs are usually light golden in colour, hands and feet black (Groves, 2001). Mittermeier *et al.* (1994) describe *P. diadema* as having principally white fur, with black on the top of the head and back of the neck; the black shades to a silvery grey in some individuals, while in others in remains golden. Hind quarters and hind limbs are usually golden, with a usually white, but sometimes golden, tail. Hands and feet are usually black. Individuals observed by Irwin (2006b) in Tsinjoarivo are much darker in colour, leading to the proposition that they are a new variant.

3.2.4. Life History

Infants are born between June and August in all *Propithecus* spp. (Richard, 2003). Infants initially cling ventrally, moving to their mother's back after a few weeks (Richard, 2003). Weaning occurs during the rainy season, when infants are six to nine months old (Richard, 2003).

The nature of dispersal within *P. diadema* is unknown due to lack of data, but it appears that both males and females disperse from their natal group. Studies in Tsinjoarivo observed two females and one male dispersing (Irwin, 2006b).

Studies at Ranomafana have found that *P. edwardsi* can live up to 27 years in the wild (King *et al.*, 2005). A female still remains fertile towards the end of her life, but the survival of her infant appears dependent on rainfall; old females are 67% more likely to lose infants in years of low rain than young females (King *et al.*, 2005). In years of high rainfall, infant survivability for older mothers is higher than in years of low rainfall (King *et al.*, 2005).

3.2.5. Group Size, Composition and Dynamics

P. diadema are thought to live in low densities, in groups of two to five individuals (Pollock, 1979a; 1979b). Powzyk (1997) habituated two groups of *P. diadema*. The larger group of six individuals contained three adult females, one sub-adult female and two adult males. The second group was comprised of one adult female, two permanent adult males and one semi-permanent adult male. These neighbouring groups therefore exhibited both polygynandry and polyandry.

Studies of *P. edwardsi* have identified variants in group structure: polygyny: one male and two or more females (27%); monogamy: one male and one female (18%); polyandry: one female and two or more males (23%); and polygynandry: two or more males and two or more females (32% [Pochron & Wright, 2003; Pochron *et al.*, 2004]). Pochron and Wright (2003) suggested this variability serves to balance coping with the seasonality of Madagascar while gaining enough protection from predators and being able to locate adequate food sources. The flexibility reported for *P. edwardsi* also appears to exist for *P. diadema*.

Differences have been found in group cohesion of *P. diadema* between fragmented and continuous forests (Irwin, 2005; 2007). In fragmented forest, where feeding patches were smaller, groups were less cohesive (Irwin, 2005; 2007). Cohesion in groups living in continuous forest was found to be lowest in the winter, associated with smaller patch sizes (Irwin, 2007). Thus, the lack of cohesion in fragmented forest appears to be linked to smaller feeding patches (Irwin, 2007). A social structure characterized by fission-fusion events has been recorded in *Eulemur albifrons* (white-fronted brown lemur), *Varecia rubra* (red-ruffed lemur [Vasey, 2000]) and *Eulemur macaco macaco* (black lemur [Johnson *et al.*, 2005]). This suggests a high degree of complexity in the nature of lemur social groupings.

P. edwardsi is largely female-dominant (Hemingway, 1999). Reasons behind female dominance are unclear. Gestating and lactating females show no increase in feeding or resting times compared to males (Pochron & Wright, 2003). Extended foraging and rest times might be expected to compensate for increased energetic costs. Differences were noted in dietary composition between sexes in some months, but lack of chemical-analysis data makes it impossible to confirm the significance of this fact (Hemingway, 1999).

3.3. *Hapalemur griseus griseus* (Link, 1795)

3.3.1. Nomenclature and Systematics

In common English the genus *Hapalemur* is known as the bamboo or gentle lemurs. The name 'bamboo lemur' originates from the primary food-stuff (bamboo) of all species in the genus (unless *Hapalemur griseus alaotrensis* is actually a distinct species as argued by Groves [2001] see below). In Malagasy *H. g. griseus* is known as bokombolo or kotrika.

Until recently there were three recognised species of bamboo lemur: *Hapalemur griseus* (grey or lesser bamboo lemur), *Hapalemur aureus* (golden bamboo lemur) and *Hapalemur simus* (greater or broad nosed bamboo lemur [Crovella & Rumpler, 1992; Mittermeier, *et al.*, 1994; Fausser *et al.*, 2002; Pastorini *et al.*, 2002; Mutschler & Tan 2003]). *H. simus* was initially classified by Gray (1871) as *Prolemur*, but it was later subsumed into the genus *Hapalemur*. However Groves (2001) returned *Hapalemur simus* to *Prolemur*, as *Prolemur simus*. Sub-fossils ascribed to *H. gallieni* are included with *P. simus* (Pastorini *et al.*, 2002). *P. simus* is today a rare species with a restricted range; however until less than a century ago, it occurred throughout the eastern rainforest (Pastorini *et al.*, 2002). The distribution of *H. aureus* is patchy, having only recently been discovered in Ranomafana (Meier & Rumpler, 1987; Meier *et al.*, 1987; Crovella & Rumpler 1992; Pastorini *et al.*, 2002). There is a suggestion of a possible fourth species of bamboo lemur on the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra (Sterling & Ramaroson, 1996): observers recorded a large-bodied, deep golden-red coloured, bamboo lemur. This patterning was observed in the same area as *P. simus* and could therefore be a variation of this species' pelage colour, although this lemur is characteristically charcoal grey (Sterling & Ramaroson, 1996).

Molecular studies on *Hapalemur* and *Prolemur* have confirmed the presence of three species (Rumpler *et al.*, 1991; Crovella & Rumpler 1992; Fausser *et al.*, 2002; Pastorini *et al.*, 2002). *P. simus* appears to have been the first species to diverge, with a closer relationship between *H. griseus* and *H. aureus* (Crovella &

Rumpler *et al.*, 1991; Rumpler 1992; Fausser *et al.*, 2002; Pastorini *et al.*, 2002;). Crovella and Rumpler (1992) found that the divergence of *P. simus* occurred early, and not long after *Lemur catta's* divergence from *Hapalemur.*

H. griseus has been divided into four subspecies, *H. g. griseus* (eastern lesser bamboo lemur), *H. g. occidentalis* (western lesser bamboo lemur), *H. g. alaotrensis* (Alaotran bamboo lemur) and *H. g. meridionalis* (southern lesser bamboo lemur [Warter *et al.*, 1987; Fausser *et al.*, 2002; Pastorini *et al.*, 2002]). *H. g. griseus* is widely distributed throughout the eastern rainforest and now includes individuals from *H. g. olivaceus* (Pastorini *et al.*, 2002). *H. g. alaotrensis* is slightly larger in size, having a shorter tail and more pointed snout. Its distribution is confined to reed beds surrounding Lac Alaotra (Pastorini *et al.*, 2002). Found in western deciduous forest, *H. g. occidentalis* is a smaller species (Pastorini *et al.*, 2002). *H. g. meridionalis* has the darkest coat and has been identified in southern Madagascar near Fort Dauphin (Warter *et al.*, 1987; Pastorini *et al.*, 2002). Fausser *et al.* (2002) examined the mitochondrial DNA of *H. griseus* spp. and suggested that *H. g. meridionalis* should be raised to *H. meridionalis.*

While Groves (2001) elevated *H. g. occidentalis* and *H. g. alaotrensis* to species level (i.e. *H. occidentalis* and *H. alaotrensis*), studies at a molecular level have led Pastorini *et al.* (2002) to suggest subsuming *H. g. alaotrensis* within *H. g. griseus*. Pastorini *et al.* (2002) conclusion was based on hybridisation between the two sub-species in captivity and the fact that their karyotypes are indistinguishable. They also suggest the possibility of a further sub-species, as an individual *H. g. occidentalis* was found to differ at the molecular level. This individual was from Tsiombikibo in northwest Madagascar, across the Betsiboka River from the other individuals tested. The Betsiboka River acts as a demarcation for *Eulemur fulvus* (common brown lemur) and *Propithecus verreauxi* subspecies (Pastorini *et al.*, 2002).

Recent cytogenetic work by Rabarivola *et al.* (2007) has further altered *Hapalemur* taxonomy. Their work supports *H. meridionalis* and *H. occidentalis* as full species, but they found no difference between *H. g. griseus* and *H.* [*g.*] *alaotrensis*. They further suggest that *H. g. griseus* should be divided into three sub-species, retaining the type location of Mantadia for *H. g. griseus* and describing two new sub-species; *H. g. ranomafanensis* found in and around Ranomafana and *H. g. gilberti* found around Beanamalao.

Hapalemur spp. and *Prolemur* are sympatric within the Parc National de Ranomafana (Wright & Randrimanantena, 1989; Tan, 1999) and the Réserve Naturelle Intégrale d'Andringitra (Sterling & Ramaroson, 1996).

3.3.2. Geographical Range

H. g. griseus lives in rainforest along the eastern coast of Madagascar from Tolagnaro (Fort-Dauphin) in the south to the Tsaratanana Massif in the north (Figure 3.3 [Mittermeier, *et al.*, 1994; Garbutt, 1999]). It has the widest altitudinal distribution of all bamboo lemurs, occupying elevations from sea level to over 2,000m (Garbutt, 1999).

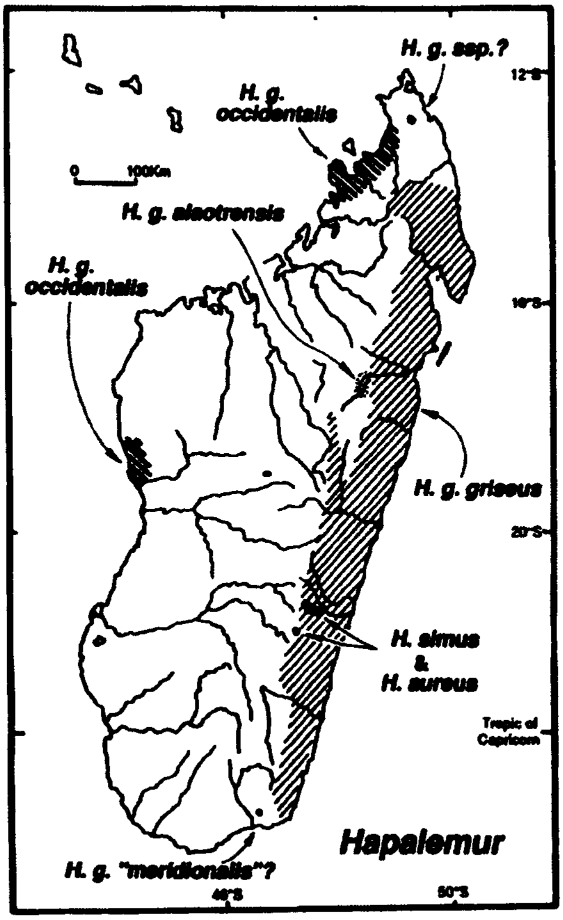


Figure 3.3. Geographic range of *Hapalemur* spp., from Mittermeier *et al.* (1994).

3.3.3. Density

At Analamazoatra, Ganzhorn (1992) calculated densities for *H. g. griseus* at 55/km^2.

3.3.4. Size and Morphology

One of the smallest bamboo lemurs, *H. g. griseus* is sexually monomorphic (Grassi, 2002) weighing between 700 and 900g (Garbutt, 1999). Meier *et al.* (1987) calculated an average weight of 830g from 4 individuals; Tan (1998) recorded mean weight as 800g, although *H. g. griseus* can reach 1kg (Mutschler & Tan, 2003). *H. griseus* have a head and body length of 250 to 310mm and tail length of 320 to 400mm (Groves, 2001).

Coat colour varies between individuals and geographic region, ranging from grey and olivaceous to rusty brown (Mutschler & Tan, 2003).

3.3.5. Life History

Mating occurs in June and July, and following a 137-day gestation, single infants are born in October and November (Wright, 1986; Tan, 1999; Mutschler & Tan, 2003). Mothers are the primary carer and the interbirth interval is roughly one year (Mutschler & Tan, 2003). Infants are initially carried in their mother's mouths, before they are old enough to cling to her fur (Mutschler & Tan, 2003). Solid food is tasted at three weeks, and eaten at six, and weaning is finished by six months (Tan, 1999).

An extended birth season was reported for *H. g. alaotrensis* from early September to February (one female giving birth in May [Mutschler, 2002]). Mutschler (2002) associated this with their non-seasonal diet.

3.3.6. Group Size, Composition and Dynamics

H. g. griseus are found in groups from four to six, often containing two adult females (Pollock, 1986b; Wright, 1986; Wright & Randrimanantena, 1989; Tan, 1999). A group studied at Ranomafana consisted of an adult pair with their two offspring from consecutive years (Wright & Randrimanantena, 1989). Two further groups contained one male with two females and their offspring (Tan, 1999). Groups within Andringitra National Park were noted as being smaller than elsewhere, although this could have been an artifact of the short study period (Sterling & Ramaroson, 1996).

Mutschler (2002) and Nievergelt *et al.* (2002) found a diverse pattern of group composition and size for *H. g. alaotrensis*. The median group size was three (78 groups observed) although the largest group contained nine individuals

(Mutschler, 2002). Over half the study groups (53%) had only one breeding female, roughly a third (35%) had two breeding females and a small percentage (12%) had no breeding female (Mutschler, 2002). Although groups had up to three males, behavioural and genetic data suggested only one male was breeding (Mutschler, 2002). Mutschler (2002) found, albeit from limited experience, that males dispersed to other groups as adults, suggesting groups contained fathers and their sons yet to disperse. It also appeared that females dispersed from their natal group, although their dispersal was as sub-adults. Genetic studies showed a variable mating system, 8% of paternities being extra-group males (Nievergelt *et al.*, 2002). Where there were two breeding females in a group, they were closely related, either mother and daughter or full sisters.

Population densities at Périnet were found to be 47 to 62 individuals per km^2, but most forests have lower densities (Mittermeier *et al.*, 1994).

3.3.7. Territorial Defence

H. griseus have been found to repeatedly use 'latrines' for defecation (Irwin *et al.*, 2004). Irwin *et al.* (2004) suggest that 'latrines' are used as an olfactory method of inter-group defence.

3.4. Summary

If we discount the possibility of *I. i. variegatus*, *I. indri* is monotypic, with a large range of pelage colouration. Historically its unusually short tail has aligned in the minds of the Malagasy people as an ancestor and has afforded it protection from hunting. Unfortunately immigration and a break down of traditional beliefs are eroding this *fady* and placing *I. indri* under increased risk of human hunting. *I. indri* has long been considered the largest of the extant lemurs, ranging from 6 to 9.5kg and although *P. diadema* can approach it, and indeed overlap, in size, this still appears an accurate assessment. Sexual dimorphism in size and pelage colour has been suggested but un-proven. *I. indri* are long-lived, with a long inter-birth interval and period of infant dependency. This puts *I. indri* at great risk if hunting levels increase as it will take populations a long time to recover. Groups consist of a monogamous adult pair with offspring, ranging from three to five individuals and are lead by the dominant female. Inter-group aggression is low and territorial defence appears to rely on long calling or 'singing'. Unusually for prosimians, habituation is difficult for *I. indri* and they are quick to vacate human disturbed forest. This indicates that protection of forest inhabited by *I. indri* is paramount. The geographic range of *I. indri* extends throughout the northeastern rainforests, sympatric with *P. diadema* over 90% of its range.

Propithecus species are undergoing revision and many sub-species have been elevated to species level. At present *P. diadema* has no sub-species, but that situation may well change. They are large bodied, second in size only to *I. indri*, ranging from 6 to 8.5kg. *P. diadema* are long lived, with a shorter period of infant dependency than *I. indri*. Group composition and size is highly variable, even between geographically closely situated groups.

H. g. griseus are small bodied folivores with a reliance on bamboo as a food source. Despite their small physical size, 700 to 900g, they have maintained a greater geographic range than either the closely related *H. aureus* or *P. simus*. *H. g. griseus* exhibit a range of group structure and size and the interbirth interval is yearly.

Chapter 4 Study Species

This chapter presents first of all a review of the challenges of living in forest fragments and edges, which proves to be a major factor in *H. g. griseus'* ecology. Background to capture and darting follows, with field methods and morphometric data collected during anaesthesia. The chapter then includes information on the field observations made on each of the study groups: habituation and choice of study groups; group size, composition and dynamics; density; territorial defence; inter-group encounters; inter-species encounters; and rest sites. While an understanding of social behaviour is not the purpose of this thesis, the ecology of a species must be affected by its social behaviour. The aim of this chapter is therefore to provide information about the study groups which may relate to other aspects of their ecology.

4.1. Living on the Edge: Disturbed, Fragmented Forest and Forest Edges

The continuous destruction of primary forest results in highly fragmented patches of natural forest with no linking corridors. Remaining forests can be left disturbed by human impact and bordered by an ever increasing 'edge' zone. Primates face a number of problems if living in disturbed and/or fragmented forest and forest edges: availability of food resources, predation risk and ability to locate a mate are all affected. Some species appear to adapt well to these conditions, even thriving, but others either do not have the capability to survive or can do so only with a decrease in health and fitness.

Forest edges are characterised by the assimilation of surrounding plants and conditions into the primary forest (Lehman *et al.*, 2006a; 2006b). Not all species are capable of living in this environment. An ability to adapt to 'poor' forest conditions is obviously a bonus to a species living in fragmented forest areas. However, living close to an edge can bring about increased likelihood of predation, not least by humans. Lehman *et al.* (2006a; 2006b) termed this the 'edge effect'. A survey 30km north of the Vohibola III Classified Forest found extensive evidence of snare-traps in forest edges (Lehman & Wright, 2000). Population densities of *H. g. griseus* did not however respond to the 'edge effect' in Vohibola III Classified Forest, being found in equal densities in edges as in more central forest areas. Lehman *et al.* (2006b) however found that *Cheirogaleus major* (greater dwarf lemur) are less common in forest edges, associated with tree diameter: fewer *C. major* were found, and tree diameters were smaller in edges.

Studies in Kibale, Uganda, found no characteristic differences between species that have an ability to live in fragmented forest and those that do not (Chapman & Lambert, 2000; Onderdonk & Chapman, 2000). Onderdonk and Chapman (2000) suggest that it is impossible to make generalisations about which primates are capable of living in fragmented forest. However they propose that in order to live in fragmented forest primates must either have small home ranges or if they have larger ranges, be able to move between patches. It was noted that ability of primates in Kibale to live in fragmented forest might be related to the ability to live on the edge of forest. For colobines in Kibale, the suggested reason for their evident ability to live on forest edges was a dietary preference for secondary growth (Onderdonk & Chapman, 2000). An increase in plant diversity in secondary growth in disturbed areas can potentially allow greater densities of certain primate species (Chiarello, 1994; Onderdonk & Chapman, 2000). There were higher concentrations of *Colobus guereza* (black-and-white colobus) in logged areas of Kibale than un-logged areas (Onderdonk & Chapman, 2000).

Chiarello (1994) suggested *Alouatta fusca* (brown howler monkey) in southeastern Brazil could benefit from forest-fragmentation and secondary growth as it resulted in a proliferation of lianas, one of their main foods. In fragmented forests *A. fusca* were found at higher-than-average densities, but with smaller-than-average home range, probably as a result of increased food resources, due both to forest disturbance and the overall dietary flexibility of *A. fusca.* A study in naturally fragmented forest in Lopé, Gabon, found that four out of eight primate species were found more commonly in forest fragments (Tutin *et al.*, 1997). For some species fragments made up only part of their home ranges, but for *Cercopithecus nictitans* (greater spot-nosed guenon) and *Cercopithecus cephus* (moustached guenon) home ranges were exclusively within fragments. Both *C. nicitans* and *C. cephus* had home ranges 8 to 25 times smaller in the fragments than in continuous forest. Tutin *et al.* (1997) therefore suggest that *C. cephus* could be a gap and edge specialist. Surprisingly a third, similarly sized guenon, *Cercopithecus pogonias* (crowned guenon), which has a similar diet to the other guenons, is only rarely found in forest fragments. Tutin *et al.* (1997) suggested that this could be because *C. pogonias* are more vulnerable to predation, although no reason why this should be the case was evident to them.

Another problem of life in fragmented forest is the difficulty individuals find in dispersing to new groups when they reach sexual maturity. Colonisation of new areas is also problematic. Lack of connectivity appears to have prevented *Alouatta palliata* (mantled howler monkey) from inhabiting available forest fragments in Mexico (Mandujano *et al.*, 2004). Mandujano *et al.* (2004) indicate the need for 'stepping stones' or corridors, linking fragments, to enable dispersal between groups.

There are differences between populations of *H. g. griseus* in disturbed and un-disturbed forest in Ranomafana (Grassi, 2006). Groups in disturbed forest are larger and *H. g. griseus* occurs at much higher densities, suggesting that *H. g. griseus* adapts well to secondary and disturbed forest. Habitat appears to affect group size and composition for *Prolemur simus* (greater bamboo lemur): mitochondrial DNA studies showed a monogamous system in the protected forest of Ranomafana and a multimale-multifemale system in the highly fragmented forest of Ambolomavo (Fausser *et al.*, 2002).

The situation is not simple however, as lower-than-usual numbers of primates have been found in forest fragments, including *H. g. griseus*. One survey found that forest fragments in southeastern Madagascar had reduced species number and/or densities of eight diurnal lemur species including *H. g. griseus* and *P. diadema* (Johnson *et al.*, 2003).

Comparisons between groups of *P. diadema* living in continuous and fragmented forest indicate that in fragments, individuals are energetically stressed and have a lower body weight (Irwin, 2006a; 2006b). There is far less group cohesion in forest fragments, higher cohesion being evident in the summer, when large food patches were available (Irwin, 2005). Irwin (2005) suggests this could lead to a greater risk of predation in fragmented forest, although this would be dependent on how many predators were able to live in the fragments. Fragments were less than 30ha (Irwin, 2005) and home ranges in these were half the size of those in continuous forest and diet more restricted (Irwin, 2006b). The reliance of *P. diadema,* living in fragments, on *Bakerella* (parasitic mistletoe) led Irwin (2006b) to suggest that parasitic plants are an important resource for primates in degraded forest fragments. This is primarily due to the 'extended phenology' of *Bakerella*, where reproductive parts are available all year (Irwin, 2005).

Anthropogenic alteration of environments can lead to increased predation risk, even where primate species survive. Ludwig *et al.* (2007) found that large-bodied *Alouatta caraya* (black-and-gold howler monkey) in Brazil were at greater risk of predation from *Puma concolor* (cougar) following the loss of tall trees from the forest, despite an overall high density of *A. caraya.*

4.2 Darting and Capture

4.2.1. Background

Capture of wild animals can be achieved by physically capturing the animal by hand, trapping, or darting with anaesthetic. Each method is appropriate for different species and circumstance. Capture by any method is risky and can, and sometimes does, result in death of the animal. This can be due to stress, physical injury sustained during capture and problems with anesthetising drugs. Studies involving capture must weigh up the risks involved against the benefits and overall increase in knowledge.

There is always a potential risk to the researcher, from an accidental dose of the anaesthetic, to injury by traps or guns, and indeed from the animal. Wild primates can transmit viruses to humans and care must be taken against being bitten and the potential viral risk must be understood. Wild macaques carry the herpesvirus simiae (B virus), fatal in 21 out of 24 recorded cases in humans (de Ruiter, 1992).

As capture is so dangerous to the animal it is necessary to recover as much information as possible. Glander *et al.* (1992) recorded body weight and measurements and used tooth wear to approximate age. Data collected by Sussman (1991) on captured *Lemur catta* (ring-tailed lemur) included: weight, reproductive state, general physical condition, internal body temperature, dermatologlyphs, hair samples, dental casts and description of dental condition and body measurements. Warren and Crompton (1997a) collected weight and morphometric data while their study animals, *Lepilemur edwardsi* (Milne Edward's sportive lemur) and *Avahi occidentalis* (western woolly lemur), were under anaesthetic. Of course increasing the amount of information obtained can extend the period under anaesthesia and this too must be considered.

4.2.2. Capture Drugs

Not only are dosages species-dependent, individual primates within a species respond differently to capture drugs, some requiring far higher doses than others (Scott, *et al.*, 1976). The best drug is one that has a wide margin of error, as body weights are not known before darting.

Cyclohexylamines are injectable general anaesthetics, producing dissociative anaesthesia, a cataleptoid state of immobility (Beck, 1976; Fowler, 1986; Swan, 1993; Wanamaker & Pettes, 1996). Cyclohexylamines are frequently combined with sedatives to counteract their cataleptic and convulsive characteristics (Swan, 1993) and include ketamine and tiletamine hydrochloride (Beck, 1976; Fowler 1986; Burroughs, 1993; Swan, 1993). Ketamine is short acting, and respiratory and cardiovascular functions are usually well maintained (Beck, 1976; de Ruiter, 1992; Burroughs, 1993; Swan, 1993; Wanamaker & Pettes, 1996). Doses vary greatly between species, from 2 to 50mg/kg, most are in the range of 10 to 20mg/kg (Fowler, 1986; Martin, 1986; Swan, 1993). There is potential for a wide margin-of-error in doses, with up to 10 times the usual dose required for toxicity (Swan, 1993). Williams *et al.* (2003) states that for captive lemurs 2.2 to10mg/kg of ketamine are sufficient for restraint, but wild lemurs require doses of up to 35mg/kg. Ketamine should be stored below 25°C and protected from light and damp, in good conditions it can be kept for over one year without potency being effected (Swan, 1993).

Ketamine should be injected intra-muscularly (de Ruiter, 1992) although this is painful (Fowler, 1986; Burroughs, 1993). It should preferably be given to an animal with an empty stomach (de Ruiter, 1992), although this is impossible to judge in wild primates. Ketamine can be given to pregnant female primates with no adverse effect (Fowler, 1986; de Ruiter, 1992), although ketamine does cross the placenta into the foetus (Fowler, 1986). Anaesthesia usually occurs within five to ten minutes (Fowler, 1986), although this can be age dependent. In *Chlorocebus aethiops* (vervet monkey), older individuals took longer to become anaesthetised (Huff *et al.*, 2003). Dependent on dosage, animals are usually ambulatory within one to two hours (de Ruiter, 1992), although it can take up to five hours (Fowler, 1986; Swan, 1993).

Following anaesthesia by ketamine, muscle tremors and jerking of limbs can occur, although this is rare in primates (Fowler, 1986; Burroughs, 1993; Swan, 1993; Wanamaker & Pettes, 1996). Tests on *C. aethiops* showed tremors are more prevalent in older individuals (Huff *et al.*, 2003). Eyelids often remain open (Fowler, 1986; de Ruiter, 1992; Burroughs, 1993) and lubrication, using a bland ophthalmic ointment, should be administered to the eyes to prevent drying and ulcers developing in the cornea (Swan, 1993; Wanamaker & Pettes, 1996). Because of this animals with open eyes should be shielded from sunlight (Burroughs, 1993; Swan, 1993). Another common side effect is salivation (Beck, 1976: Fowler, 1986; Burroughs, 1993), found more often in older animals (Huff *et al.*, 2003). Due to side effects, depth of anaesthesia must be measured by the animal's response to pain and handling, rather than by reflex, respiration and ocular effect (Swan, 1993). A further side effect due to the catatonic effects of the drug is hyperthermia, and effort must be made to keep the animals temperature down (Fowler, 1986; Burroughs, 1993; Swan, 1993).

Experiments have shown that ketamine at low doses (up to 1.78mg/kg) impairs cognition in *Macaca mulatta* (rhesus monkey [Taffe *et al.*, 2003]). Higher doses (15mg/kg) affected locomotion and object manipulation of infant *M. mulatta* for at least 24 hours after injection (Pierre *et al.*, 2003). Behavioural studies should therefore lag behind anaesthesia to rule out adverse effects of the drugs.

Cyclohexylamines accidentally absorbed through broken human skin or membranes are not immediately life-threatening, and serious problems are only likely if the full contents of a dart were injected into a human (Morkel, 1993). Agitation, un-coordination, aggression, self mutilation and other bizarre behaviour can occur; large doses can result in coma, serious respiratory depression and death (Morkel, 1993).

4.2.3. Studies using Ketamine to Anesthetise Primates

Table 4.1. Dosages of ketamine (mg/kg) used in primate capture.

Dosage	Species	Author(s)
30 to 35 mg/kg	*Avahi laniger* *Eulemur rufus* *Eulemur rubriventer* *Hapalemur aureus* *Hapalemur griseus griseus* *Propithecus edwardsi*	Glander *et al.*, 1992
20 mg/kg	*Eulemur rufus*	Ostner & Kappeler, 1999
13.5 mg/kg	*Cebus capucinus*	Glander *et al.*, 1991
20 mg/kg	*Aotus azarai*	Fernandez-Duque & Rotundo, 2003
6.3 mg/kg	*Lemur catta*	Pye *et al.*, 2000
10 mg/kg	*Macaca fascicularis*	de Ruiter, 1992

Ketamine has been used by a number of researchers across the primate clade (Table 4.1). Unfortunately not all accounts of anaesthesia include specific dosages and when dosages are given it can be in either mg/kg, or less usefully simply the mg; *Saguinus fuscicollis* (saddle-backed tamarin) were anaesthetised with ketamine following trapping, but no dosages are given (Terborgh & Goldizen, 1985).

Warren and Crompton (1997a; 1997b) used ketamine hydrochloride to anaesthetise *Lepilemur edwardsi* (0.1ml) and *Avahi occidentalis* (0.2ml), the concentration of ketamine is not recorded so mg/kg cannot be calculated. Rehydration using a pipette was carried out frequently by mouth and recovery was made within one hour, animals held for a maximum of 1.5 hours (Warren & Crompton, 1997a; 1997b). Larger doses were used for *A. occidentalis* as they were injected by darting, and the entire dose was found not to be injected into the animal (Warren & Crompton, 1997b) by the explosive-based Distinject 'flip' darts used, propelled by blowpipe.

Glander *et al.* (1989) darted *Hapalemur* spp. using a carbon dioxide powered rifle and non-barbed darts with 3/8-inch needles contained 40mg of Ketamine hydrochloride (100mg/ml). Six species of lemur were captured at Ranomafana; *Avahi laniger* (eastern woolly lemur), *Eulemur rufus* (red-fronted brown lemur), *Eulemur rubriventer* (red-bellied lemur), *Hapalemur aureus* (golden bamboo lemur), *H. g. griseus* and *Propithecus edwardsi* (Milne-Edward's simpona [Glander *et al.*, 1992]). A carbon dioxide powered rifle using disposable non-barbed darts with 9mm needles was used for capture and ketamine hydrochloride (100mg/ml) used at doses of 30 to 35mg/kg. Ketaset (20mg/kg) was used to anaesthetise *E. rufus* (Ostner & Kappeler, 1999). In this study all individuals were returned to their groups within one hour, with no adverse reactions observed.

4.2.4. Methods of Capture and Administration of Drugs

Anaesthetic drugs are administered intramuscularly by injection. The simplest method is by hand-held syringe, but this assumes there is contact with the animal. This method is appropriate when the animal has been captured by hand, or has been trapped. Indirect administration can be by blowpipe or rifle.

Direct physical capture has been used to remove nocturnal primates from their sleep sites. *Lepilemur ruficaudatus* (red-tailed sportive lemur) were captured by hand in Kirindy (Zinner *et al.*, 2003). *L. edwardsi* were captured with a noose from their daily sleep sites (Warren & Crompton, 1997a; 1997b). In the same study, *Avahi occidentalis* were anaesthetised using with darts fired from both blowpipes and air guns. It was found that darts only injected part of the dose into the animal.

Mist netting can capture small nocturnal primates, such as *Tarsius* spp. (tarsiers [Crompton & Andau, 1987; Gursky, 2000]). Nets are set around sleep sites to catch the primates when they first move, and Crompton and Andau (1987) used up to a dozen at a time, checking all nets four times a night. Traps have been used to capture a variety of primates including lemurs. Harcourt (1987a) used Sherman traps baited with banana to capture *Microcebus rufus* (brown mouse lemur). Traps can be used at the entrance of tree holes to capture nocturnal lemurs as they leave their sleep sites, as with *L. ruficaudatus* (Zinner *et al.*, 2003).

Carbon dioxide powered rifles and blowpipes have been used to capture a number of primate species, such as *Ateles geoffroyi* (Geoffroy's spider monkey), *Cebus capucinus* (white-throated capuchin [Glander *et al.*, 1991]) and *Alouatta palliata* (Scott *et al.*, 1976; Glander *et al.*, 1991). Glander *et al.* (1991) found blowpipes effective for distances of less than 5m, with de Ruiter (1992) finding them accurate up to 7m: as with all darting, aim is taken on the hindquarters, perpendicular to the target surface to ensure complete injection of the drug, and no shots should be attempted unless the animal is faced away from the shooter so as to miss dangerous areas: chest, thorax, lumbar region, abdomen, shoulder, neck, head or face. Nylon mesh nets held by two or three people catch darted individuals; animals which do not fall can be removed by climbing the tree or cutting the branch (Glander *et al.*, 1991). Fernandez-Duque and Rotundo (2003) darted 70 *Aotus azarai* (Azara's night monkey). One metre long blowpipes were used when individuals were less than 6 or 7m away from the researcher and a carbon dioxide powered rifle used for distances up to 20m.

4.2.5. Field Methods

Darting in this study was carried out in January 2005 by Nicole Volosoa Andriaholinirina using either a Distinject air-pump rifle (Delta Model: 45) with a SKS Renkompressor foot pump or Telinject air-pump rifle (Figure 4.1). For *I. indri* and *P. diadema* 1000mg/ml ketamine (Imalgène) was utilised, while the *H. g. griseus* was darted using 100mg/ml ketamine (Table 4.2). Individuals were caught in a cloth.

Animals were fitted with TW-3 medium mammal tag-and-collars from Biotrack Ltd. These are brass collars with a soft heat-shrunk sleeving.

Figure 4.1. **A**: Field assistant Finomana Andriamasitoly 'Toly' weighing the adult male *P. diadema*. **B**: Field assistants Lantonirina Claudia Natache Randrianarivony, Finomana Andriamasitoly and darter Nicole Volosoa Andriaholinirina pumping up air rifle. Photographs: Mary Blanchard, 29 January 2005.

Animals were weighed under anaesthesia by placing the animal in a cloth sack (Figure 4.1) using a 10kg Pesola scale for *I. indri* and *P. diadema* and 2.5kg Pesola scale for the smaller *H. g. griseus*. Animals were measured using a standard 1m haberdashery tape measure. Individuals were released by placing them on a vertical or angled branch as soon as they were capable of maintaining balance. Observers remained with individuals until they were capable of moving off on their own, to protect them from potential predation.

Table 4.2. Date, position and amount of anaesthetic used for each individual darted and radio-collared during the study.

	I. indri		*P. diadema*		*H. g. griseus*
Sex	A female	SA female	A male	SA female	A female
Date	20-Jan-05	20-Jan-05	29-Jan-05	22-Jan-05	26-Jan-05
GPS position	S18°48.853 E48°25.309	S18°48.852 E48°25.242	S18°48.831 E48°25.032	S18°48.927 E48°26.208	S18°48.746 E48°25.850
Anaesthetic	0.6ml of 1000mg/ml Imalgene	0.5ml of 1000mg/ml Imalgene	3x0.6ml of 1000mg/ml Imalgene, 1x0.3ml of 100mg/ml ketamine	2x0.5mg of 1000mg/ml Imalgene, 2x0.3mg of 100mg/ml ketamine	0.3ml of 100mg/ml ketamine
Approximate mg/kg	82	75	340	196	43

A: adult; SA: sub-adult.

4.2.6. Morphometric results

Table 4.3. Weights (kg) and lengths (cm) of individuals darted and anaesthetised during the present study.

	I. indri		*P. diadema*		*H. g. griseus*
Sex	A female	SA female	A male	SA male	A female
Weight	6.7	7.3	5.3	5.1	0.7
Length tibia-fibula	15	26	24	22	10
Length femur	17	26	22	22	10.5
Length foot	12	14	14	13.5	6
Length hallux	11	12	11.5	12	4
Length fore-arm	18	19	15	16	7.7
Length humerus	15	16	13	16	5.5
Length hand	14	14	13	12.5	4.3
Length thumb	6.5	8.5	6.5	7	2.3
Length neck-pubic	39	37	30	31	16
Chest circumference	40	44	37	38	17.5
Length ear	3	5	3	3	2
Length nose to tail base	60	63	46	44	24
Length tail	5	5	52	56	35
Total length	65	66	95	96	58
Length eyes to nose	4	4	3	3	1.5
Length eye to eye	4.5	3.2	5	3.5	2.5

A: adult; SA: sub-adult.

4.3. Field Observations

4.3.1. *Indri indri*

4.3.1.1. Habituation

Habituation began in November 2004, continuing until January 2005. Habituation of *I. indri* proved difficult and they were the hardest of the study species to habituate. Other than randomly finding *I. indri* they could initially be located only by listening for their territorial call. Days would pass during habituation where no *I. indri* were observed. Details of the habituation process can be found in Appendix C1.

It was discovered in April (16 April 2005) that the adult female's radio collar had fallen off. Following this the group could only be located by the sub-adult female's radio collar.

4.3.1.2. Pelage Colour

Although pelage colouration of *I. indri* follows a north-south gradient, considerable variation was observed in the pelage of *I. indri* in Mantadia and Analamazoatra. During the preliminary visit to Mantadia in May 2004 the *I. indri* observed were distinctly black and white, with the appearance seen in Figure 4.2. This pelage pattern was also observed for the often-photographed *I. indri* at Analamazoatra Special Reserve (Figure 4.3); for the 'white-head' *I. indri* group, which attempts were initially made to habituate, and in other groups and individuals of *I. indri* glimpsed in the study area. However, the study group, the 'black-heads', not only displayed black heads, but were substantially blacker over their bodies (Figure 4.4 and Figure 4.5). Rather than having white arms and legs, they were black, ranging to grey.

Figure 4.2. Adult *I. indri*, from habituated 'tourist' group in Mantadia National Park. Photograph: Mary Blanchard, May 2004.

Figure 4.3. *I. indri* from habituated 'Tourist Group One' at Analamazoatra Special Reserve. Photograph: Mary Blanchard, 25 June 2005.

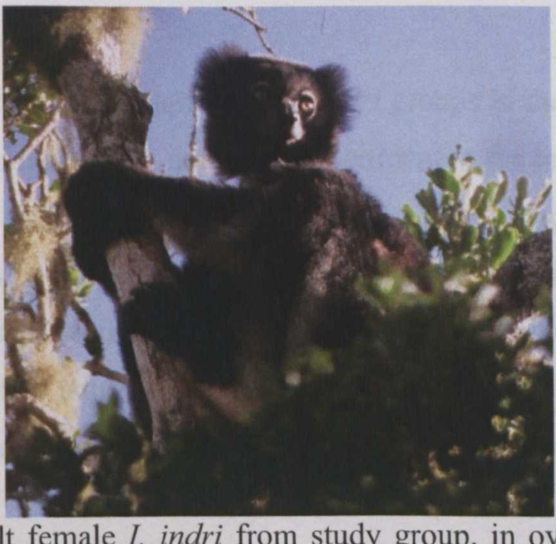


Figure 4.4. Sub-adult female *I. indri* from study group, in overnight rest position. Photograph: Mary Blanchard, 04 July 2005.

Figure 4.5. Adult male *I. indri* from study group, in overnight rest spot. Photograph: Mary Blanchard, 04 July 2005.

4.3.1.3. Group Size, Composition and Dynamics

The study group comprised an adult male and female pair, a sub-adult female, and an infant that at the beginning of the study was carried on its mother's back. In January 2005 the infant was often seen moving and feeding on its own. The infant disappeared in May 2005; the cause of the disappearance is unknown. The neighbouring 'white-headed' *I. indri* were comprised of an adult male and female pair, a sub-adult and infant. The infant in this group appeared smaller and presumably slightly younger than the infant in the study group. During a preliminary study in May 2004, group of *I. indri* habituated for tourists was observed. This group contained an adult pair, a sub-adult (probably female) and on 17 May 2004 a new-born *I. indri* was observed, carried ventrally by the adult female.

4.3.1.4. Density

A specific survey of the number of *I. indri* groups in the vicinity of the study area was not carried out as it was not deemed pertinent to the investigation. However ad-hoc observations suggest a minimum of five other groups of *I. indri* in and surrounding the study area (Figure 4.6). They also indicate overlap between different groups' territories. The specifics of these sightings can be found in Appendix C2. If each group contains two adults, it would seem reasonable to assume a local density of 10adults/km^2, with the study area covering approximately 1km^2.

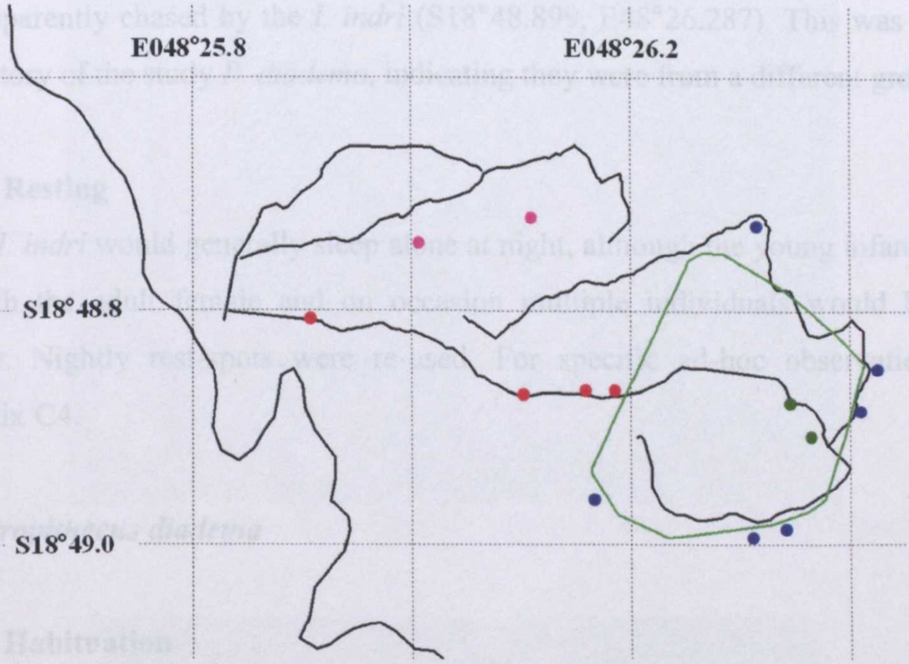


Figure 4.6. Known and approximate locations of non-study group *I. indri* during study period. Study group's home range as determined by the minimum convex polygon method (____). Trails and road indicated by ____. ● White-head group. ● White-headed solitary individuals. ● Black- and white-headed group. ● Approximate positions of non-study group *I. indri* territorial calls heard while following study group.

4.3.1.5. Inter-Group Encounters

One of the guides, Joseph, observed an encounter between two groups of *I. indri* in the Special Reserve in January 2004. An adult male was observed entering the territory of a neighbouring group. The itinerant male was then attacked by the group male and bitten on the leg. He fell from the tree and was initially taken to the park office and after discussion this male was returned to the forest. Previous studies have concluded that the long-calling of *I. indri* serves as territorial defence (Pollock, 1975; 1986). Details of long 'territorial' calls recorded on an ad-hoc basis during the present study are in Appendix C3.

4.3.1.6. Inter-Species Encounters

I. indri appeared to ignore other lemur species. In August (11 August 2005) *Eulemur rubriventer* and *H. g. griseus* were seen in close proximity to *I. indri*. Although the *H. g. griseus* alarm called, *I. indri* ignored them. *H. g. griseus* were also seen close to *I. indri* on 13 February 2005. In September (15 September 2005) the study group of *I. indri* were observed in close proximity to two *P. diadema* at 08:43 (S18°48.891, E48°26.357). At midday, presumably the same two, *P. diadema* were apparently chased by the *I. indri* (S18°48.899, E48°26.287). This was outside the territory of the study *P. diadema*, indicating they were from a different group.

4.3.1.7. Resting

I. indri would generally sleep alone at night, although the young infant would rest with the adult female and on occasion multiple individuals would be seen together. Nightly rest-spots were re-used. For specific ad-hoc observations see Appendix C4.

4.3.2. *Propithecus diadema*

4.3.2.1. Habituation

Two groups of *P. diadema* were observed in the study area prior to habituation. The chosen group appeared to be the only group whose home range overlapped with the study *I. indri*. They were frequently seen while searching for *I. indri* and although not followed were observed for as long as possible. The group was not properly followed until the darting in January. The first *P. diadema* was darted 22 January 2005 and the second 29 January 2005. The group was first followed all day in February (10 February 2005). Subsequent to this one day of following there were no difficulties in following the group to within 3m.

4.3.2.2. Pelage Colour

P. diadema in this study (Figure 4.7 and Figure 4.8) and an individual captured locally and held on the nearby 'Vakona Island' (Figure 4.9) had golden limbs, with black hands and feet. They had white face rings with black on the top of their heads, extending down their necks. Their backs were silvery grey and tails white to golden, with silvery grey to black fronts.

Figure 4.7. Adult *P. diadema* from the study group. Photograph: Mary Blanchard, 25 July 2005.

Figure 4.8. Collared adult male *P. diadema*. Photograph: Mary Blanchard, 01 October 2005.

Figure 4.9. Adult *P. diadema*, Vakona Island. Photographs: Mary Blanchard, 29 August 2005.

4.3.2.3. Group Size, Composition and Dynamics

The study group of *P. diadema* consisted of seven individuals, four males and three females. There were three adult males (the collared adult male, an adult male with no collar and an adult male that was previously collared) and a sub-adult male (collared). There were two adult females and one individual that appeared to be a juvenile. This indicates that this group was polygynandric: multi-male and multi-female, as were 32% of *P. edwardsi* groups at Ranomafana (Pochron and Wright, 2003; Pochron *et al.*, 2004). There was a lack of cohesion observed in the group of *P. diadema* and the group would often disperse throughout the daily period of observation. Details of these observations can be found in Appendix C5.

One of the adult females had an infant, first observed 10 July 2005. The infant was small, clinging low on its mother's stomach and was probably only a day old. We had last followed this group four days previously (06 July 2005) and the infant had not been observed. The infant continued to grow and appeared healthy, becoming more and more active. On 01 October 2005 it was noticed that the infant was missing. There is no evidence as to the cause of this disappearance. Predation is a possibility, although the female displayed no apparent wounds. It is also possible that the infant fell and either died or was abandoned by its mother. We had previously followed the entire group fourteen days previously (17 September 2005). On this day the infant was still on its mother's stomach, and its arms were starting to turn the adult orange.

Figure 4.10. Adult female *P. diadema* carrying her infant on her front. Photograph: Mary Blanchard, 13 August 2005.

A second group of *P. diadema* frequently encountered, contained five adult individuals with a infant being carried by its mother.

4.3.2.4. Density

Ad-hoc observations of other groups of *P. diadema* can be found in Appendix C2. These sightings indicate the presence of at least two more groups of *P. diadema* with territories partly within the study area (Figure 4.11). They also show that *P. diadema* territories overlap, leading to inter-group encounters.

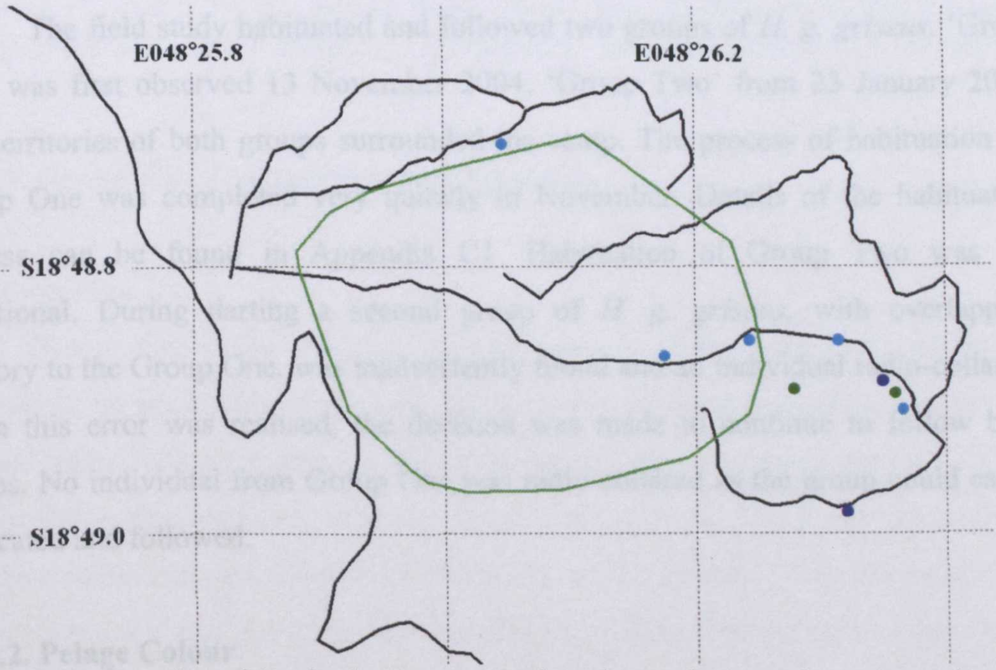


Figure 4.11. Density of *P. diadema* compared to the study group's territory (____). Trails and road indicated by ____. ● Known positions of second group. ● Positions of two *P. diadema* observed and chased by *I. indri*. ● Positions of third group of *P. diadema*.

4.3.2.5. Inter-Group Encounters

Two groups of *P. diadema* were observed in December (21 December 2004). Ten individuals were counted and there appeared to be a dispute although no fighting was observed. In February a guide, Laurent Randrianirina, observed an encounter between the study group and a neighbouring group of *P. diadema*. There was no fighting, but obvious displacement. The territory of the study *P. diadema* either overlapped with the neighbouring group, or boundaries altered during the study period. Both groups were observed slightly south of 'Hapa' trail.

4.3.2.6. Inter-Species Encounters

We observed *P. diadema* in close proximity to other lemur species, when they ignored each other. They were frequently seen near *H. g. griseus*. In June (05 June 2005) we observed a group of six *Eulemur fulvus* (common brown lemur) feeding in the same trees as *P. diadema*.

4.3.3. *Hapalemur griseus griseus*

4.3.3.1. Habituation and Group Choice

The field study habituated and followed two groups of *H. g. griseus*. 'Group One' was first observed 13 November 2004, 'Group Two' from 23 January 2005. The territories of both groups surrounded the camp. The process of habituation for Group One was completed very quickly in November. Details of the habituation process can be found in Appendix C1. Habituation of Group Two was not intentional. During darting a second group of *H. g. griseus*, with overlapping territory to the Group One, was inadvertently found and an individual radio-collared. When this error was realised, the decision was made to continue to follow both groups. No individual from Group One was radio-collared as the group could easily be located and followed.

4.3.3.2. Pelage Colour

Study *H. g. griseus* (Figure 4.12 and Figure 4.13) had grey faces, with a distinctive brown on their heads, extending down their back. Fur on arms, legs and the tail merged into grey, while their fronts were paler.

Figure 4.12. Adult *H. g. griseus* from Group One. Photograph: Mary Blanchard, 25 September 2005.

Figure 4.13. Adult *H. g. griseus* from Group Two feeding on *Cathariostachys madagascariensis* (giant bamboo). Photograph: Mary Blanchard, 19 September 2005.

4.3.3.3. Group Size, Composition and Dynamics

A: Group One

Group One was initially (13 November 2004) comprised of seven individuals: an adult male, three adult females, two juveniles (including one female) and one infant (unknown sex) carried by its mother. This continued until at least 09 January 2005, the last time the entire group was followed. The group consisted of only five individuals on the next observations on 28 January 2005; the infant and juvenile were missing. An adult female disappeared from Group One in June. On 07 June 2005 Group One consisted of five individuals, on 22 June 2005 there were four individuals: an adult male, two adult females and a juvenile female. This composition continued to the end of the field study (25 September 2005). One of the surviving adult females had bad skin and fur on her leg, first noticed in March (20 March 2005).

B: Group Two

Group Two was initially (23 January 2005) comprised of six individuals: an adult male, two adult females, one juvenile female and two infants (unknown sex) carried by their mothers. On 29 May 2005 the collared adult female was missing, she had been present on the previous follow 28 April 2005 (Chapter 10). The group contained the remaining five individuals at the end of the study period (19 September 2005). The collared adult female had an infant when she disappeared. The infant was capable of moving around and feeding on its own, but remained close to its mother. Following her death this infant appeared to remain close to one of the remaining adult females.

4.3.3.4. Density

Details of ad-hoc observations of non-study groups of *H. g. griseus* can be found in Appendix C2. These sightings (Figure 4.14) suggest the presence of at least four additional groups in the study area, and two groups on the opposite side of the road.

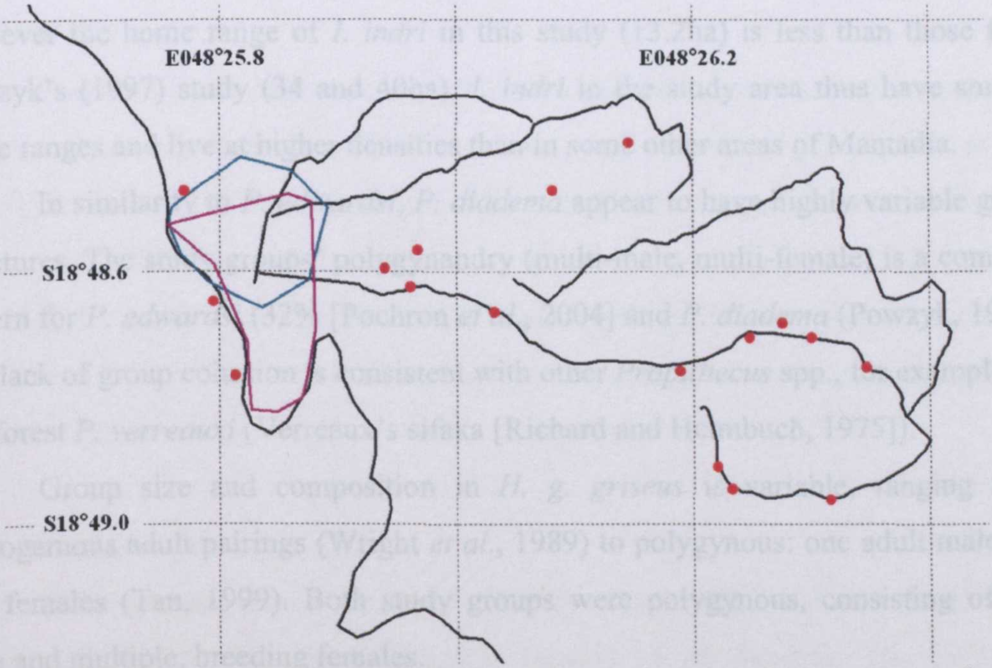


Figure 4.14. Known positions of *H. g. griseus* observed during the study (●), compared to territory of Group One (—) and Group Two (—).Trails and road indicated by —.

Both study groups of *H. g. griseus* border the road and additional groups were observed on the miners' road. Along the miners' road towards Andasibe, *H. g. griseus* could be observed in small, fragmented patches of forest and bamboo including areas bordered by small 'tavy' farms.

4.3.3.5. Inter-Group Encounters

The home range of the two *H. g. griseus* groups overlapped around camp. This allowed for ad-hoc observations of inter-group encounters outside of the study, detailed in Appendix C3. Encounters at territorial boundaries were aggressive.

4.4 Discussion

The group structure and size of *I. indri* appears consistent throughout their range: a monogamous adult breeding pair with offspring. The study group, consisting of an adult pair, sub-adult female and infant did not deviate from this. The controlling factors behind group size are not fully understood, but include predation risk, foraging advantages and avoidance of conspecific threat (Chapman and Pavelka, 2005). There is variation in pelage colour of *I. indri* in Mantadia, although no individuals were all black as are those of the far north.

The approximate density of *I. indri* in the study area (10 adults/km^2) is higher than the density Powzyk (1997) reported in the same reserve (5.3individuals/ km^2). However the home range of *I. indri* in this study (13.2ha) is less than those from Powzyk's (1997) study (34 and 40ha). *I. indri* in the study area thus have smaller home ranges and live at higher densities than in some other areas of Mantadia.

In similarity to *P. edwardsi*, *P. diadema* appear to have highly variable group structures. The study groups' polygynandry (multi-male, multi-female) is a common pattern for *P. edwardsi* (32% [Pochron *et al.*, 2004] and *P. diadema* (Powzyk, 1997). The lack of group cohesion is consistent with other *Propithecus* spp., for example the dry forest *P. verreauxi* (Verreaux's sifaka [Richard and Heimbuch, 1975]).

Group size and composition in *H. g. griseus* is variable, ranging from monogamous adult pairings (Wright *et al.*, 1989) to polygynous: one adult male and two females (Tan, 1999). Both study groups were polygynous, consisting of one male and multiple, breeding females.

The body weight of the *H. g. griseus* (700g), although low, falls within the accepted range for the species (700g to 1kg [Mittermeier *et al.*, 2006]). The body weights of the female *I. indri* (6.7 and 7.3kg) fall well within the accepted range for the species (6 to 9.5 kg [Mittermeier *et al.*, 2006]). However the body weights of the two male *P. diadema* (5.1 and 5.3kg) fall outside the accepted range for the species (6 to 8.5 kg [Mittermeier *et al.*, 2006]).

Chapter 5 Activity Patterns

For any folivorous species, energy budgets will be a core influence, and in turn any consideration of energy budgets requires that we first understand activity patterns, since they are intimately linked to basal metabolic costs. This chapter commences with background on the nature of cathemerality (activity covering both the diurnal and nocturnal phase) in lemurs before discussing the effects of seasonality on activity. Following this, data on activity budgets and cycles, derived from this study, are presented and analysed.

5.1 Introduction

Primate activity patterns can be broadly classified as diurnal (e.g. *Lemur catta* [ring-tailed lemur]: Kappeler, 1997), nocturnal, (e.g. *Avahi laniger* [eastern woolly lemur]: Harcourt, 1987b) or cathemeral (e.g. *Eulemur mongoz* [mongoose lemur]: Curtis *et al.*, 1999). Activity patterns can vary seasonally and even intra-specifically: for example, activity patterns of *Gorilla gorilla beringei* (eastern mountain gorilla) were found to vary between different habitats, depending on varying quality of food resources (Watts, 1988).

5.1.1. Cathemerality

While several lemur species do display cathemeral behaviour (Hill, 2006) cathemerality is rarely seen in primates outside of Madagascar. However, one example of a non-lemurid cathemeral primate is the South American *Aotus azarai* (Azara's night monkey [Fernandez-Duque, 2003; Erkert, 2004]). Suggestions for the causes of *A. azarai* cathemerality range for a lack of diurnal predators (Hill, 2006) to nocturnal light levels: low moonlight conditions leading to increased diurnal activity (Fernandez-Duque, 2003). While Hill (2006) argues that cathemerality usually results from a lowering of the diurnal predation risk, Fernandez-Duque (2003) denies that the predation risk for cathemeral *A. azarai* is lower.

Patterns of cathemerality vary; for example, three types of cathemerality are displayed by *Eulemur* species. In seasonally dry forest *E. mongoz* alternate activity between day and night dependent on the season; while *E. fulvus* (common brown lemur) and *E. rufus* (red-fronted brown lemur), in seasonally dry forest, shift between purely diurnal activity and 24 hour activity depending on the season, and all rainforest *Eulemur* spp. display year-round 24 hour activity (Curtis & Rasmussen, 2002). *Hapalemur griseus alaotrensis* (Alaotran bamboo lemur), found in lakeside reed beds, are active day and night throughout the year (Curtis & Rasmussen, 2002).

Three ecological causes of cathemerality have been suggested: predator avoidance, thermoregulation (Curtis & Rasmussen, 2002) or food availability (Colquhoun, 2006; Hill, 2006). Curtis & Rasmussen (2002) suggested that avoidance of diurnal raptors may be served by adoption of cathemerality, especially in seasonally dry forests, where canopy cover is limited in the dry season. Curtis and Rasmussen (2002) further state that *Eulemur macaco macaco* (black lemur) only feeds in exposed areas with little canopy cover at night, when there is no risk from diurnal raptors. Although the large *Asio madagascariensis* (Madagascar long eared owl) is present in Curtis and Rasmussen's (2002) study sites, its largest known prey is *Avahi laniger* at 1.3kg (Goodman *et al.*, 1993c), whereas *E. m. macaco* weigh up to 2.5kg. No differences were found in food items eaten during the night and day for *E. m. macaco* at Ambato and cathemerality showed no link with seasonal food resources (Colquhoun, 1998).

Hill (2006) suggested that the high frequency of cathemerality among Malagasy lemurs is a consequence of the activity pattern of one unique predator in Madagascar, namely *Cryptoprocta ferox* (fossa), which is also cathemeral, with a peak in activity during the middle of the nocturnal phase (Hawkins, 1998). This pattern contrasts with that in cathemeral lemurs, which tend to have peaks in activity during the crepuscular periods: dawn and dusk (Hill, 2006). Hill (2006) suggests that heightened activity during crepuscular periods avoids predation risk both from diurnal predators and the cathemeral *C. ferox*. Hawkins (1998) found that the cathemeral *E. fulvus* were under-represented in the diet of *C. ferox*, while nocturnal genera (*Microcebus* [mouse lemurs], *Lepilemur* [sportive lemurs], *Phaner* [fork-marked lemurs] and *Mirza* [dwarf lemurs]) and the diurnal *Propithecus verreauxi* (Verreaux's sifaka) were over-represented in relation to their abundance. The cause of cathemerality in *C. ferox* is not understood. If it evolved in response to cathemerality in lemurs, then it follows that *C. ferox* predation cannot also be considered a driving force behind lemur adoption of cathemerality (Hill, 2006) unless this is a case of co-evolution or predator/prey scramble competition.

In winter months, when night-time temperatures are low, nocturnal activity patterns may help conserve energy, although conversely, during periods of high diurnal temperatures, nocturnal activity patterns may serve to minimise heat stress, as with *H. g. alaotrensis* (Curtis & Rasmussen, 2002; Mutschler, 2002).

There are two competing hypotheses to explain the evolution of cathemerality in lemurs. On the one hand it has been suggested that cathemerality is transitional between nocturnal and diurnal behaviour, caused by an evolutionary disequilibrium, itself brought about by human activities and relatively recent extinction of large-bodied lemurs and large aerial predators (van Schaik & Kappeler, 1996); or, on the other hand, cathemerality might be a stable evolutionary strategy (Curtis & Rasmussen, 2002; 2006). Hill (2006) theorises that the crepuscular period, although safe from predation risk in Madagascar, was not long enough for small bodied *Eulemur* spp. and *Hapalemur* spp. to conduct all essential activity, so that they expanded activity into the diurnal or nocturnal phases. Hill (2006) continues by arguing that cathemerality could be the ancestral state for both *Eulemur* and *Hapalemur*, the diurnal lifestyle presently exhibited by *Hapalemur* being a recent adoption, associated with a reduction in the risk of predation from diurnal raptors.

Visually, *Hapalemur* spp. have adaptations both for diurnal and nocturnal living. The retina of *Hapalemur* spp. has a distinct *area centralis* (the point at which the maximum spatial resolution is achieved), an adaptation for diurnal vision found in species which require resolution of fine detail but also retains a tapetum, an adaptation for nocturnal vision (high visual sensitivity [Oyster, 1999]). An examination of eye morphology in *Eulemur* spp. found they have corneal size comparable to other cathemeral mammals, and intermediate in size between those of diurnal and nocturnal mammals (Kirk, 2006). Kirk (2006) therefore concluded that the cathemerality of *Eulemur* spp. is an ancient adaptation, present in the last common ancestor of the genus, approximately 8 to12 million years ago.

If predator behaviour were, as Curtis and Rasmussen (2002) suggest, a major influence on the activity patterns of Malagasy lemurs, we would thus expect that: **Hypothesis 5.1: *I. indri* and *P. diadema* as larger bodied folivores will be diurnal; *H. g. griseus* as a much smaller folivore will be cathemeral.**

5.1.2. Seasonal Effects on Activity

We know from Powzyk (1997) at Mantadia and Britt *et al.* (2002) at Betampona that *I. indri* and *P. diadema* as inhabitants of mid-montane Eastern rainforest are subject to strong seasonal influences. Seasonality has been linked with day length, ambient temperature, humidity, precipitation and food abundance (Morland, 1993; Wright, 1999). Mutschler (2002) for example found a relationship between temperature and activity for *H. g. alaotrensis*: low levels of activity occurred during the hottest time of the day, with increased periods of activity at night in the hot, wet season. Powzyk (1997) found for *Indri* that the period of daily activity was correlated positively with maximum temperature as well as hours of daylight, although a negative correlation was also found with rainfall.

Separating effects is difficult, as day length is inextricably linked to temperature and humidity, which in part control plant growth and therefore food abundance. Erkert and Kappeler (2004) examined environmental controls of activity in *P. verreauxi* in Kirindy, southwest Madagascar. Although in many endothermic species periods of activity match the hours of daylight (Daan & Aschoff, 1975), Erkert and Kappeler (2004) found that although activity periods did decrease with decreasing hours of daylight, the pattern was not stable. Thus from the above we can expect that: **<u>Hypothesis 5.2</u>: *I. indri*, *P. diadema* and *H. g. griseus* will be more active in summer months (long hours of daylight) compared to winter months (short hours of daylight)** and **<u>Hypothesis 5.3</u>: the start and end of the active period will run parallel to sunrise and sunset for the diurnal *I. indri* and *P. diadema*** and assuming that the species act primarily as to conserve energy, while time taken to eat food is a constant, it is logical that we should expect that: **<u>Hypothesis 5.4</u>: for *I. indri*, *P. diadema* and *H. g. griseus* resting (during the active period) will increase in the austral winter, when availability of good-quality food should be relatively low, while travelling and indeed feeding will proportionately decrease.**

5.2. Methods

5.2.1. Field Methods

Data required for analysis of activity patterns were collected by Sabine Day using continuous focal-animal sampling (Altmann, 1974), the aim being to follow a single individual throughout the daily observation period. If an individual was lost, observation continued on the physically-closest alternative animal. Records were made on whether focal animals were participating in one of three activities: feed, rest or travel (Table 5.1). Records were made every time the focal animal changed activity. The time at the start and end of each bout was recorded as: hour; minute; seconds.

Table 5.1. Schedule of observations conducted by Day on feeding behaviour.

1	Date
2	Species and focal animal identification
3	Time at start of activity
4	Time at end of activity
5	Activity: rest, travel, feed

5.2.2. Statistical Methods

The Pearson correlation coefficient has previously been used for determining environmental correlations of activity in *P. verreauxi* (Erkert & Kappeler, 2004); however climatic variables and hours of daylight have non-normal distributions (Chapter 2). It was decided that the non-parametric equivalent, Spearman's rank order correlation coefficient (ρ), was more suitable for assessing the strength of correlations between activity period and environmental factors (hours of daylight, temperature and rainfall) in *I. indri* and *P. diadema*. A correlation is deemed significant when $\rho \leq 0.05$. One-way ANOVAs (ANalysis Of VAriance [F]) were used to examine relationships of activity between species. One-way ANOVA is a parametric test, robust to departures from normality and can be used with even considerable kurtosis and skewness (Zar, 1999). Significance is accepted when $p \leq 0.05$.

Only data from complete day-long follows (i.e. when observations were from nightly resting period to nightly resting period) are included. Spearman's correlation is also used to examine the relationship between the time *I. indri* and *P. diadema* spend in each activity in the daily active periods and individual environmental factors such as hours of daylight, temperature and rainfall and the total length, in hours, of the active period. Again only data from full days' observation are included. Rest periods are included only when they occurred between the first and last feeding or travelling bout, so as not to include periods of night-time resting.

5.3. Results

5.3.1. *Indri indri*

5.3.1.1. Schedule of Observations

I. indri were followed on 25 days throughout 2005. Activity-pattern data, totalling 173 hours, was only collected on 23 of these days due to observer absence. For 18 of these days activity was from nightly rest to nightly rest (Table 5.2).

Although no nocturnal observations were conducted, it is reasonable to assume that *I. indri* are a purely diurnal species. They were frequently observed while collecting GPS readings on the day following observations occupying the same rest-spots (Table 5.2). It must be remembered that an absence of a record of *I. indri* in the same rest spot the following day does not mean that they were not followed to final rest, but that GPS readings were not collected on the subsequent day or not collected early enough to observe the *I. indri*.

Table 5.2. Observation days for *I. indri*, including time at the start and end of observations; whether or not they were resting at these times, and if they were seen in the same rest spot the following day. Dates are from 2005.

Date	Time at start	Resting?	Time at end	Resting?	Next day?
05 February	11:12	No	17:01	Yes	Yes 07:15
13 February	07:10	Yes	17:02	Yes	No
20 February	09:31	No	16:22	No	No
02 March	08:05	Yes	17:03	No	Yes
09 March	07:45	Yes	16:46	Yes	No
23 March	09:15	No	16:31	Yes	No
31 March	08:14	Yes	16:00	Yes	No
08 April	08:10	Yes	15:53	Yes	Yes at 09:00
16 April	11:35	No	16:15	Yes	No
22 April	08:00	Yes	16:00	Yes	Yes at 08:40
18 May	09:15	Yes	15:20	Yes	No
31 May	07:28	Yes	15:00	Yes	Yes
09 June	08:53	Yes	14:53	Yes	Yes at 08:05
10 June	08:05	Yes	15:10	Yes	No
17 June	08:17	Yes	15:03	Yes	Yes
04 July	07:49	Yes	14:35	Yes	Yes at 08:50
12 July	08:00	Yes	15:35	Yes	No
21 July	08:15	Yes	14:55	Yes	Yes at 08:45
30 July	08:20	Yes	15:18	Yes	Yes at 09:12
11 August	08:10	Yes	15:15	Yes	Yes at 08:55
30 August	08:20	Yes	16:02	Yes	No
05 September	07:55	Yes	14:40	Yes	No
15 September	07:30	Yes	14:40	Yes	Yes
23 September	07:40	Yes	15:22	Yes	No
03 October	08:15	No	16:17	Yes	No

5.3.1.2. Hours of Daily Activity

For the 18 days for which there are data spanning from rest to rest, *I. indri* were active between 4.7 and 9.1 hours of daylight (Figure 5.1), the duration of activity (defined as being from the first to the last 'activity' [feed or travel] recorded each day) being longer during summer than in winter.

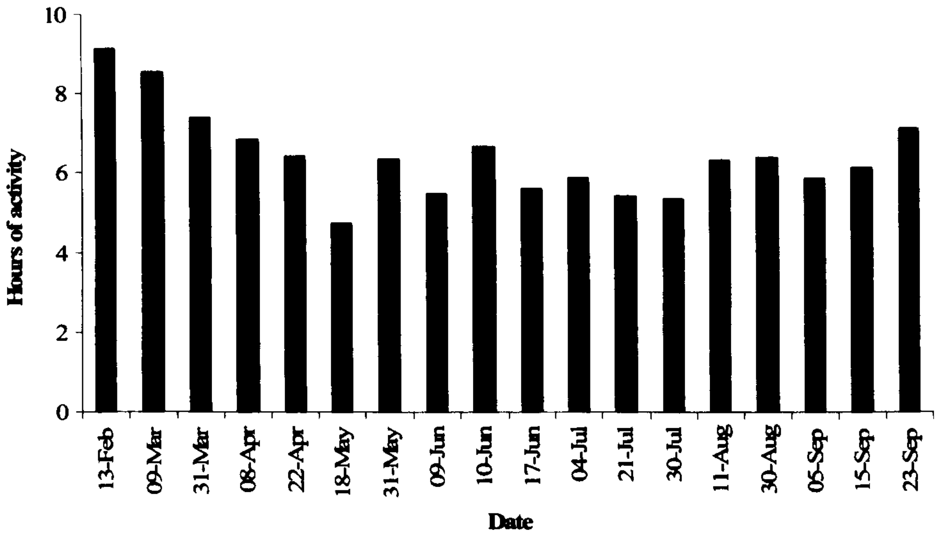


Figure 5.1. Hours of activity for *I. indri* for each day of observation which spanned from nightly rest to nightly rest, dates from 2005.

5.3.1.3. Environmental Correlations of Total Daily Activity Period

The strongest correlation, at the 0.01 level (Table 5.3), for the daily activity period for *I. indri* is with the number of hours of daylight ($\rho = 0.669$ [Figure 5.2]): a decrease in the number of hours of daylight correlates with a decrease in the number of hours of activity. Maximum temperature correlates with the activity period at the 0.01 level ($\rho = 0.549$ [Figure 5.3]). There is a weaker correlation ($\rho = 0.504$), significant at the 0.05 level, between minimum temperature and hours of activity. There is no correlation between rainfall and activity period.

Table 5.3. Spearman's rank order correlation co-efficient for hours of activity against maximum and minimum temperature (°C) and rainfall (mm).

	Hours of daylight	Maximum temperature (°C)	Minimum temperature (°C)	Rainfall (mm)
ρ	0.669**	0.549*	0.504*	-0.127
p	0.002	0.018	0.033	0.615
N	18	18	18	18

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

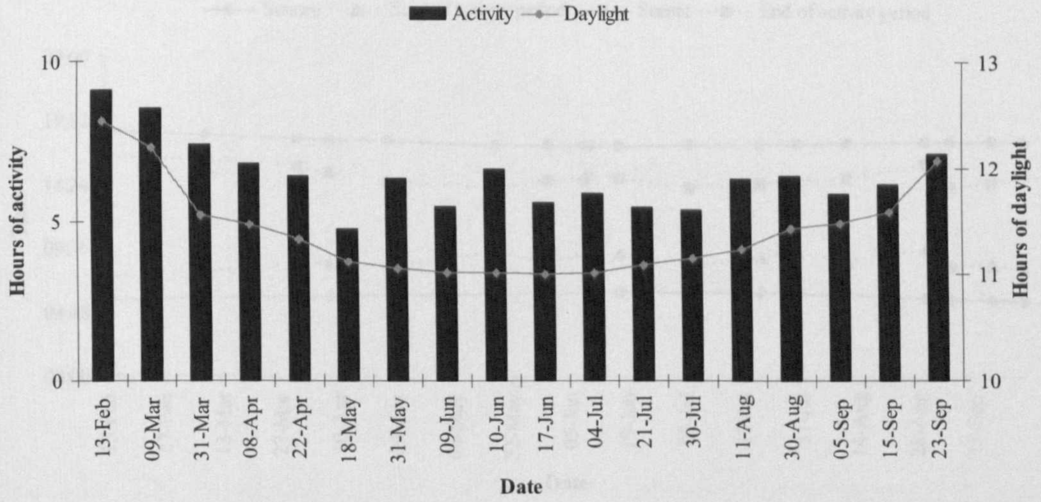


Figure 5.2. Hours of daylight against hours of activity for *I. indri* (2005).

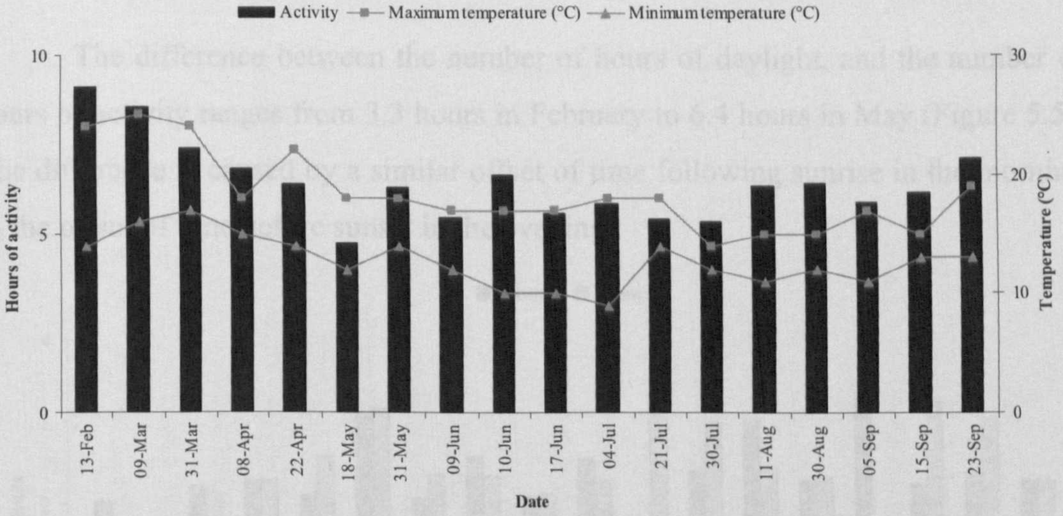


Figure 5.3. Maximum and maximum temperature (°C) against activity period in *I. indri* (2005).

5.3.1.4. Time at Start and End of Activity Compared to Sunrise and Sunset

The time of the beginning of the daily activity period of *I. indri* changes seasonally, following the progression of sunrise (Figure 5.4). The time of cessation of the active period also changes seasonally as sunset become earlier. The time differences between on the one hand sunrise and the start of the active period, and on the other, the end of the active period and sunset do not remain constant throughout the year.

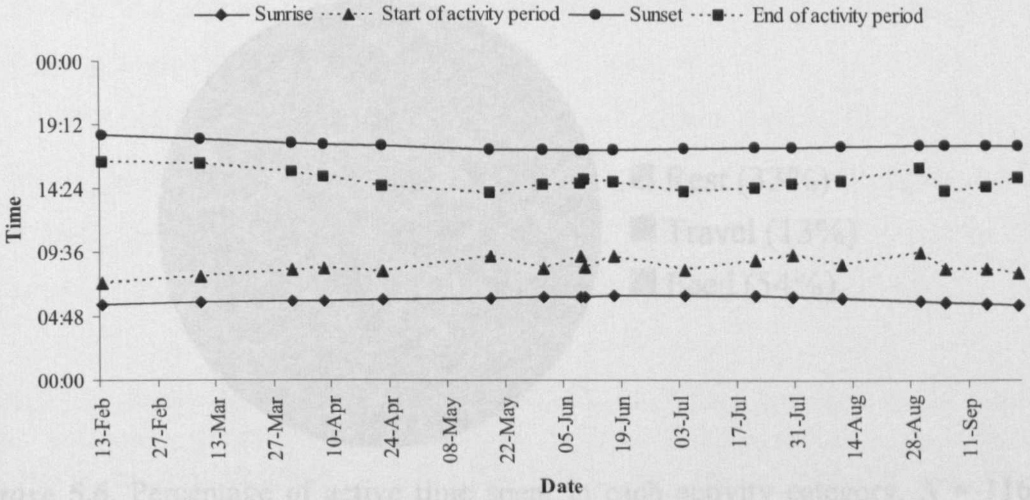


Figure 5.4. A comparison of the daily start and end of the activity period of *I. indri* with sunrise and sunset times (2005).

The difference between the number of hours of daylight, and the number of hours of activity ranges from 3.3 hours in February to 6.4 hours in May (Figure 5.5). The difference is caused by a similar offset of time following sunrise in the morning as the offset of time before sunset in the evening.

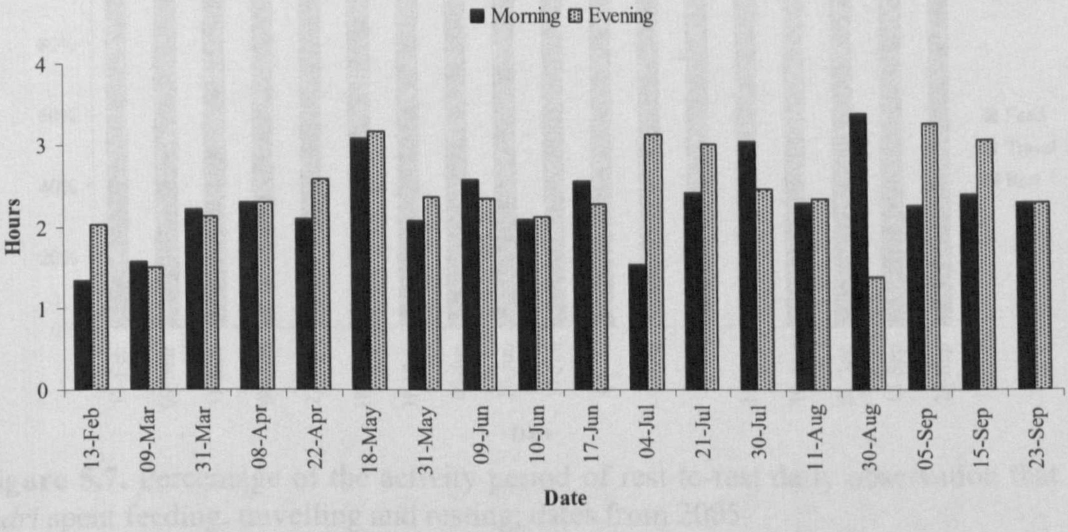


Figure 5.5. Time offset between sunrise and start of activity in the morning and between end of activity and sunset in the evening for *I. indri* (2005).

5.3.1.5. Time Spent in Each Activity

Considering only the daily duration of activity, *I. indri* spent 33% of their time resting, 13% travelling and 54% feeding (Figure 5.6).

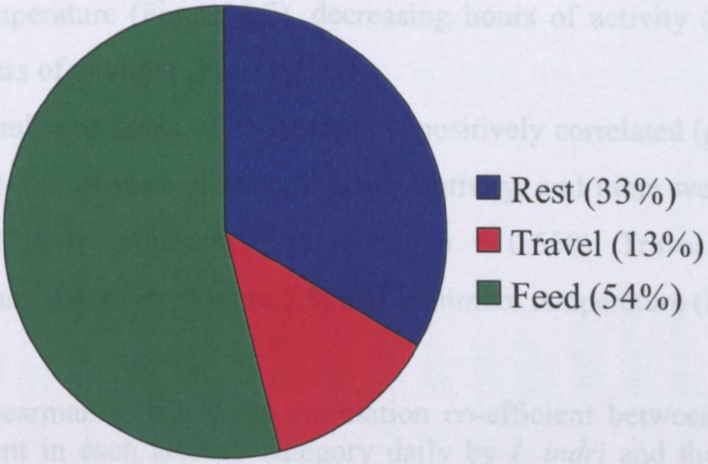


Figure 5.6. Percentage of active time spent in each activity category, N = 116.37 hours.

There appear to be seasonal differences in the percentage of the daily active period *I. indri* spent in each activity (Figure 5.7). The total time spent each day resting decreases in winter months, as does the time spent travelling, while the time spent feeding increases.

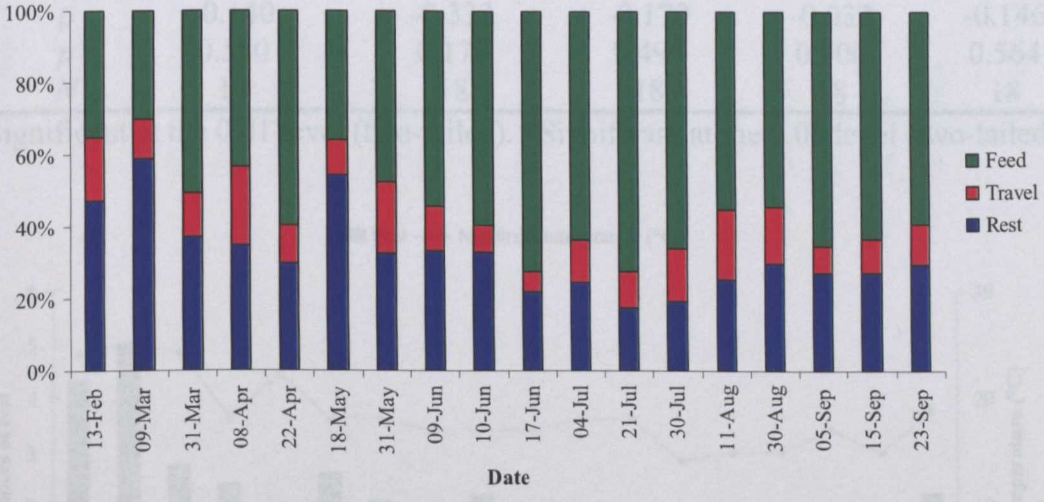


Figure 5.7. Percentage of the activity period of rest-to-rest daily observation that *I. indri* spent feeding, travelling and resting, dates from 2005.

5.3.1.6. Correlations of Other Variables with Time Spent in Each Activity

Feeding showed no correlation with any environmental factor recorded (Table 5.4). The time spent resting each day is strongly correlated at the 0.01 level with the maximum daily temperature (ρ = 0.682), hours of daily activity (ρ = 0.719), and at the 0.05 level with the minimum daily temperature (ρ = 0.577) and hours of daylight (ρ = 0.562 [Table 5.4]). The number of hours of daily rest decreases with decreasing temperature (Figure 5.7), decreasing hours of activity (Figure 5.8) and decreasing hours of daylight (Figure 5.9).

The number of hours of daily travel is positively correlated (ρ = 0.620) at the 0.01 level with the number of hours of daily activity; and more weakly at the 0.05 level with the daily minimum temperature (ρ = 0.550). Travel decreases with decreasing hours of activity (Figure 5.8) and minimum temperature (Figure 5.10).

Table 5.4. Spearman's rank order correlation co-efficient between the amount of daily time spent in each activity category daily by *I. indri* and the maximum and minimum daily temperature (°C), rainfall (mm), hours of daily activity and hours of daylight.

		Maximum temperature	**Minimum temperature**	**Rainfall**	**Hours of activity**	**Hours of daylight**
Rest	ρ	0.682**	0.577*	-0.165	0.719**	0.562*
	p	0.002	0.012	0.512	0.001	0.015
	N	18	18	18	18	18
Travel	ρ	0.264	0.550*	0.123	0.620**	0.466
	p	0.290	0.018	0.627	0.006	0.051
	N	18	18	18	18	18
Feed	ρ	-0.140	-0.332	-0.170	-0.032	-0.146
	p	0.580	0.178	0.499	0.900	0.564
	N	18	18	18	18	18

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

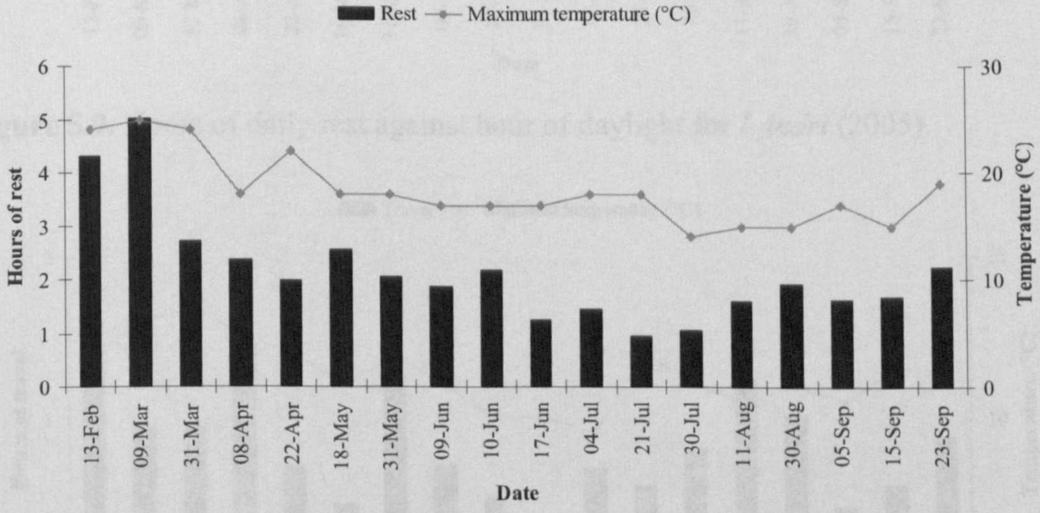


Table 5.5. Hours of daily rest against maximum temperature (°C) for *I. indri* (2005).

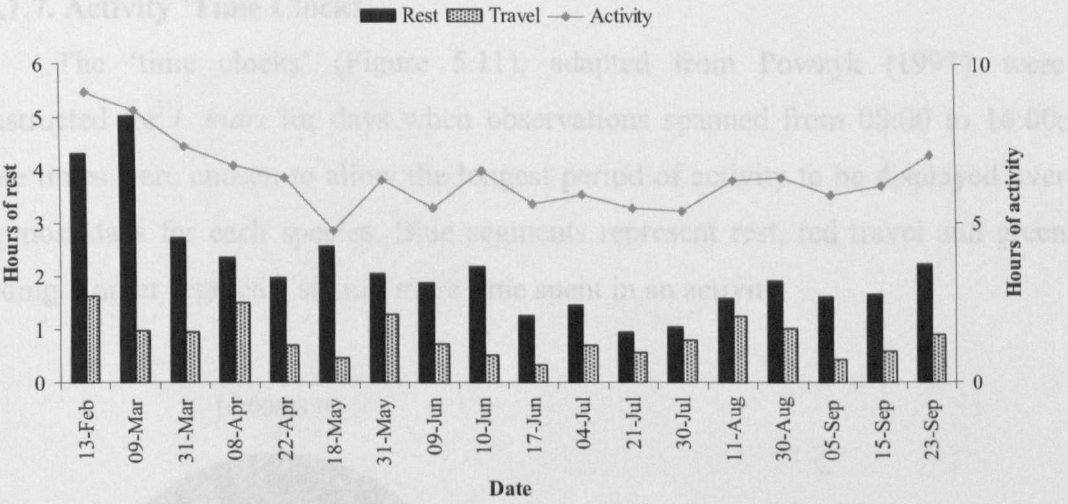


Figure 5.8. Hours of daily rest and travel against hours of daily activity for *I. indri* (2005).

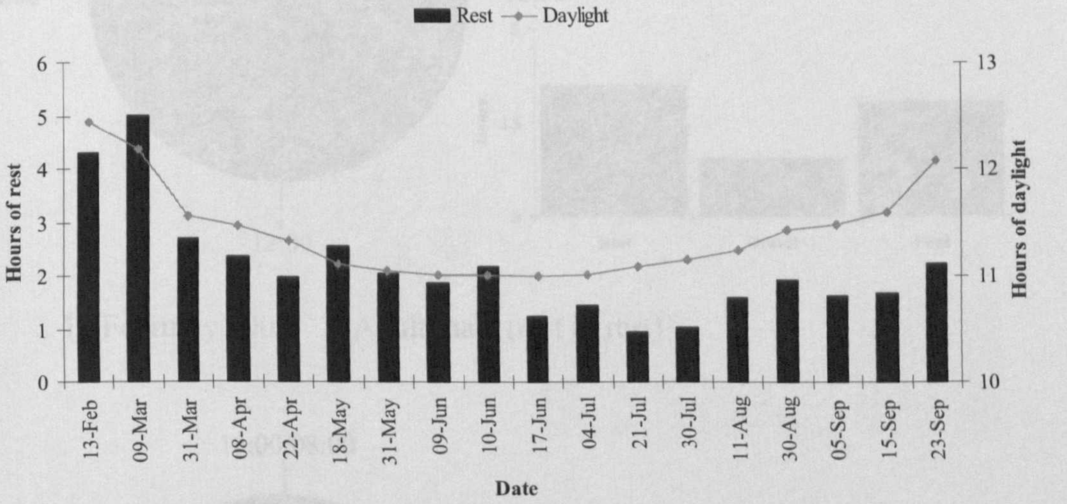


Figure 5.9. Hours of daily rest against hour of daylight for *I. indri* (2005).

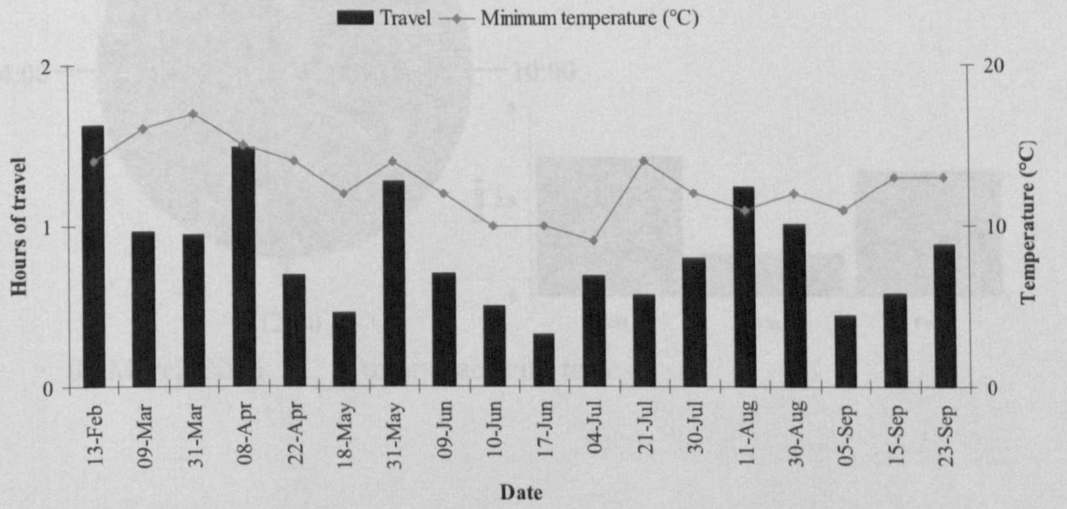
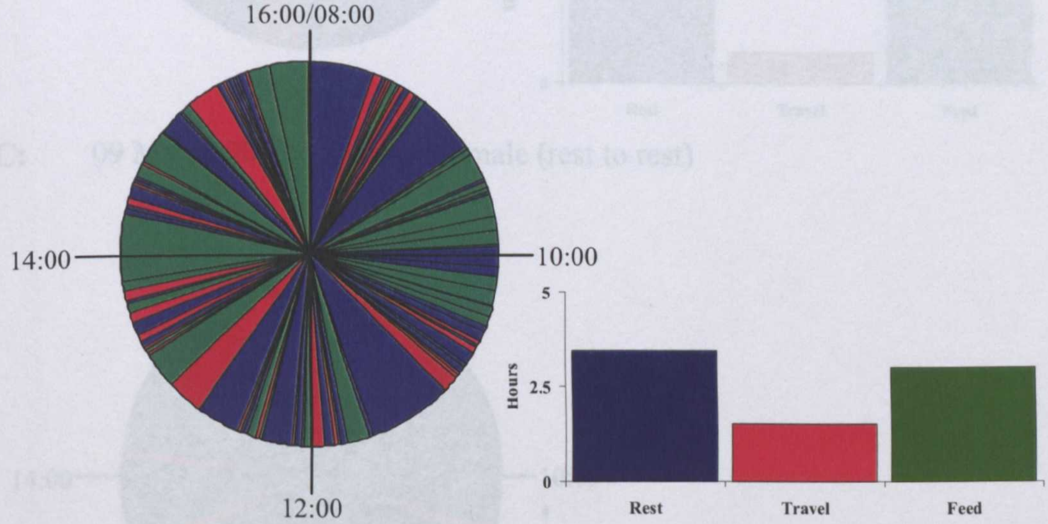


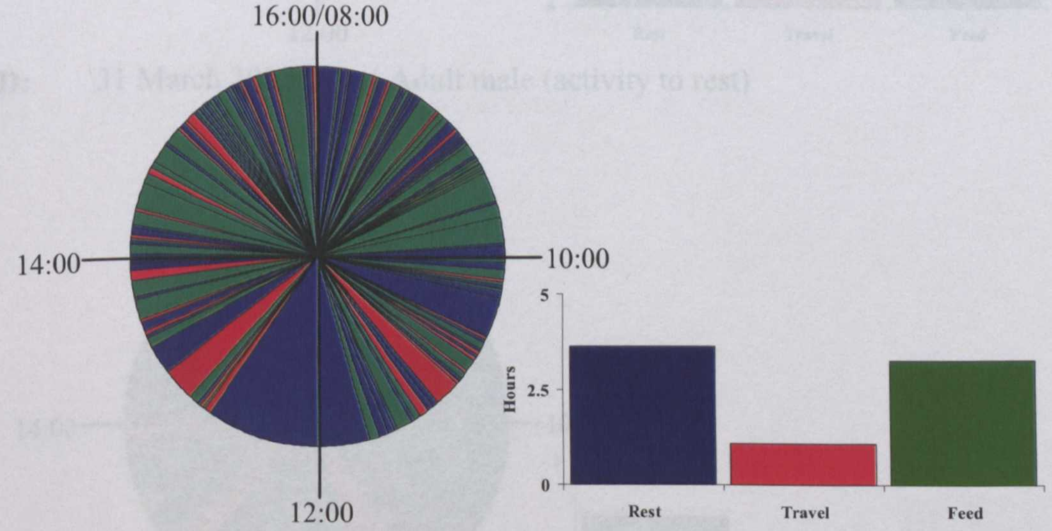
Figure 5.10. Hours of daily travel plotted against minimum daily temperature (°C) for *I. indri* (2005).

5.3.1.7. Activity 'Time Clocks'

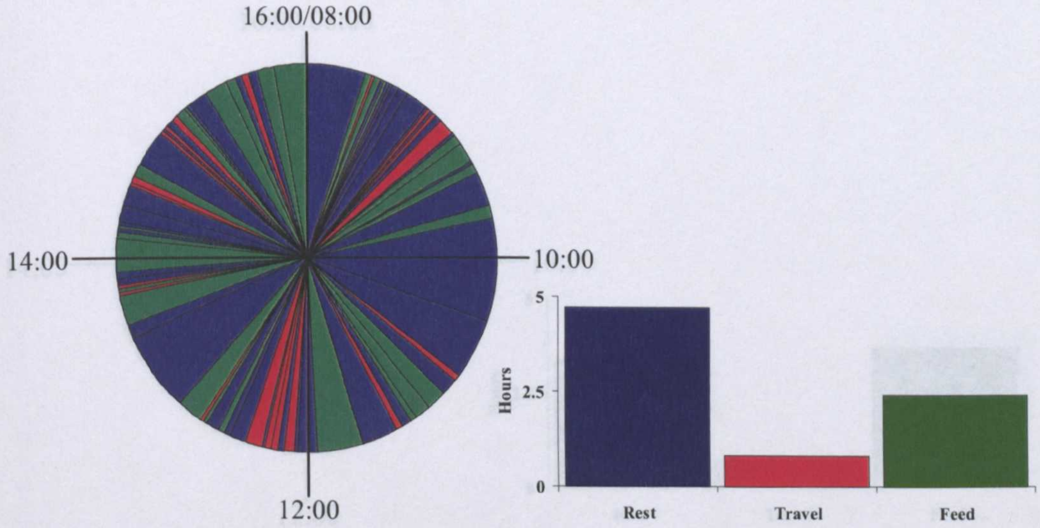
The 'time clocks' (Figure 5.11), adapted from Powzyk (1997), were constructed for *I. indri* for days when observations spanned from 08:00 to 16:00; these times were chosen to allow the longest period of activity to be displayed over the most days for each species. Blue segments represent rest, red travel and green feeding. Larger segments signify more time spent in an activity.



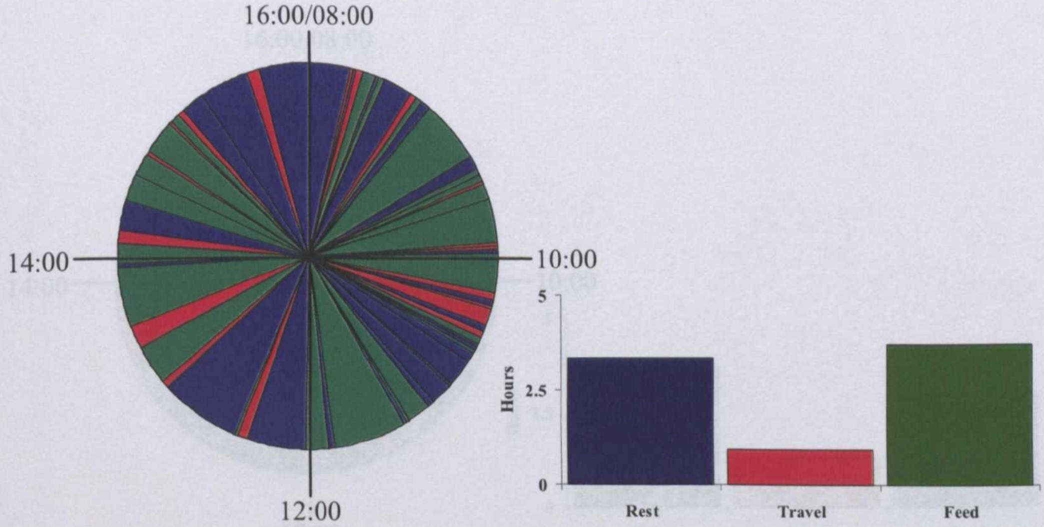
A: 13 February 2005: Adult male (rest to rest)



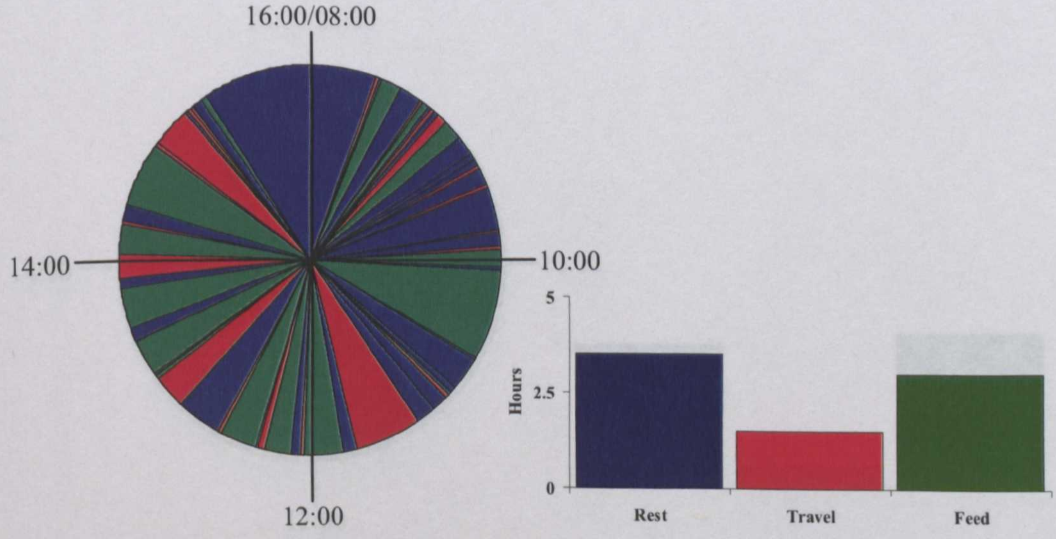
B: 02 March 2005: Infant (activity to rest)



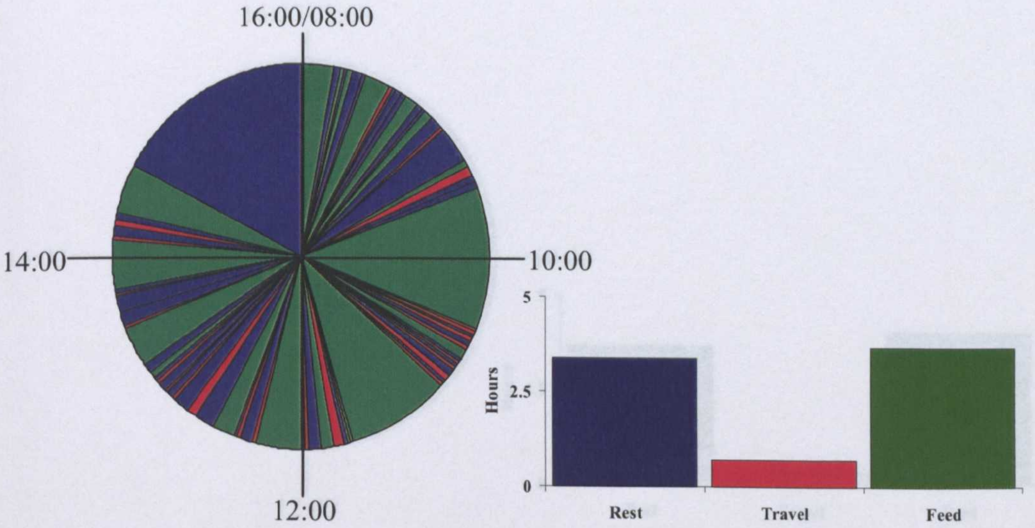
C: 09 March 2005: Adult male (rest to rest)



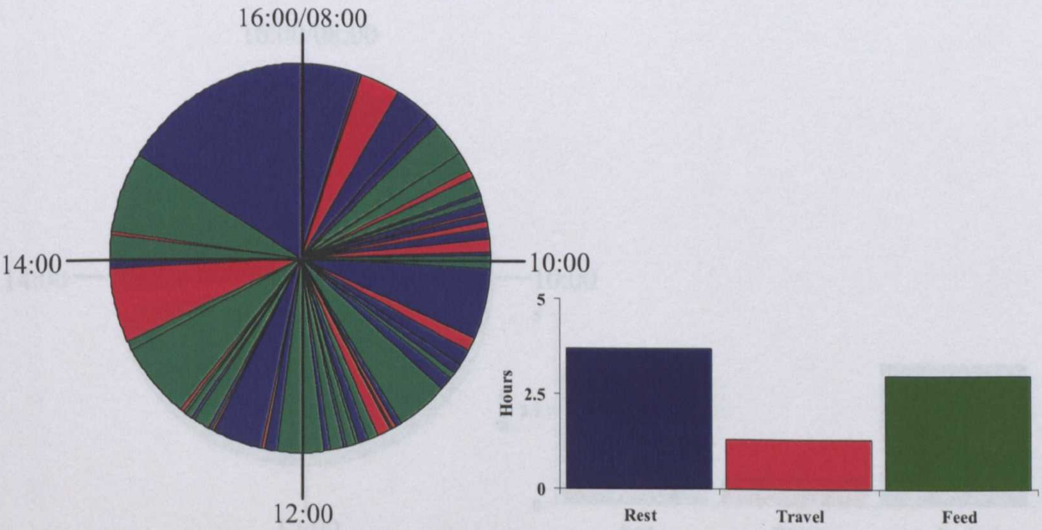
D: 31 March 2005: Adult male (activity to rest)



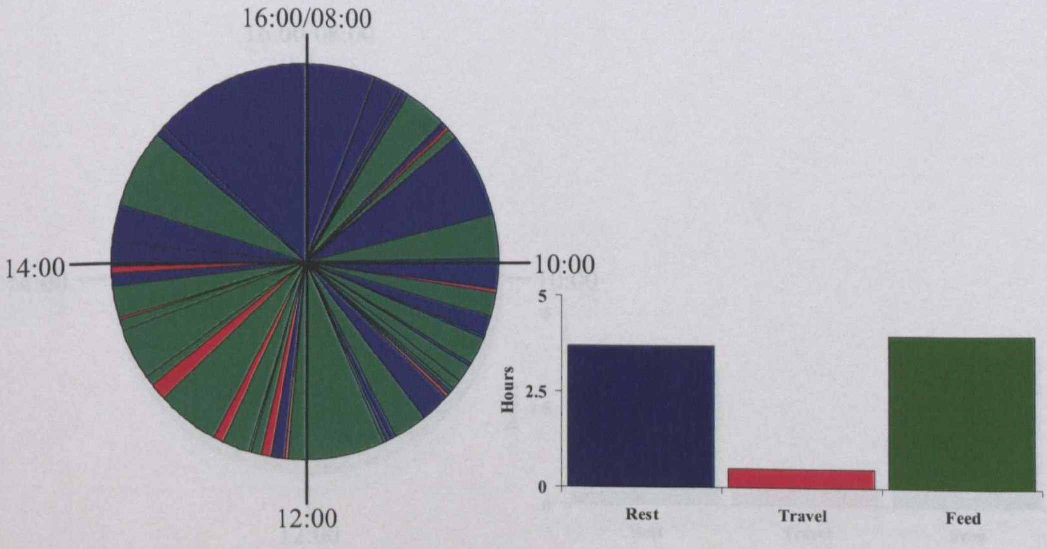
E: 08 April 2005: Sub-adult female (rest to rest)



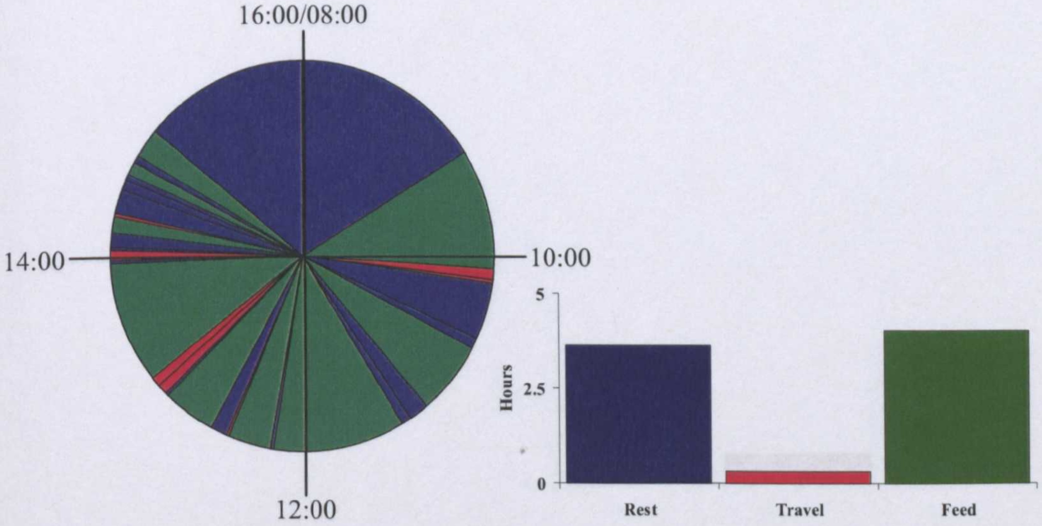
E: 22 April 2005: Adult female (activity to rest)



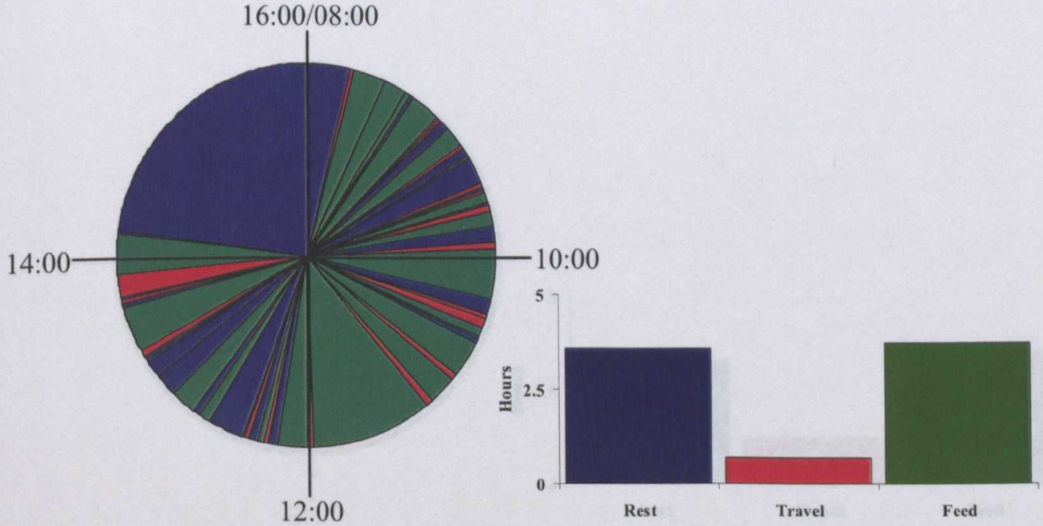
F: 31 May 2005: Sub-adult male (rest to rest)



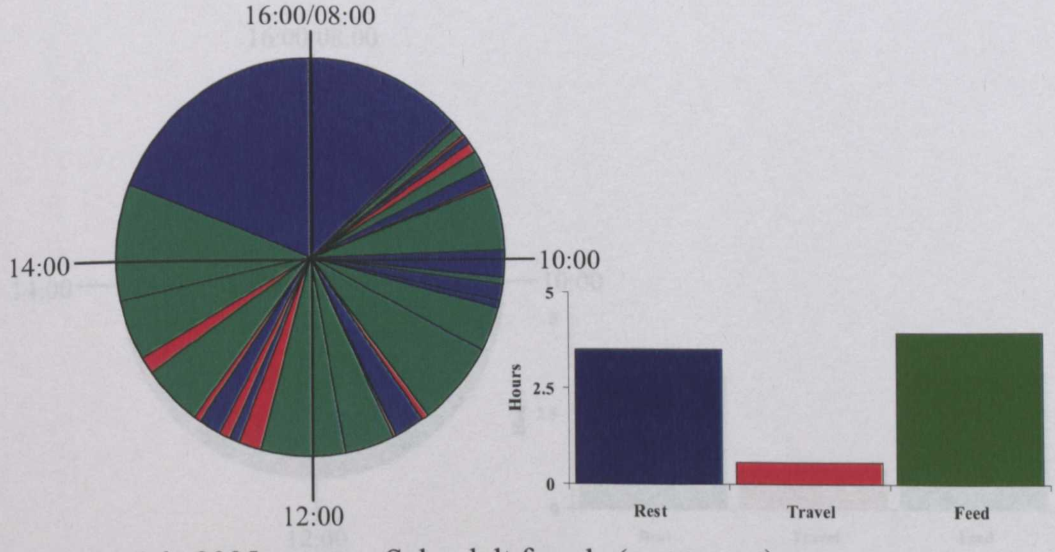
G: 10 June 2005: Sub-adult female (rest to rest)



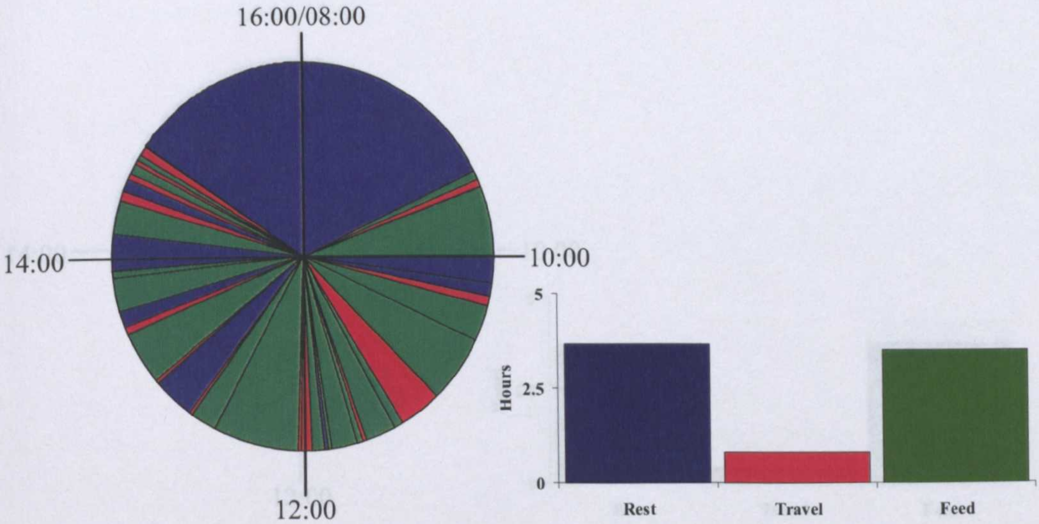
H: 17 June 2005: Sub-adult female (rest to rest)



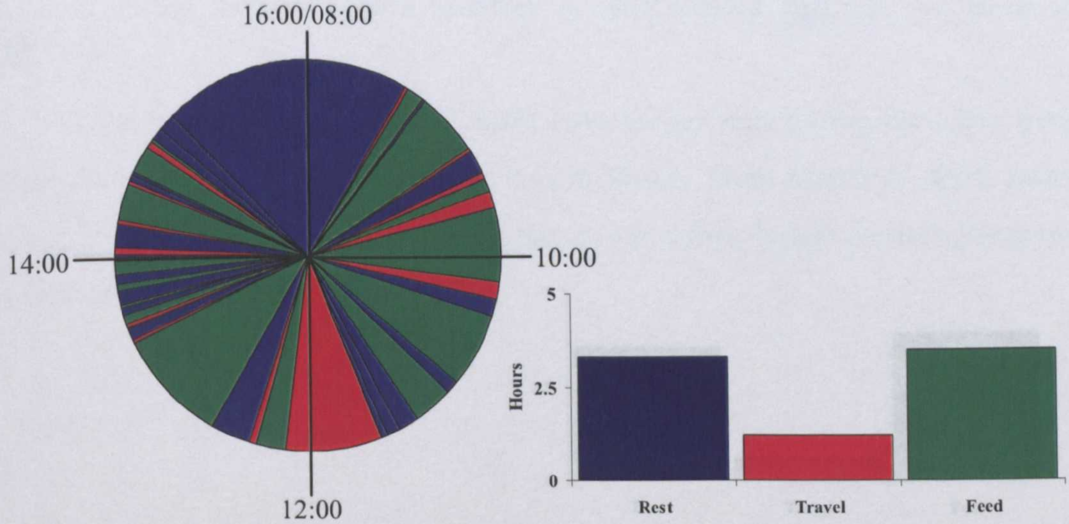
I: 04 July 2005: Adult male (rest to rest)



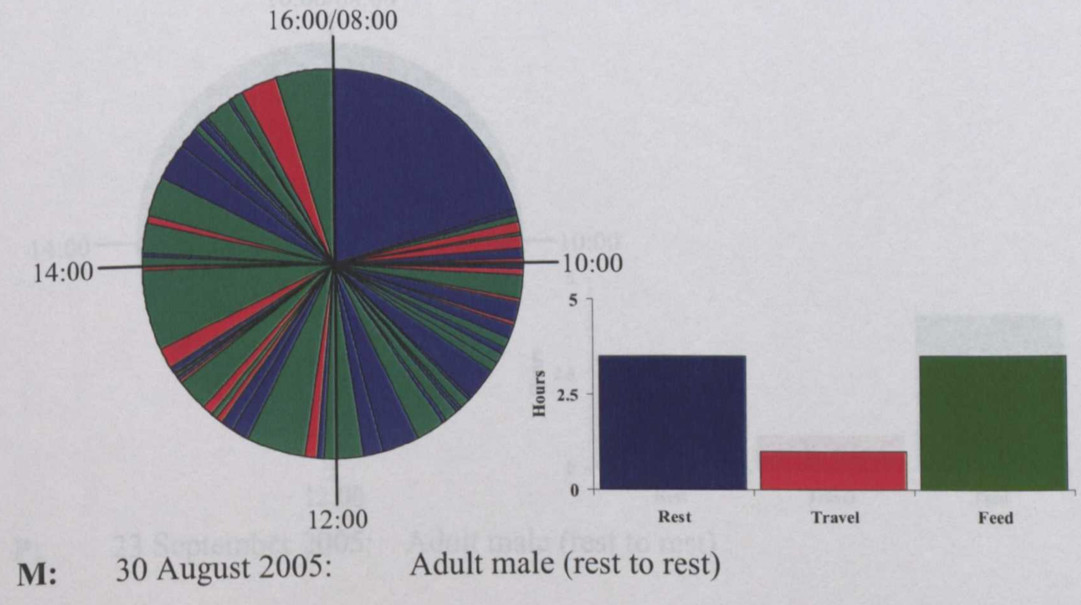
J: 21 July 2005: Sub-adult female (rest to rest)



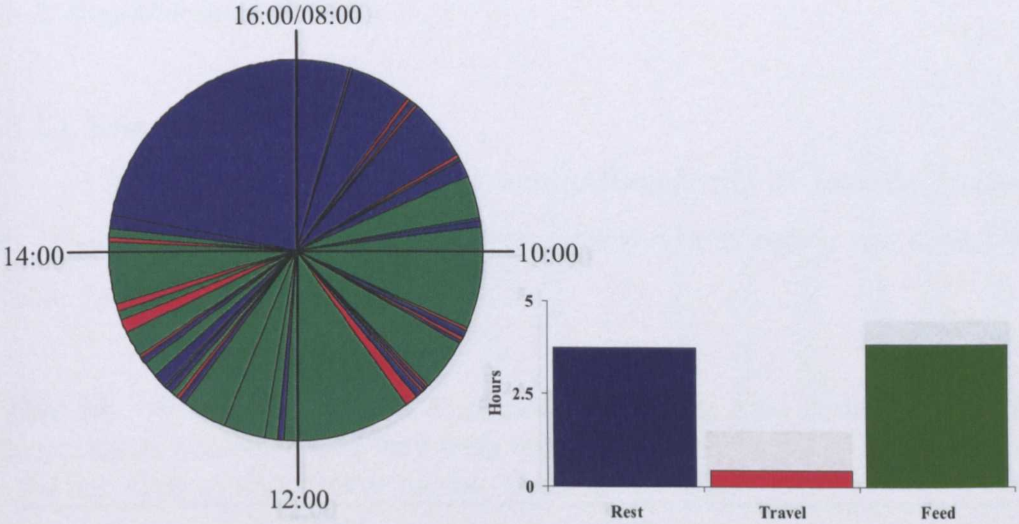
K: 30 July 2005: Adult male (rest to rest)



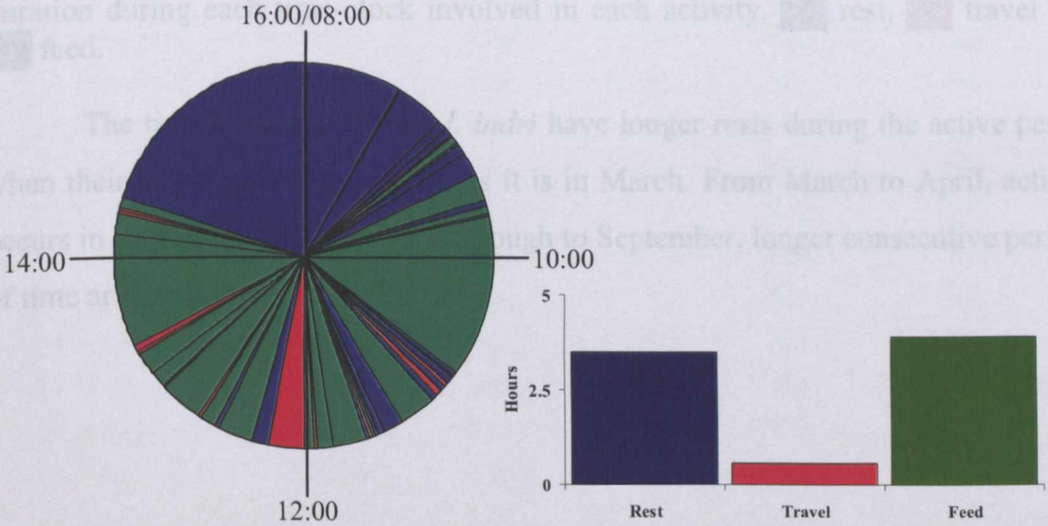
L: 11 August 2005: Sub-adult female (rest to rest)



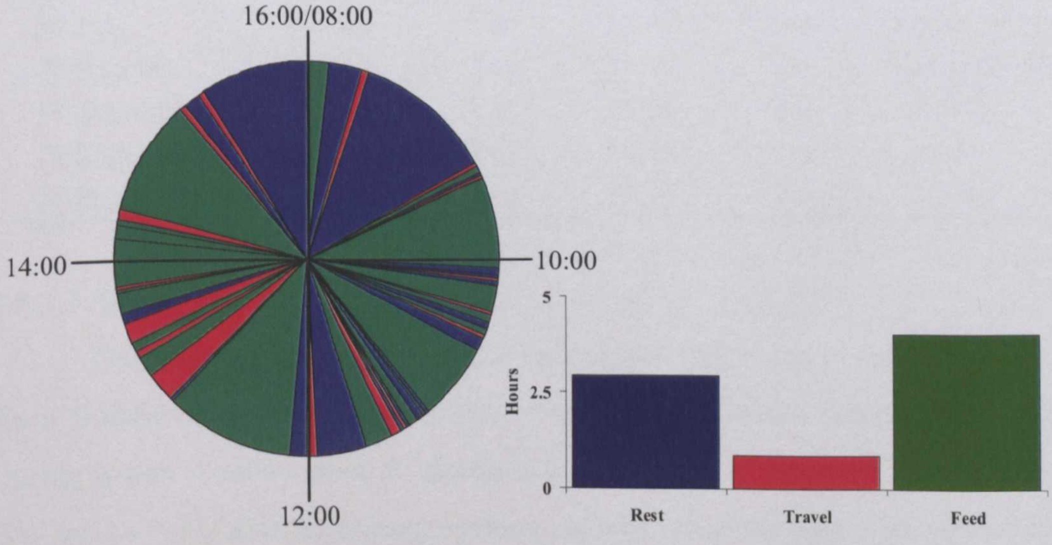
M: 30 August 2005: Adult male (rest to rest)



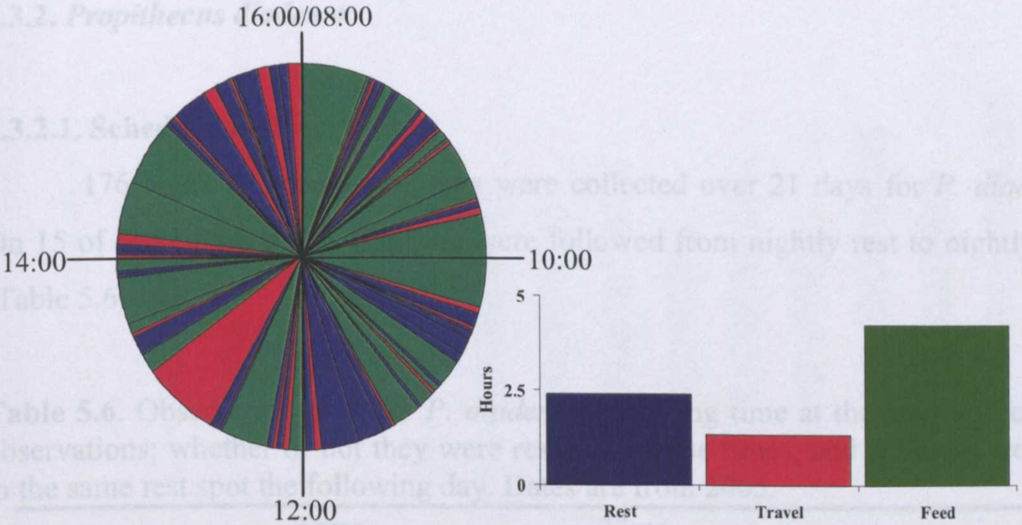
N: 05 September 2005: Adult male (rest to rest)



O: 15 September 2005: Sub-adult female (rest to rest)



P: 23 September 2005: Adult male (rest to rest)



Q: 03 October 2005: Sub-adult female (activity to rest)

Figure 5.11. A-Q: Time clocks for *I. indri* from 08:00 to 16:00, with the total duration during each time-clock involved in each activity. 🟦 rest, 🟥 travel and 🟩 feed.

The time clocks show that *I. indri* have longer rests during the active period when their active period is longest, as it is in March. From March to April, activity occurs in shorter bursts. From June through to September, longer consecutive periods of time are spent in each activity.

5.3.2. *Propithecus diadema*

5.3.2.1. Schedule of Observations

176 hours of behavioural data were collected over 21 days for *P. diadema*. On 15 of these days the *P. diadema* were followed from nightly rest to nightly rest (Table 5.6).

Table 5.6. Observation days for *P. diadema*, including time at the start and end of observations; whether or not they were resting at these times, and if they were seen in the same rest spot the following day. Dates are from 2005.

Date	Time start	Resting?	Time end	Resting?	Next day?
10 February	08:10	Yes	16:45	Yes	No
15 February	07:15	Yes	14:08	No	No
26 February	07:05	Yes	17:07	Yes	No
04 March	07:59	No	16:31	No	No
11 March	08:05	Yes	16:43	No	No
26 March	07:35	Yes	17:00	Yes	No
02 April	07:33	No	17:45	Yes	No
10 April	07:20	Yes	17:21	Yes	No
17 April	08:08	No	17:31	No	No
24 April	07:51	No	17:00	No	No
27 May	07:47	Yes	16:46	Yes	Yes at 09:50
05 June	07:34	Yes	15:50	Yes	No
12 June	08:58	Yes	16:05	Yes	No
19 June	07:57	Yes	15:47	Yes	Yes
06 July	07:57	Yes	15:55	Yes	No
10 July	09:50	Yes	16:00	Yes	Yes at 07:30
24 July	08:23	Yes	16:47	Yes	Yes at 09:10
03 August	07:30	Yes	16:10	Yes	Yes at 09:30
17 September	08:15	Yes	17:20	Yes	No
27 September	07:45	Yes	16:18	Yes	No
01 October	07:30	Yes	17:22	Yes	No

5.3.2.2. Hours of Daily Activity

The active period of *P. diadema* ranged from 5.2 hours in July to 9.7 hours in April (Figure 5.12); that is, active time was shorter in winter compared to summer. During winter months, when *P. diadema* were frequently followed from rest to rest, they were strictly diurnal. During summer months the group was often left feeding at dusk, suggesting that they were active at dusk and probably at dawn.

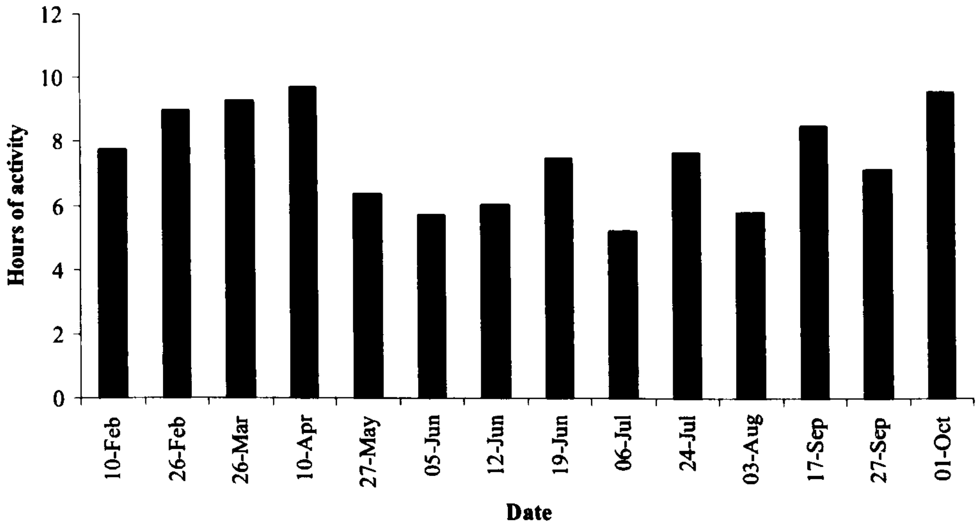


Figure 5.12. Hours of activity for *P. diadema* for each day of observation which spanned from nightly rest to nightly rest (2005).

5.3.2.3. Environmental Correlations of Total Daily Activity Time

There is a strong positive correlation at the 0.05 level (ρ = 0.637 [Table 5.7]) between the active period and hours of daylight (Figure 5.13). The number of hours of activity is more strongly (ρ = 0.690) correlated at the 0.01 level with the maximum daily temperature (Figure 5.14): shorter activity periods are found on colder days. There is no correlation between the active period and minimum temperature. There is a negative correlation at the 0.05 level (ρ = -0.763) between rainfall and period of activity: activity greater on days of lower rainfall (Figure 5.15).

Table 5.7. Spearman's rank order correlation coefficient for hours of daylight, maximum and minimum temperature (°C) and rainfall (mm) against the number of hours of activity of *P. diadema* each day of full observation.

	Hours of Daylight	**Maximum temperature**	**Minimum temperature**	**Rainfall**
ρ	0.637*	0.690**	0.355	-0.763*
p	0.014	0.006	0.213	0.014
N	14	14	14	14

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

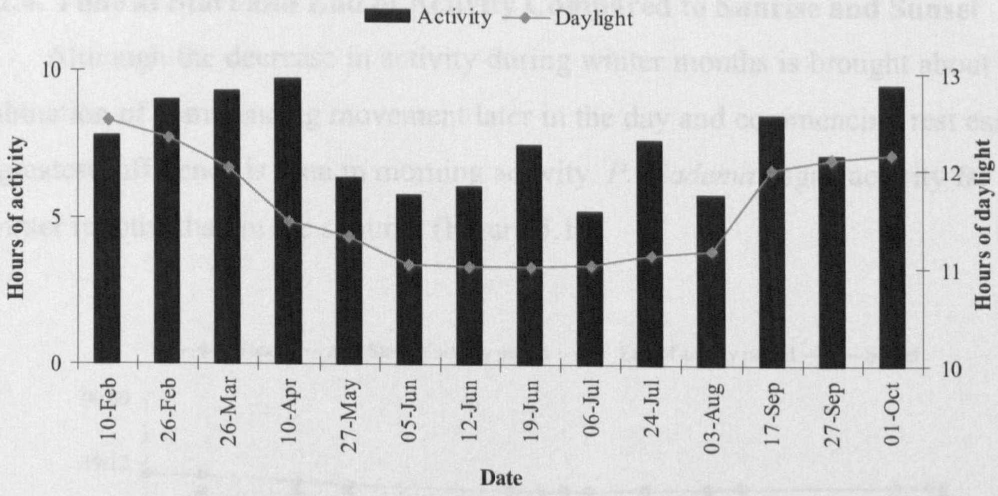


Figure 5.13. Hours of activity of *P. diadema* plotted against hours of daylight (2005).

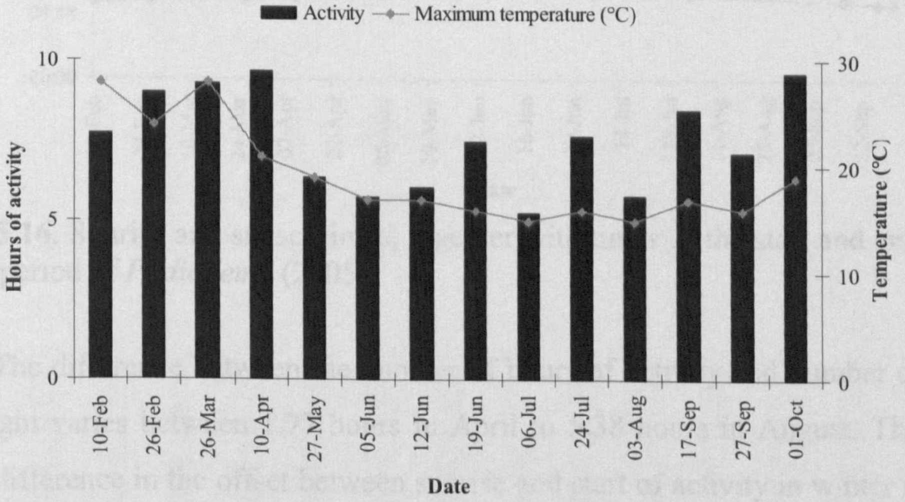


Figure 5.14. Hours of activity of *P. diadema* plotted against daily maximum temperature (°C [2005]).

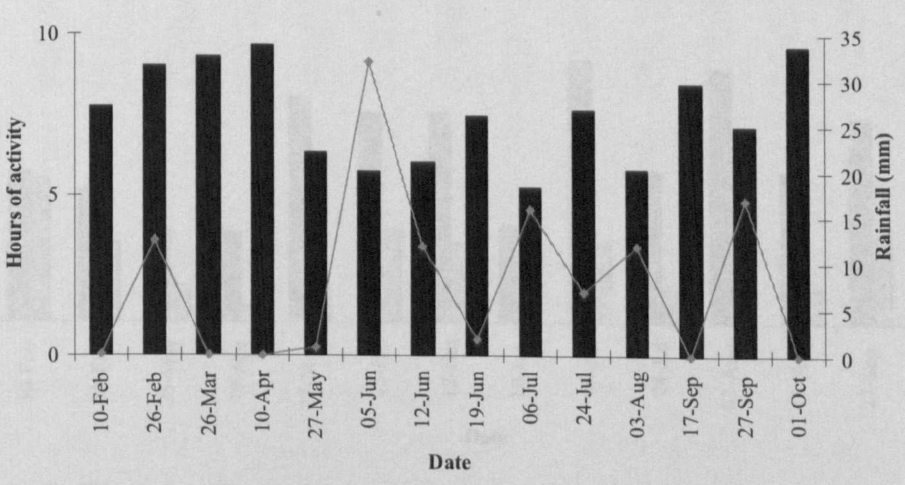


Figure 5.15. Hours of activity of *P. diadema* plotted against daily rainfall (mm[2005]).

5.3.2.4. Time at Start and End of Activity Compared to Sunrise and Sunset

Although the decrease in activity during winter months is brought about by a combination of commencing movement later in the day and commencing rest earlier, the greatest difference is seen in morning activity. *P. diadema* began activity far later in winter months than in the summer (Figure 5.16).

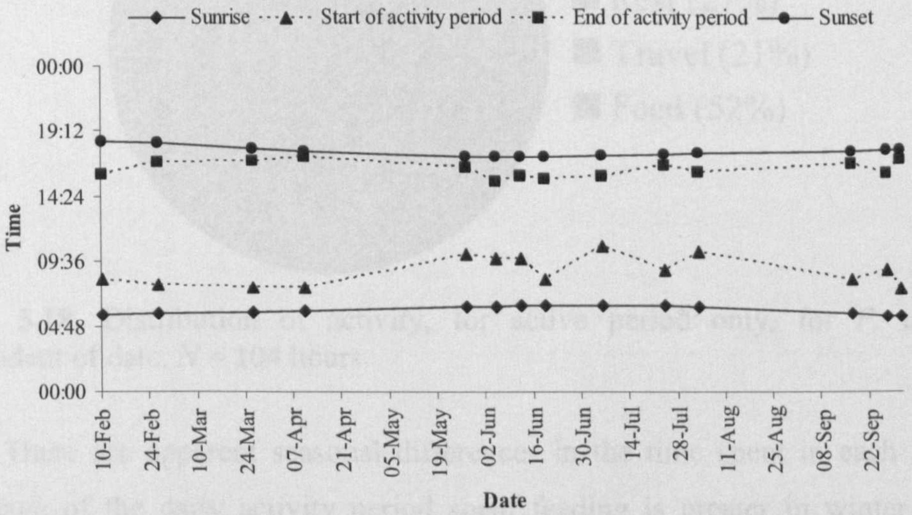


Figure 5.16. Sunrise and sunset times, together with times of the start and end of the activity period of *P. diadema* (2005).

The difference between the number of hours of activity and number of hours of daylight varies between 1.77 hours in April to 5.38 hours in August. There is a greater difference in the offset between sunrise and start of activity in winter months, compared to that between the end of activity and sunset (Figure 5.17).

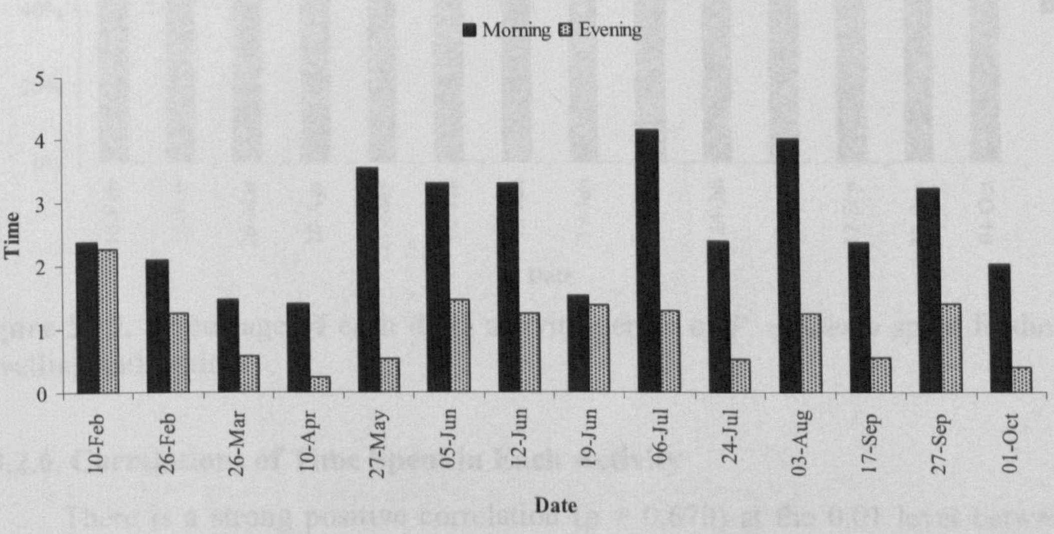


Figure 5.17. Time lag between sunrise and start of activity in the morning and between end of activity and sunset in the evening for *P. diadema* (2005).

5.3.2.5. Time Spent in Each Activity

P. diadema spend 27% of their daily activity period in rest, 21% travelling and 52% feeding (Figure 5.18).

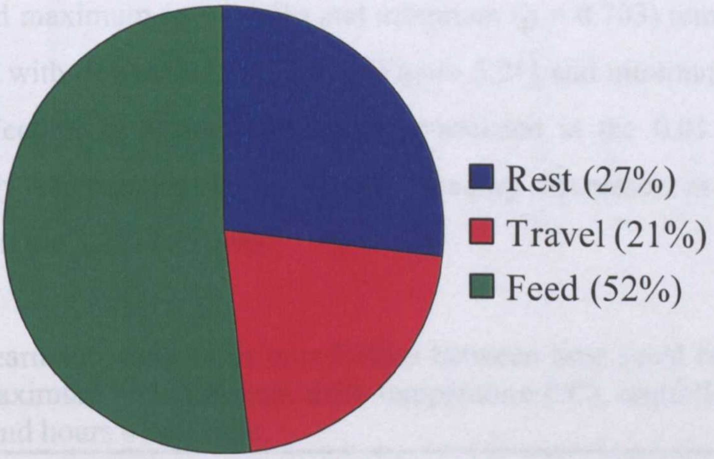


Figure 5.18. Distribution of activity, for active period only, for *P. diadema* independent of date. $N = 104$ hours.

There are apparent seasonal differences in the time spent in each activity. Percentage of the daily activity period spent feeding is greater in winter months (Figure 5.19).

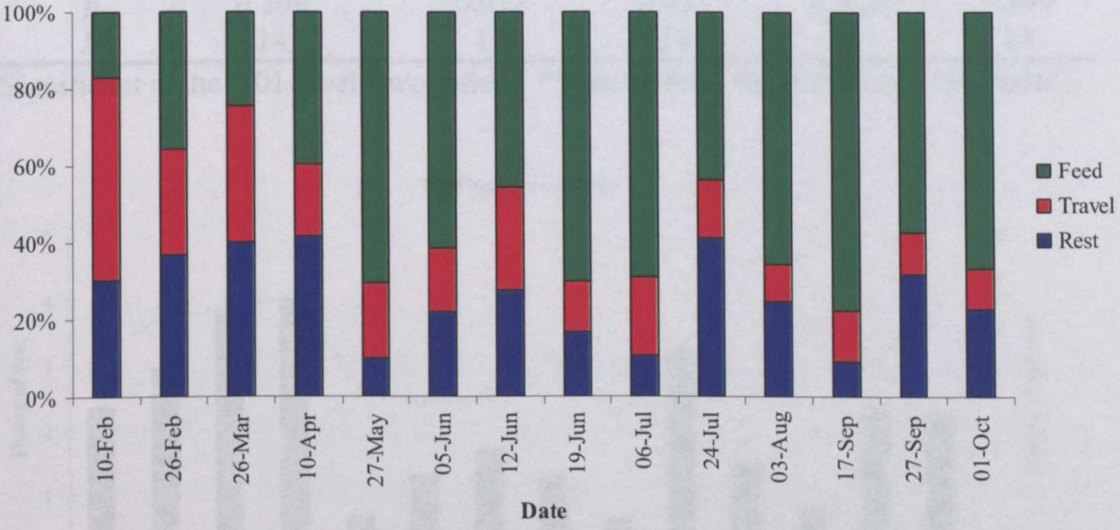


Figure 5.19. Percentage of each daily activity period of *P. diadema* spent feeding, travelling and resting.

5.3.2.6. Correlations of Time Spent in Each Activity

There is a strong positive correlation ($\rho = 0.670$) at the 0.01 level between hours of daily rest and hours of daily activity and a weaker correlation of duration of daily rest with maximum ($\rho = 0.532$) and minimum temperature ($\rho = 0.650$ [Table

5.8]) at the 0.05 level: daily rest period decreases with increasing hours of daily activity (Figure 5.20), and maximum (Figure 5.21) and minimum (Figure 5.22) temperatures. There is a strong positive correlation at the 0.01 level between hours of daily travel and maximum (ρ = 0.808) and minimum (ρ = 0.703) temperature: travel time decreases with decreasing maximum (Figure 5.21) and minimum (Figure 5.22) temperature. Feeding is strongly negatively correlated at the 0.01 level with the minimum daily temperature (ρ = -0.648): feeding decreases as the minimum temperature (Figure 5.22) increases.

Table 5.8. Spearman's rank order correlations between time spent each day in each activity and maximum and minimum daily temperature (°C), rainfall (mm), hours of daily activity and hours of daylight.

		Maximum temperature	**Minimum temperature**	**Rainfall**	**Hours of activity**	**Hours of daylight**
Rest	ρ	0.532*	0.650*	-0.280	0.670**	0.450
	p	0.050	0.012	0.332	0.008	0.107
	N	14	14	14	14	14
Travel	ρ	0.808**	0.703**	-0.467	0.525	0.379
	p	0.000	0.005	0.092	0.054	0.181
	N	14	14	14	14	14
Feed	ρ	-0.358	-0.648*	-0.227	0.081	-0.060
	p	0.209	0.012	0.435	0.782	0.840
	N	14	14	14	14	14

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

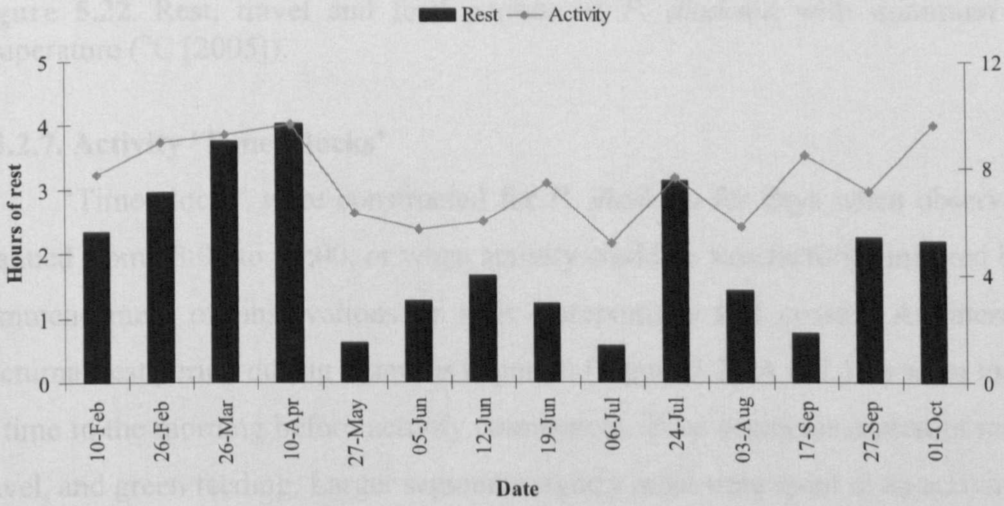


Figure 5.20. Rest period of *P. diadema* with hours of activity (2005).

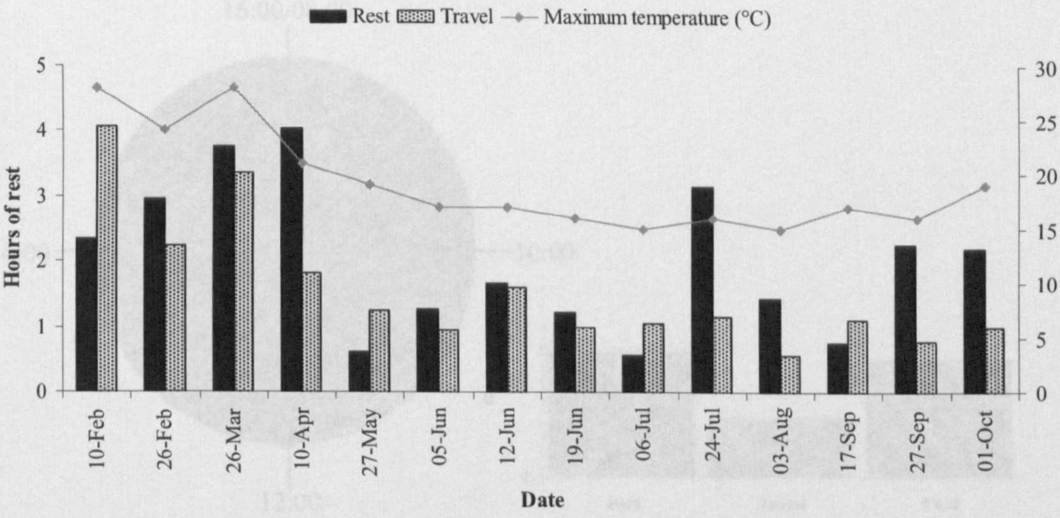


Figure 5.21. Rest and travel period of *P. diadema* with maximum daily temperature (°C [2005]).

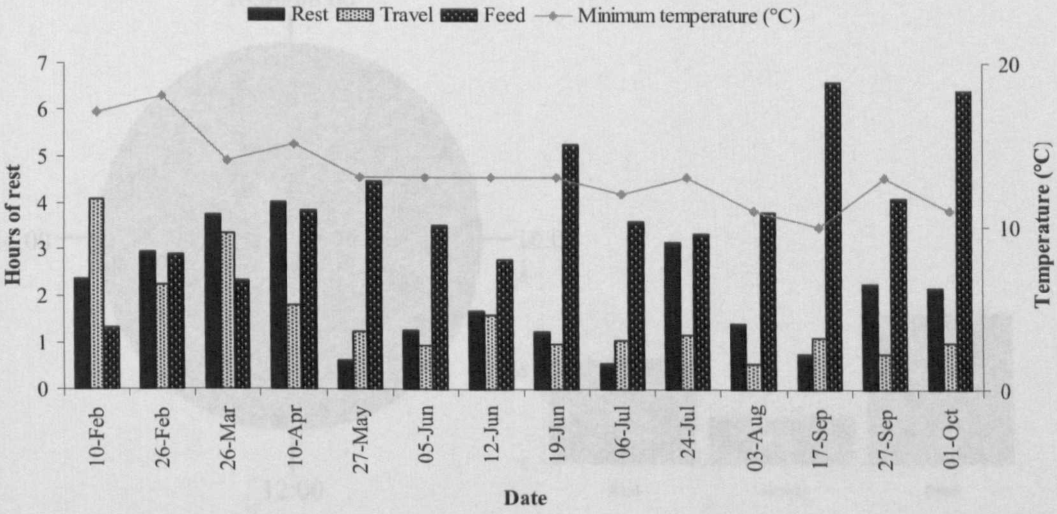
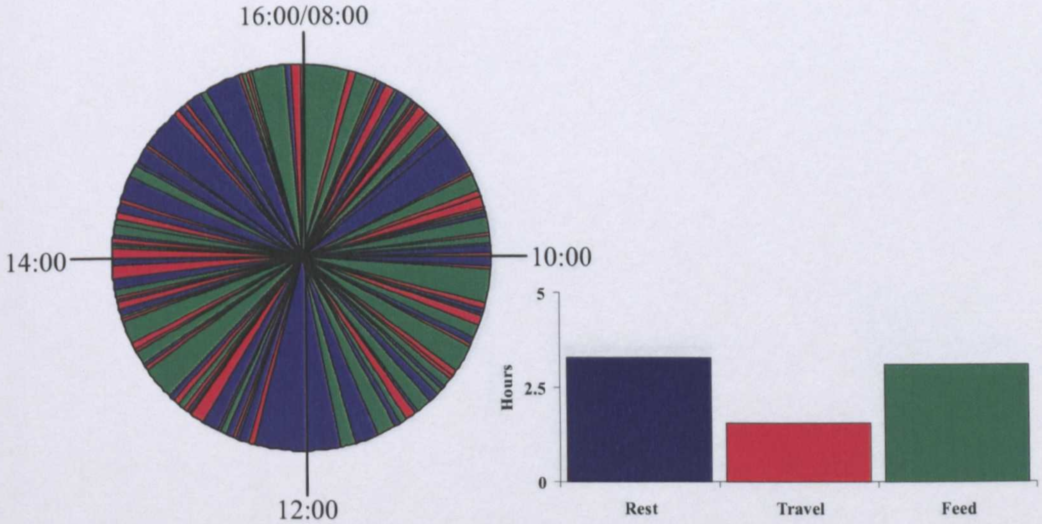


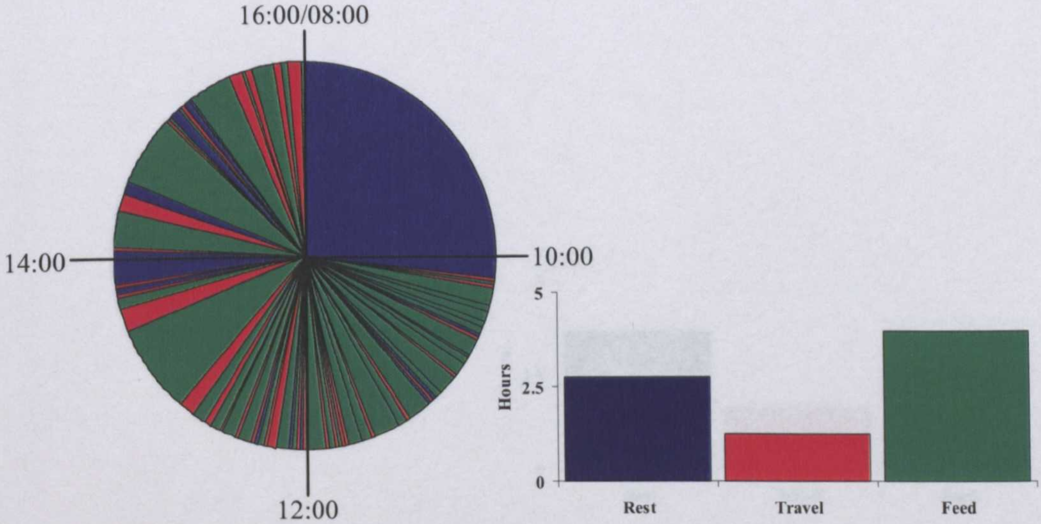
Figure 5.22. Rest, travel and feed periods of *P. diadema* with minimum daily temperature (°C [2005]).

5.3.2.7. Activity 'Time Clocks'

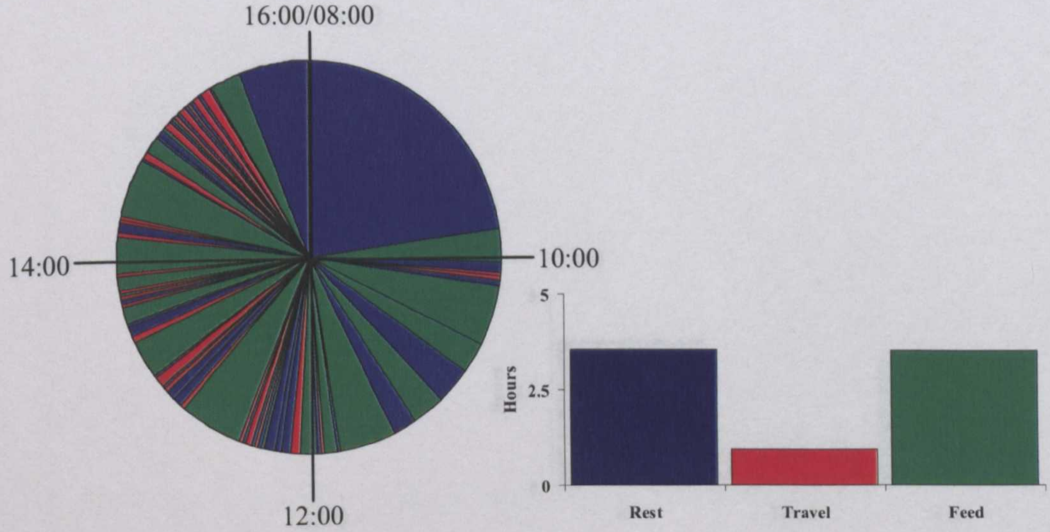
'Time clocks' were constructed for *P. diadema* for days when observations spanned from 08:00 to 16:00, or when activity could be satisfactorily inferred before commencement of observations or after observations had ceased. An increasing nocturnal rest period during winter is apparent (Figure 5.23 A to L), as is an increase in time in the morning before activity commences. Blue segments represent rest, red travel, and green feeding. Larger segments signify more time spent in an activity.



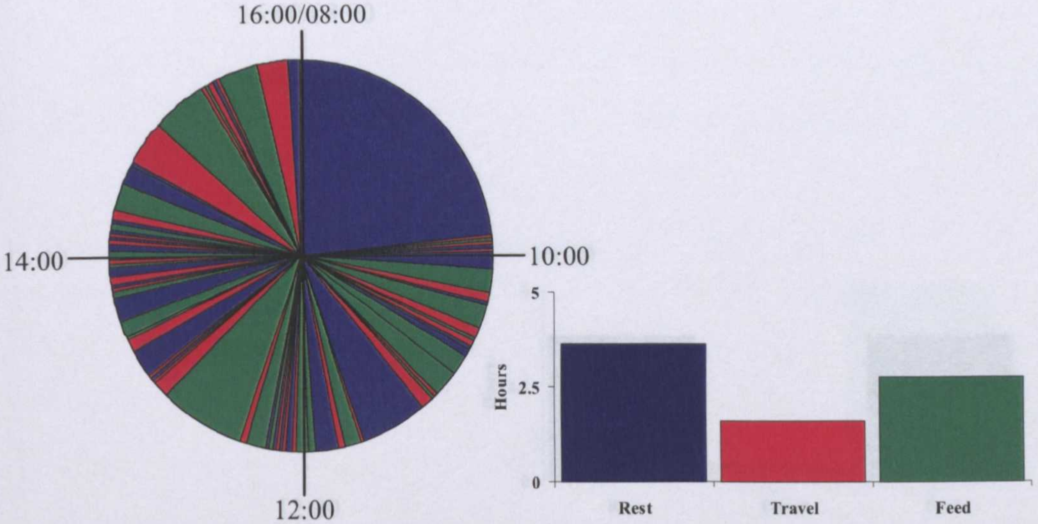
A: 10 April 2005: Sub-adult collared male (activity to activity)



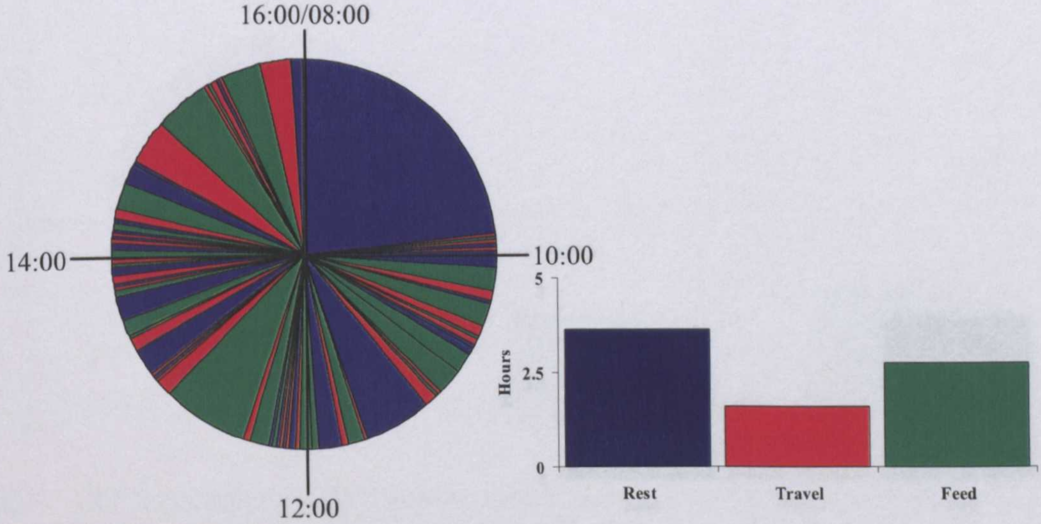
B: 27 May 2005: Sub-adult collared male (rest to activity)



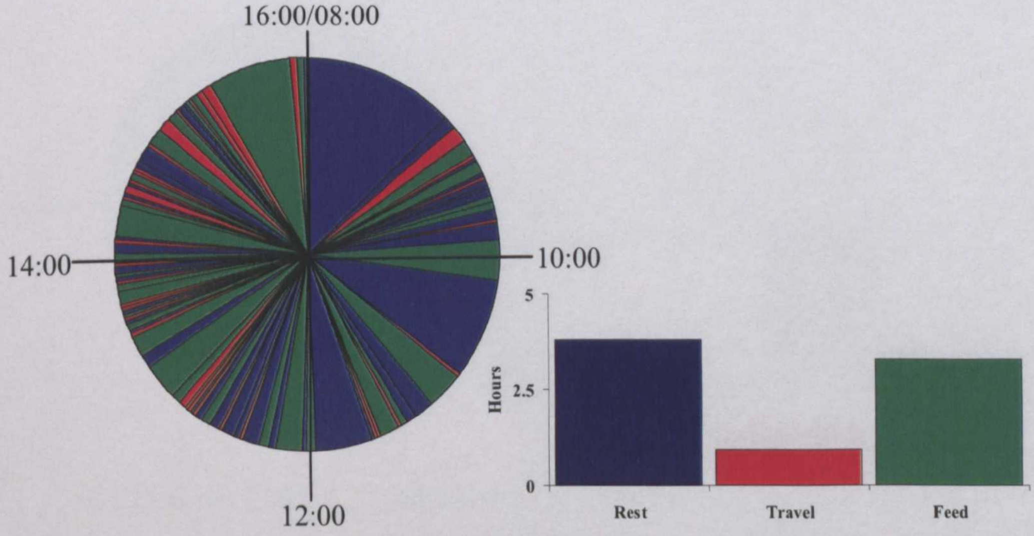
C: 05 June 2005: Mixed (rest to rest)



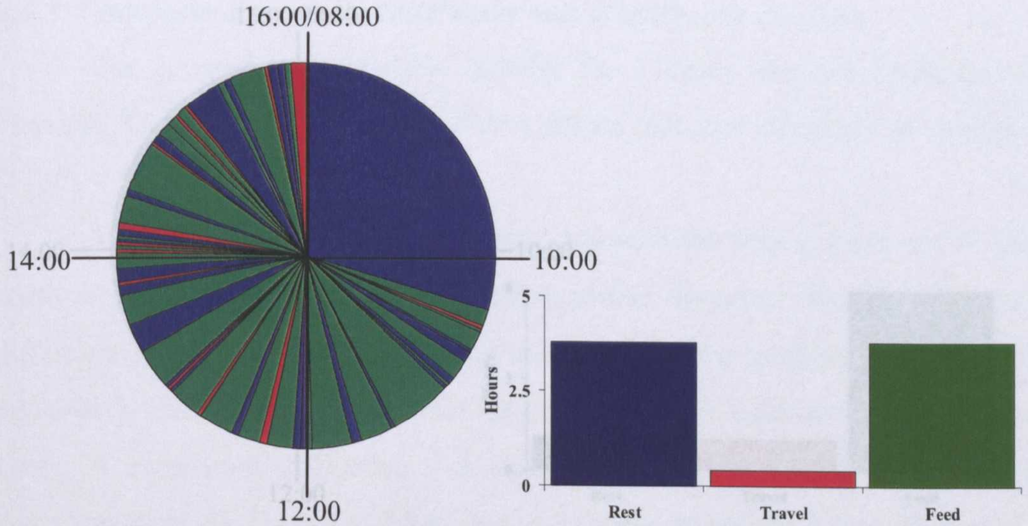
D: 12 June 2005: Adult female (rest to rest)



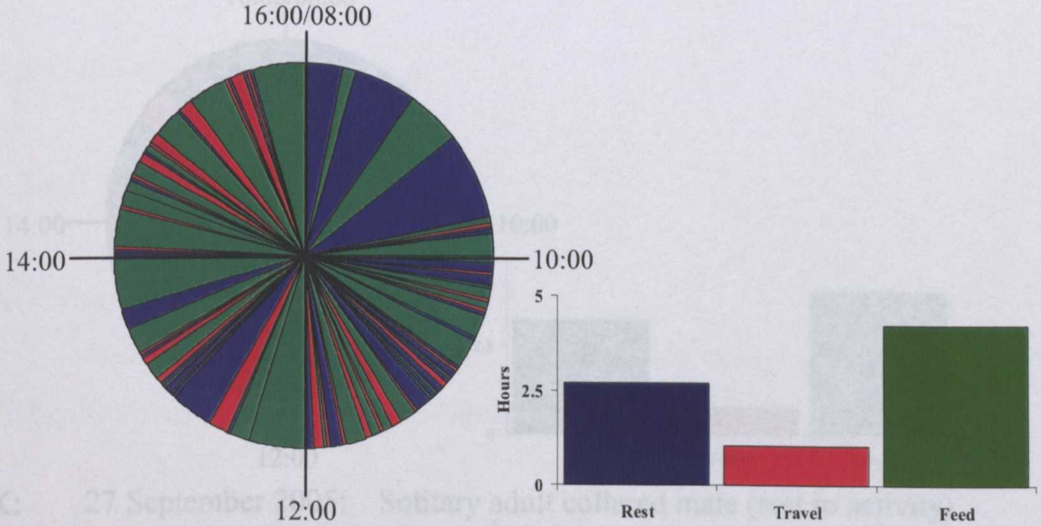
E: 19 June 2005: Mixed (rest to rest)



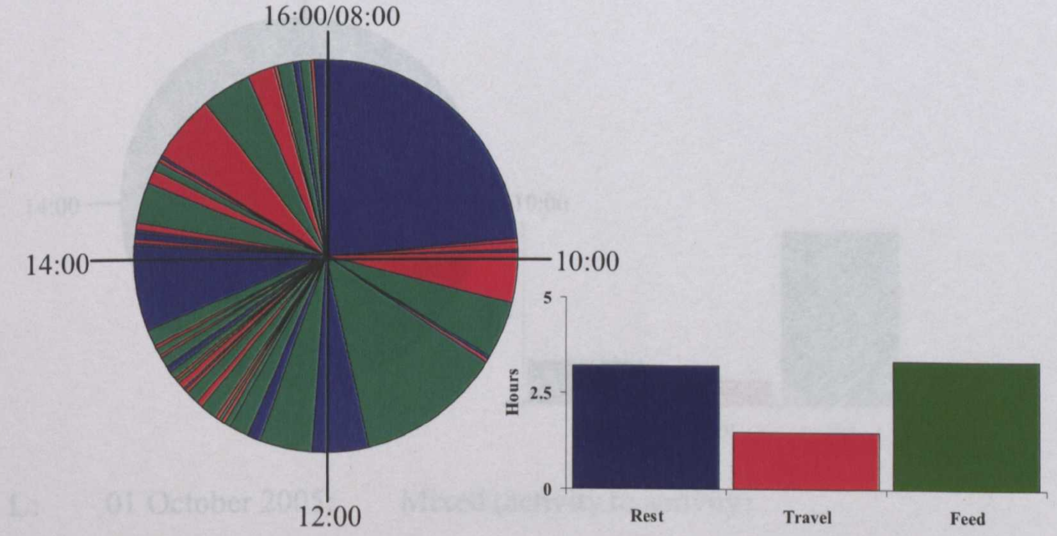
F: 24 July 2005: Mixed (rest to rest)



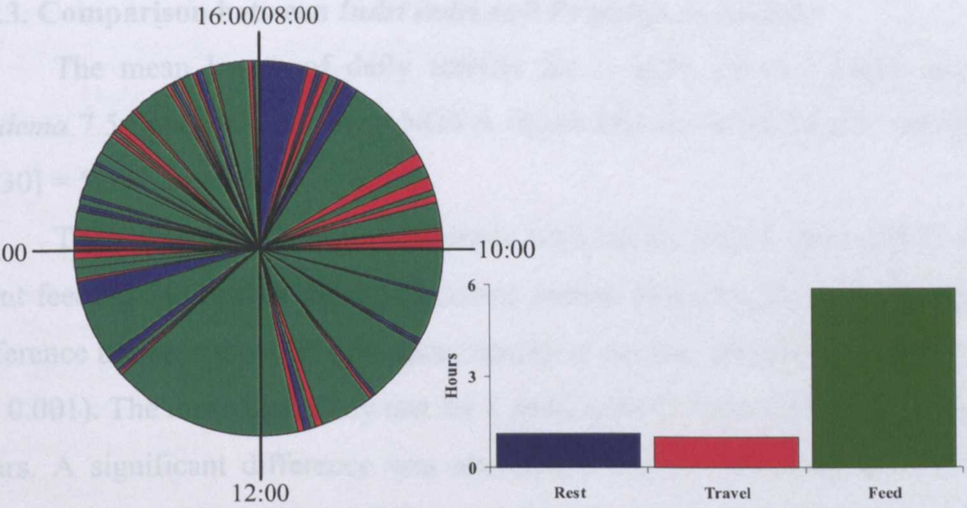
G: 03 August 2005: Mixed (rest to activity)



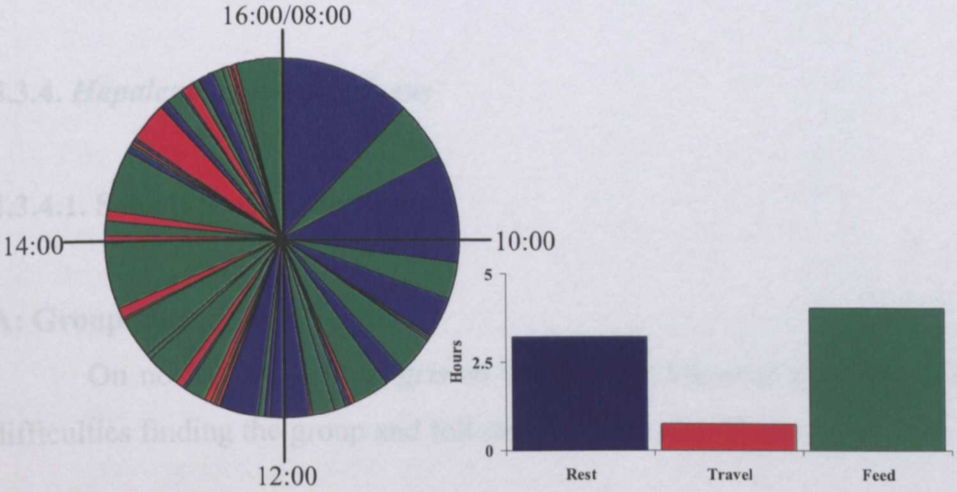
H: 13 August 2005: Mixed (rest to activity)



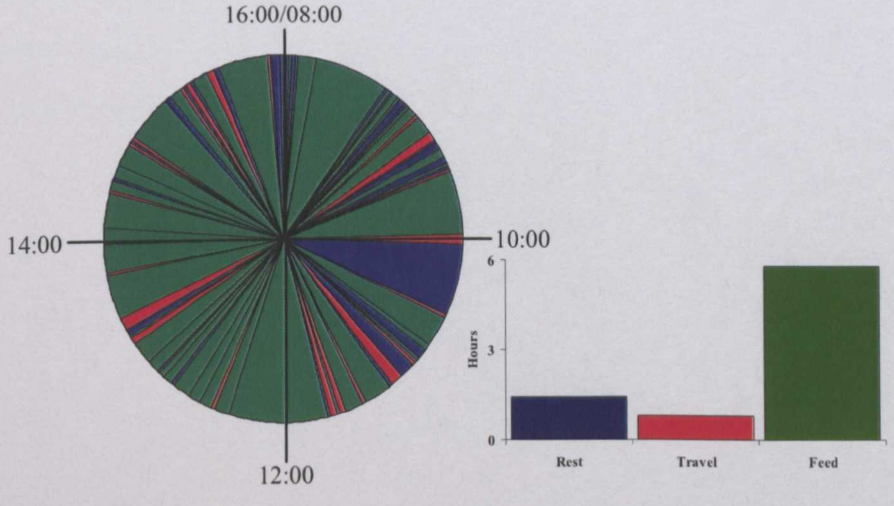
I: 03 September 2005: Mixed (rest to rest)



J: 17 September 2005: Mixed (rest to activity)



K: 27 September 2005: Solitary adult collared male (rest to activity)



L: 01 October 2005: Mixed (activity to activity)

Figure 5.23. A-L: Time clocks for *P. diadema* from 08:00 to 16:00, with the total duration during each time-clock involved in each activity. 🟦 rest, 🟥 travel and 🟩 feed. 'Mixed' refers to observations on multiple individuals.

5.3.3. Comparison between *Indri indri* and *Propithecus diadema*

The mean length of daily activity for *I. indri* was 6.4 hours and for *P. diadema* 7.5 hours. A one-way ANOVA shows that this difference is significant (F [1, 30] = 5.521, $p < 0.05$).

There was no significant difference between the time *I. indri* and *P. diadema* spent feeding and resting during the active period. However, there was a significant difference between the total time spent resting in the two species (F [1, 30] = 13.224, $p < 0.001$). The mean total daily rest for *I. indri* was 9.7 hours and for *P. diadema* 8.6 hours. A significant difference was also found between the time the two species spent travelling (F [1, 30] = 7.996, $p < 0.01$). The mean daily travelling time for *I. indri* was 50 minutes and for *P. diadema* 1.5 hours.

5.3.4. *Hapalemur griseus griseus*

4.3.4.1. Schedule of Observations

A: Group One

On no day were *H. g. griseus* Group One followed from rest-to-rest due to difficulties finding the group and following in darkness (Table 5.9).

Table 5.9. Observation days for *H. g. griseus* Group One, including time at the start and end of observations and whether or not they were resting at these times.

Date	Time start	Resting?	Time end	Resting?
17 November 2004	06:10	No	07:30	No
20 November 2004	05:00	No	18:05	No
27 November 2004	07:30	No	16:15	No
01 December 2004	06:25	No	13:25	No
10 December 2004	06:30	No	17:25	No
11 December 2004	08:35	No	17:30	No
18 December 2004	10:00	No	16:45	No
09 January 2005	05:00	Yes	10:40	No
28 February 2005	07:00	No	16:50	No
20 March 2005	08:10	No	17:10	No
04 April 2005	08:00	No	17:00	No
20 April 2005	07:15	No	17:15	No
20 May 2005	07:30	No	16:00	No
07 June 2005	07:35	No	16:45	No
22 June 2005	07:30	No	16:00	No
08 July 2005	07:40	No	08:40	No
14 July 2005	07:40	No	16:00	No
26 July 2005	08:30	No	17:00	No
19 August 2005	08:10	No	17:15	No
07 September 2005	08:40	No	16:00	No
25 September 2005	07:20	No	16:02	No

B: Group Two

No observations were carried out from rest-to-rest on *H. g. griseus* Group Two, because of difficulties with locating the group and with nocturnal observations (Table 5.10).

Table 5.10. Observation days for *H. g. griseus* Group Two, including time at the start and end of observations and whether or not they were resting at these times.

Date	Time start	Resting?	Time end	Resting?
01 February 2005	07:05	No	16:56	No
08 February 2005	10:20	No	18:00	No
18 February 2005	07:17	No	17:46	No
06 March 2005	09:55	No	18:00	No
29 March 2005	09:57	No	18:00	No
13 April 2005	07:00	No	18:00	No
28 April 2005	07:00	No	17:00	No
29 May 2005	07:00	No	15:20	No
15 June 2005	08:00	No	16:05	No
24 June 2005	07:30	No	16:00	No
08 July 2005	08:51	No	16:00	No
09 August 2005	06:15	No	16:30	No
01 September 2005	07:45	No	17:00	No
19 September 2005	07:45	No	16:45	No

5.3.4.2. Total Observation Period Compared to Sunrise and Sunset

In this study there were seven occasions when *H. g. griseus* were followed, and known to be active, prior to sunrise and following sunset (Figure 5.24). On 20 November 2004 and 09 January 2005 Group One were followed and active before sunrise, Group Two were followed and active from sunrise on 09 August 2005. On 20 November 2004 and 06 March 2005, Group One were followed, and active, to sunset and Group Two were followed, and active, to sunset on 29 March 2005 and 13 April 2005. On 09 January 2005 they were followed from their nightly rest, starting activity at 05:00. On 29 September 2005 Group One were observed feeding in trees over camp at 17:45. They spent the night resting and were heard to move at 05:18 the following morning.

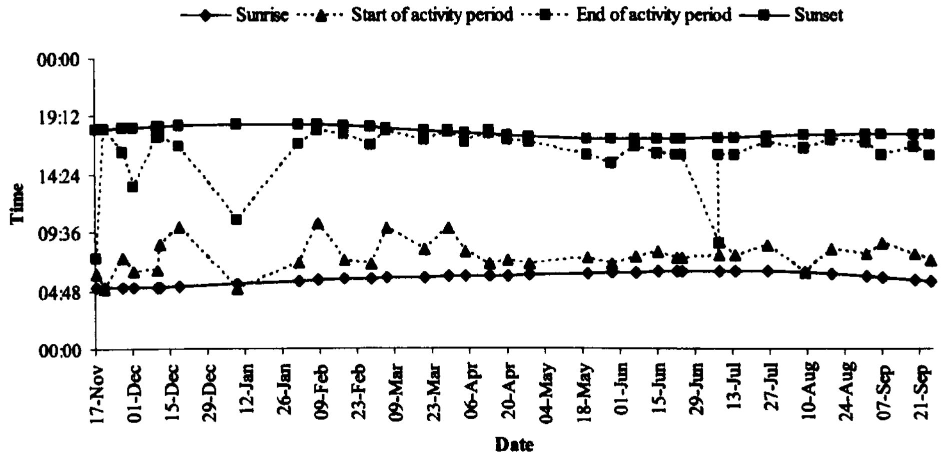
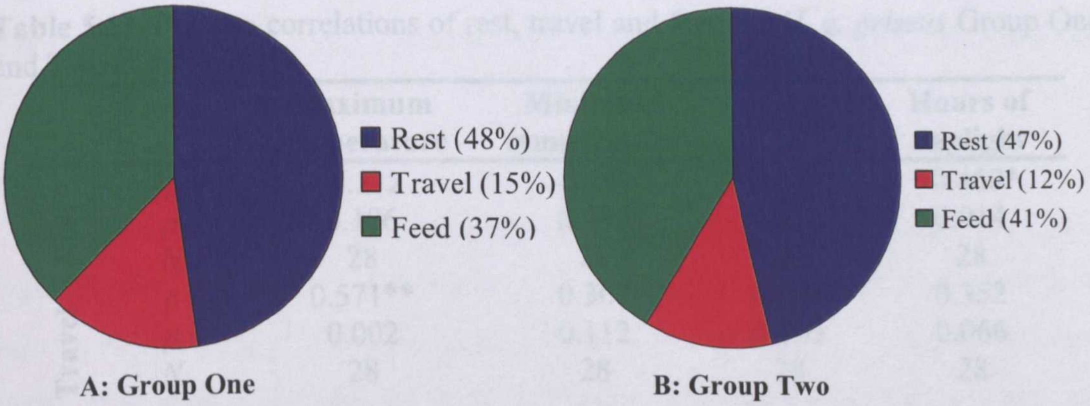


Figure 5.24. Hours of observation for Group One and Group Two *H. g. griseus* combined compared to sunrise and sunset.

5.3.4.3. Proportion of Time Spent for Each Activity

As we lack complete rest-to-rest data for *H. g. griseus*, proportions of time spent in each activity are not complete for the activity period and can only be used as an approximation.

Group One and Two spent similar proportions of time in each of the three activity classes (Figure 5.25). The greatest proportion of their active period was spent resting. Group One spent more time travelling and less time feeding than Group Two. *H. g. griseus* spend longer resting in winter and less time feeding (Figure 5.26).



A: Group One **B: Group Two**

Figure 5.25. Activity budget for *H. g. griseus* **A**: Group One and **B**: Group Two.

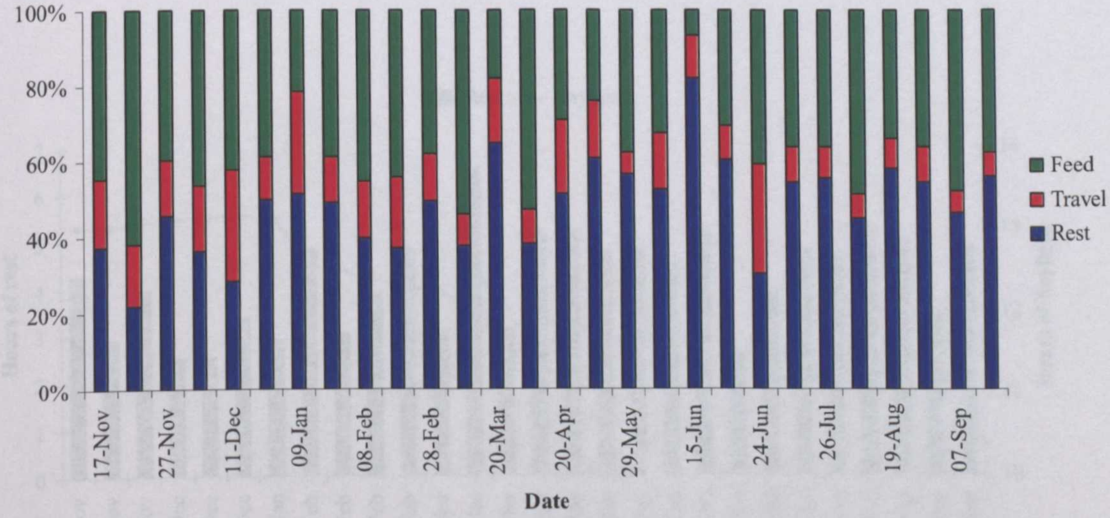


Figure 5.26. Percentage of time each day spent feeding, travelling and resting for *H. g. griseus* Group One and Group Two combined.

5.3.4.4. Environmental Correlations of Time Spent Resting, Travelling and Resting.

There was no correlation between time spent feeding and maximum and minimum temperature, rainfall or hours of daylight (Table 5.11). Rest was weakly negatively correlated with hours of daylight (ρ = -0.460) at the 0.05 level, (Figure 5.27): *H. g. griseus* rest more with decreasing hours of daylight. Travel is weakly positively correlated (ρ = 0.571) with the maximum temperature at the 0.05 level (Figure 5.28): travel time increases as maximum temperature decreases.

Table 5.11. Pearson correlations of rest, travel and feed for *H. g. griseus* Group One and Two combined.

		Maximum temperature	**Minimum temperature**	**Rainfall**	**Hours of daylight**
Rest	ρ	-0.312	-0.230	0.046	-0.460*
	p	0.106	0.239	0.816	0.014
	N	28	28	28	28
Travel	ρ	0.571**	0.307	-0.315	0.352
	p	0.002	0.112	0.103	0.066
	N	28	28	28	28
Feed	ρ	0.340	0.135	-0.333	0.350
	p	0.077	0.492	0.083	0.083
	N	28	28	28	28

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

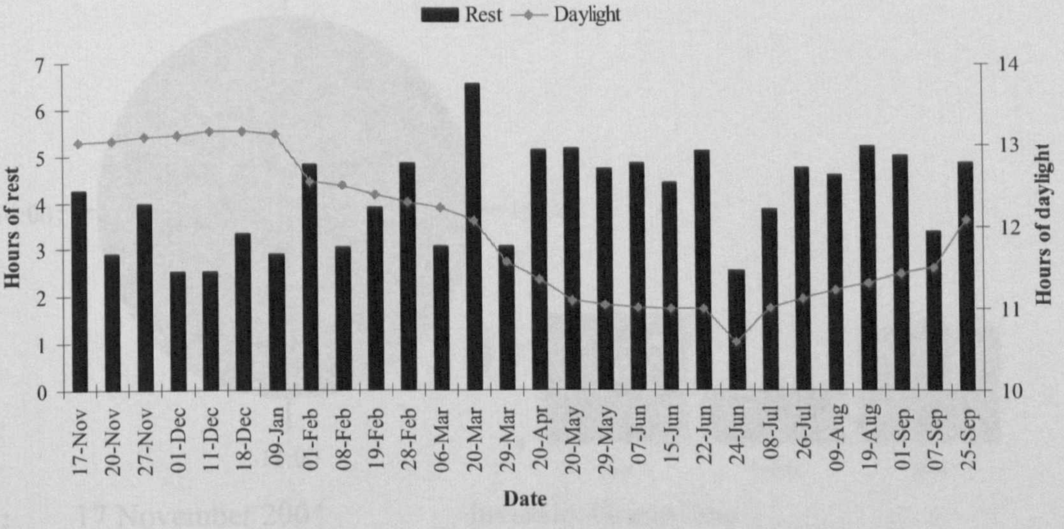


Figure 5.27. Hours of rest and hours of daylight for each day of observation for *H. g. griseus* Group One and Two combined.

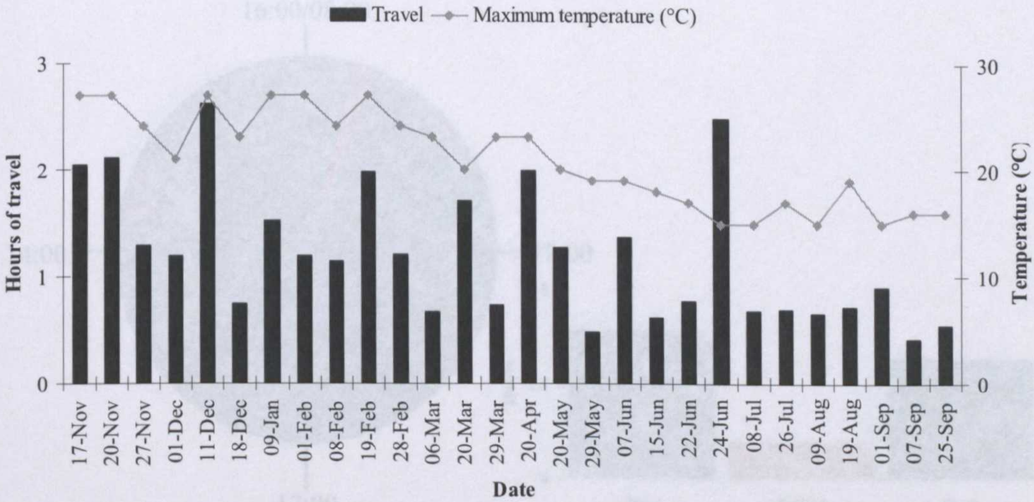
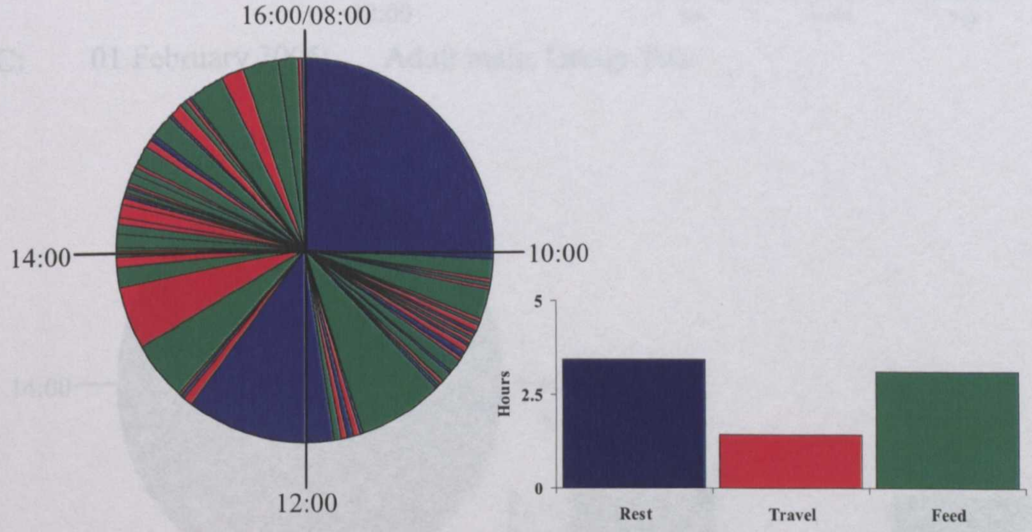


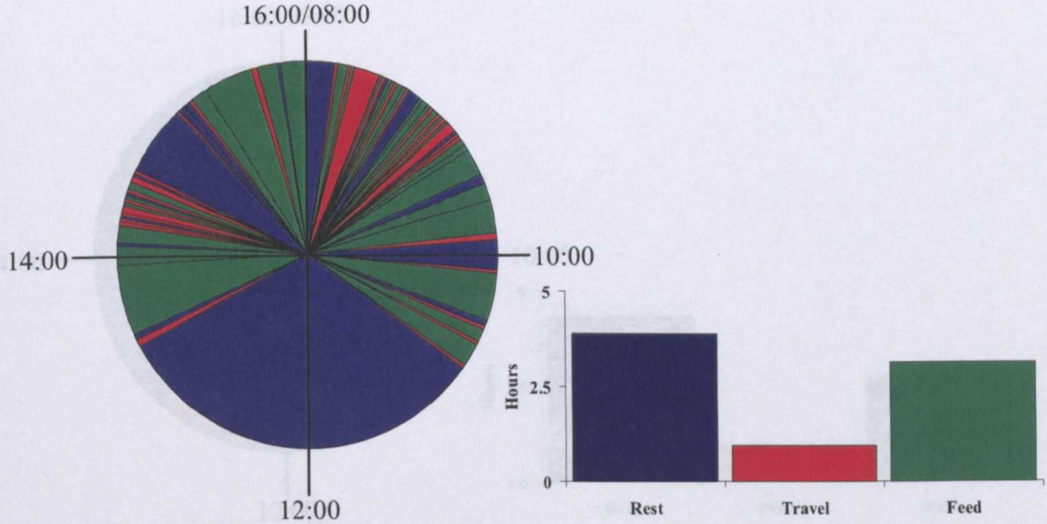
Figure 5.28. Hours of travel compared with maximum temperature (°C) for each day of observation for *H. g. griseus* Group One and Two combined.

4.3.4.5. Time Clocks

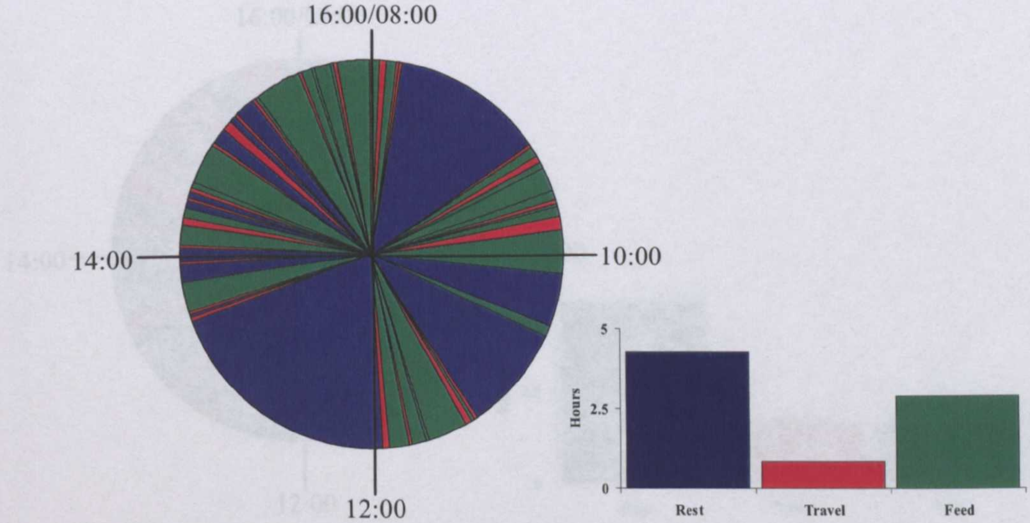
Time clocks for *H. g. griseus* Group One and Two (Figure 5.29 A to L) run from 08:00 to 16:00. They show that *H. g. griseus* have a prolonged rest period from late morning to early afternoon, lasting up to four hours. *H. g. griseus* intersperse bouts of feeding and travelling with short rests. Blue segments represent rest, red travel and green feeding. Larger segments indicate more time spent in a given activity. No time clocks are representative of rest to rest activity.



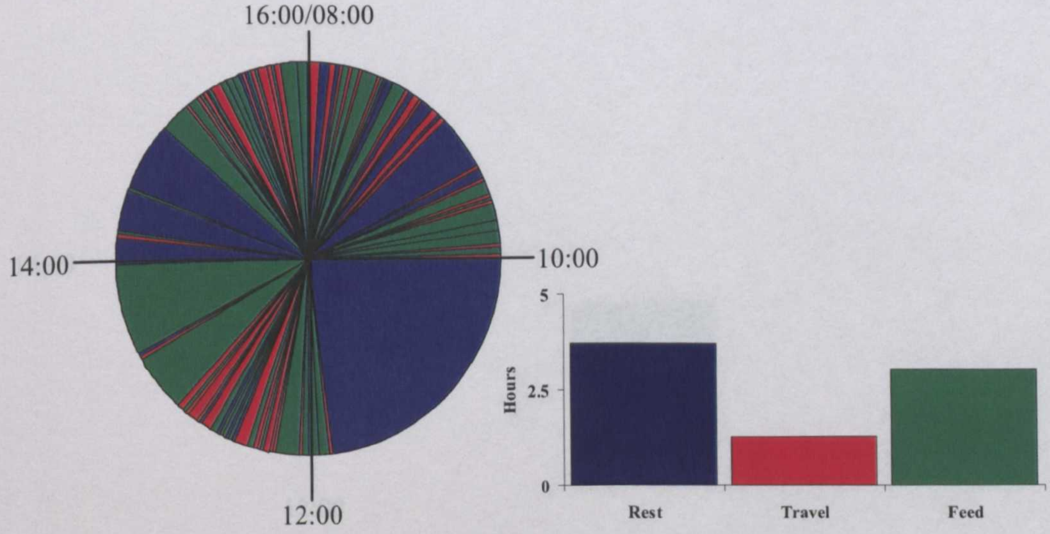
A: 17 November 2004: Juvenile: Group One



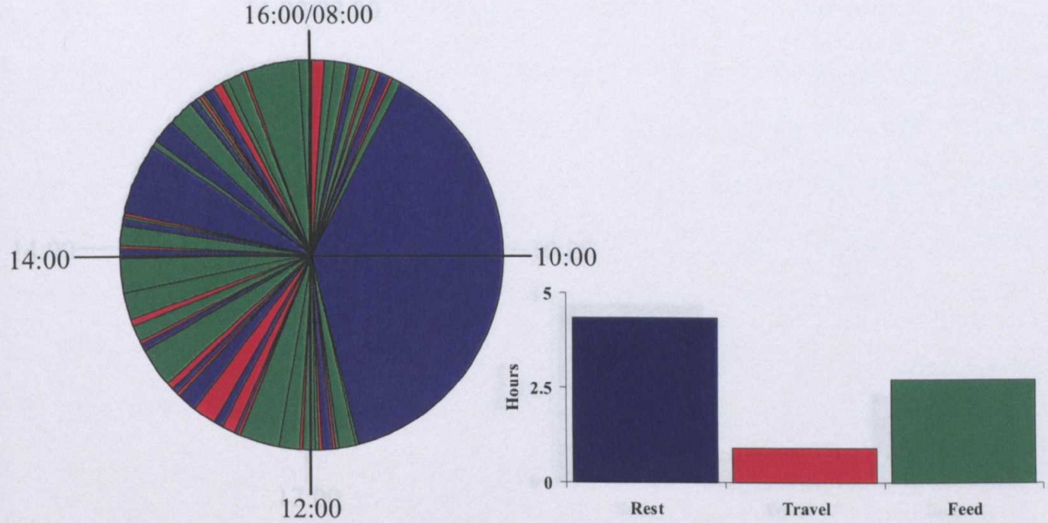
B: 27 November 2004: Adult: Group One



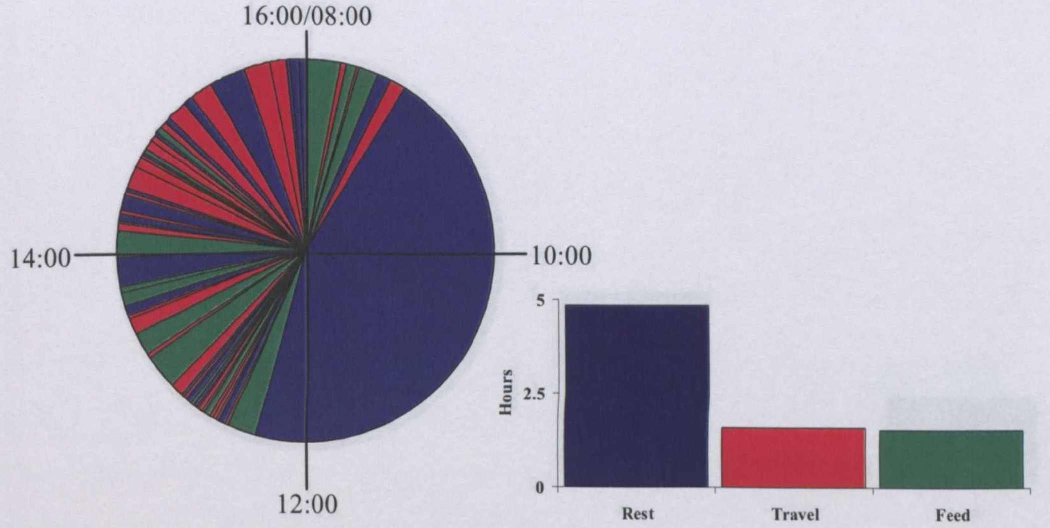
C: 01 February 2005: Adult male: Group Two



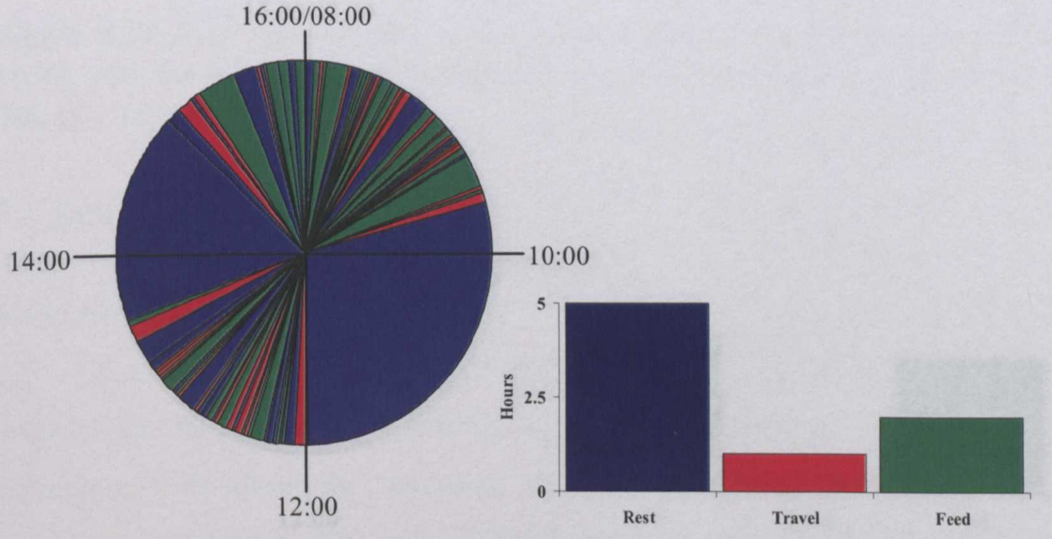
D: 18 February 2005: Mixed: Group Two



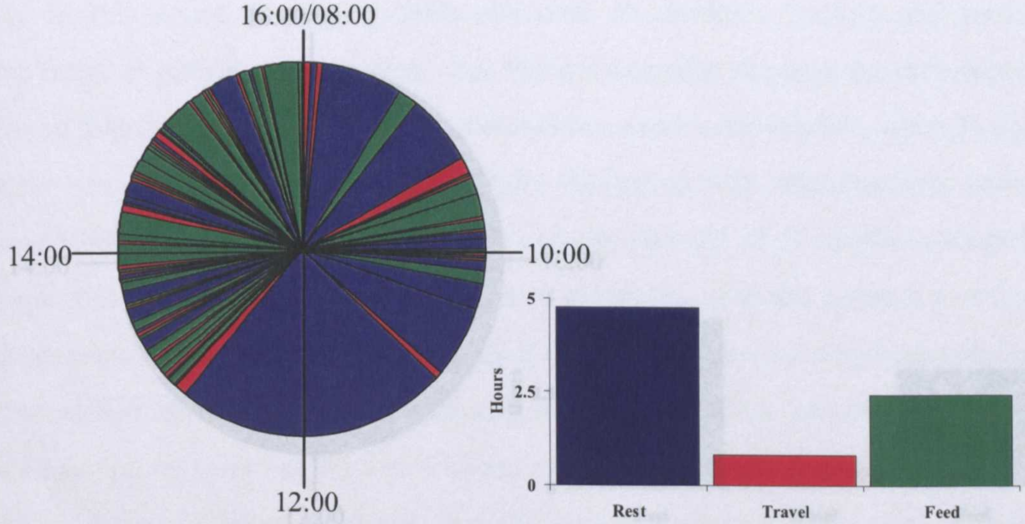
E: 28 February 2005: Adult male: Group One



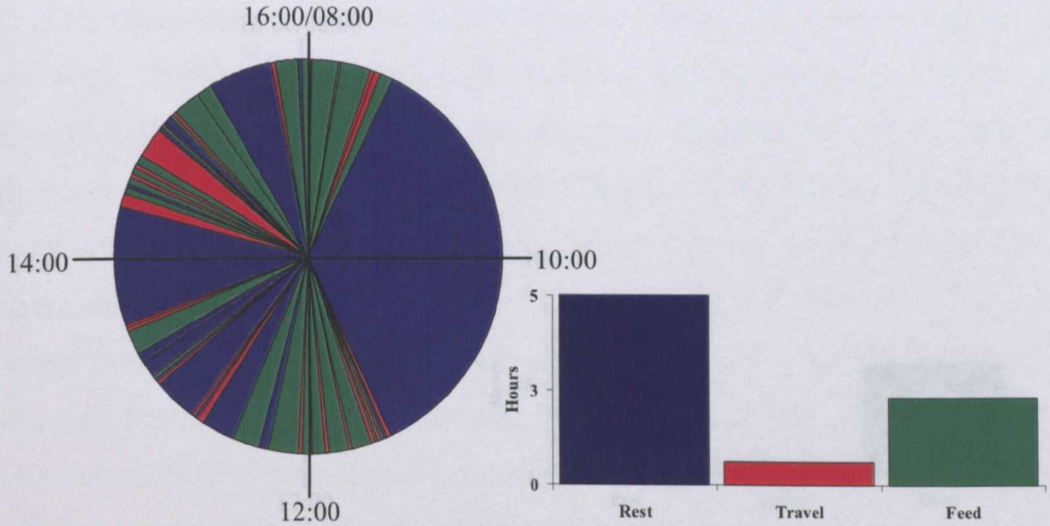
F: 20 April 2005: Mixed: Group One



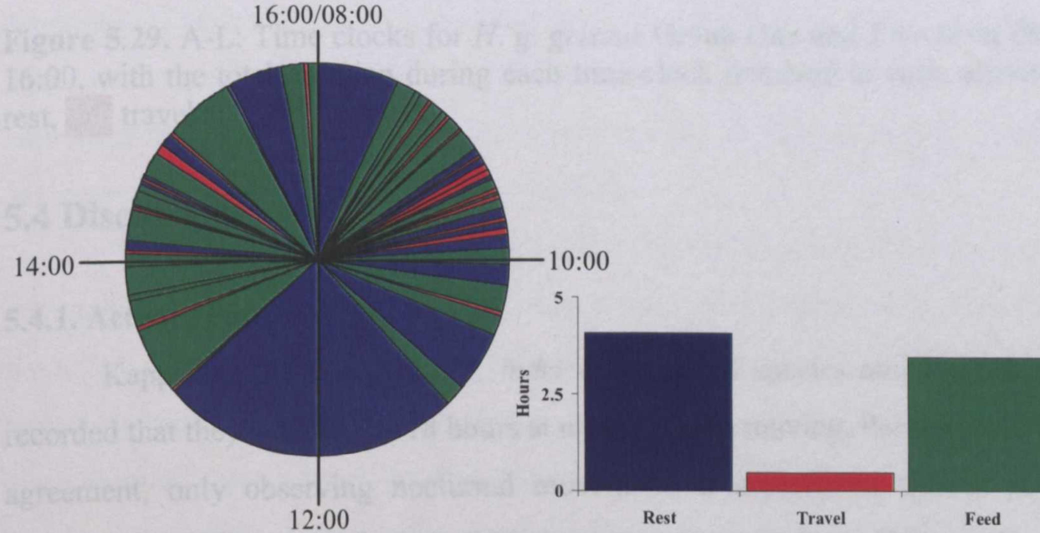
G: 20 May 2005: Mixed: Group One



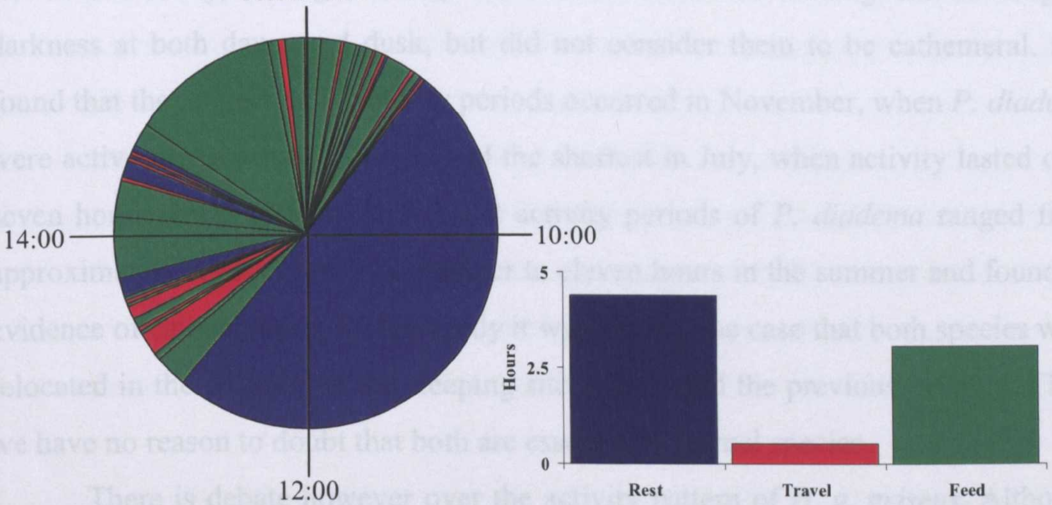
H: 07 June 2005: Adult female: Group One



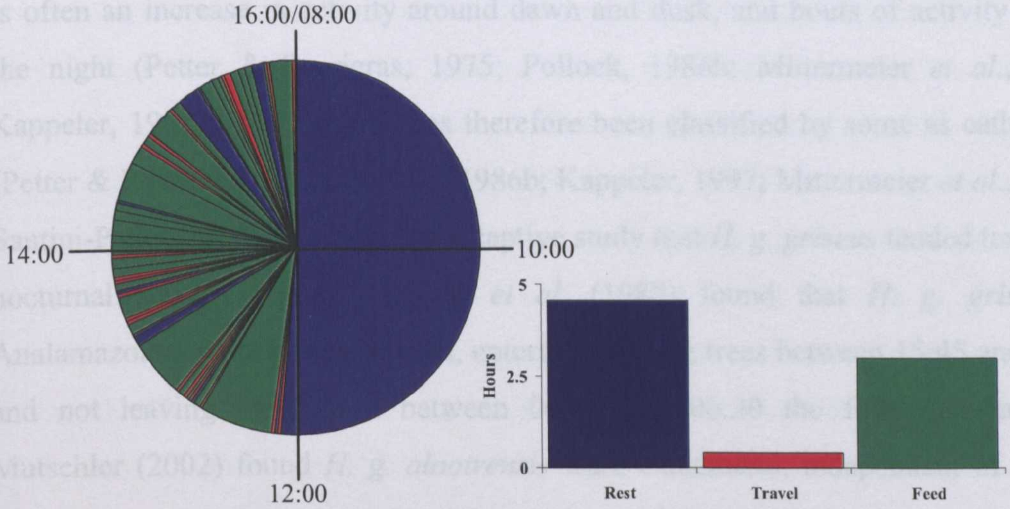
I: 22 June 2005: Adult male: Group One



J: 24 June 2005: Juvenile female: Group Two



K: 09 August 2005: Mixed: Group Two



L: 25 September 2005: Juvenile: Group One

Figure 5.29. A-L: Time clocks for *H. g. griseus* Group One and Two from 08:00 to 16:00, with the total duration during each time-clock involved in each activity. 🟦 rest, 🟥 travel and 🟩 feed.

5.4 Discussion

5.4.1. Activity Pattern

Kappeler (1997) regarded *I. indri* as a diurnal species and Pollock (1975) recorded that they can rest for 18 hours at night without moving. Powzyk (1997) is in agreement, only observing nocturnal movement in association with a powerful nocturnal disturbance, such as a predation attempt or cyclone. Britt *et al*. (2002) observed that in Betampona *I. indri* activity would begin around 09:00 and end after six hours at 15:00. There is no conclusive evidence that *P. diadema* are cathemeral.

As in this study, Powzyk (1997) observed *P. diadema* feeding and moving in darkness at both dawn and dusk, but did not consider them to be cathemeral. She found that the longest daily activity periods occurred in November, when *P. diadema* were active for just over 13 hours and the shortest in July, when activity lasted only seven hours. Irwin (2006b) found that activity periods of *P. diadema* ranged from approximately seven hours in the winter to eleven hours in the summer and found no evidence of cathemerality. In this study it was usually the case that both species were relocated in the morning at the sleeping site determined the previous evening. Thus, we have no reason to doubt that both are essentially diurnal species.

There is debate however over the activity pattern of *H. g. griseus*. Although principally a diurnal species, and at Ranomafana purely diurnal (Grassi, 2002), there is often an increase in activity around dawn and dusk, and bouts of activity during the night (Petter & Peyrieras, 1975; Pollock, 1986b; Mittermeier *et al.*, 1994; Kappeler, 1997). *H. g. griseus* has therefore been classified by some as cathemeral (Petter & Peyrieras, 1975; Pollock, 1986b; Kappeler, 1997; Mittermeier *et al.*, 1994). Santini-Palka (1994) found during a captive study that *H. g. griseus* tended towards a nocturnal activity pattern. Wright *et al.* (1989) found that *H. g. griseus* at Analamazoatra were purely diurnal, entering sleeping trees between 15:45 and 17:25 and not leaving them until between 06:00 and 06:30 the following morning. Mutschler (2002) found *H. g. alaotrensis* were cathemeral, independent of season, activity occurring throughout the night, not just at dawn and dusk.

There was no unambiguous evidence of cathemerality in *H. g. griseus* at Mantadia. However there is a tendency for concentration of activity at dawn and dusk, with a prolonged period of rest during the day. Activity at dawn and dusk, combined with the lull in activity during the middle of the day, suggest that *H. g. griseus* may tend towards crepuscular behaviour.

Study observations do not support Hill's (2006) suggestion that the diurnality of *Hapalemur* is a secondary characteristic caused by the decrease in diurnal raptor predation. Many *H. g. griseus* 'disappeared' during the study and it is likely that a high proportion of these disappearances were due to predation by diurnal raptors, since diurnal raptors (such as *Polyboroides radiatus* [Madagascar harrier hawk]) capable of predating a lemur the size of a *H. g. griseus* were locally abundant and active in the study area.

It appears unjustified to assume that the extinction of the very large Malagasy raptors has removed raptor predation as a factor in determining activity patterns, and hence it is unlikely that a supposed decrease in raptor predation could have lead to the adoption of cathemerality. Karpanty (2006) came to a similar conclusion after finding significant rates of predation by diurnal raptors on both diurnal and nocturnal lemurs. These findings are more consistent, therefore, with Curtis and Rasmussen's (2006) conclusion that it is far more likely that the origin of cathemerality was an ancient event.

5.4.2. Seasonality and Activity

Seasonality has been linked with day length, ambient temperature, humidity, precipitation and food abundance (Morland, 1993; Wright, 1999). Many lemur species rest more during cold weather when food resources are low: *Varecia variegata variegata* (black-and-white ruffed lemur [Morland, 1993]); *Lepilemur ruficaudatus* (red-tailed sportive lemur [Schmid & Ganzhorn, 1996]); *Microcebus* spp. (Schmid, 1998). This is observed in other primate species such as *Colobus polykomos* (black-and-white colobus [Dasilva, 1992]). The increase in rest allows considerable energy to be saved (Mutschler, 1999) and this 'energy minimising' strategy has been described for *Lepilemur* spp. (Nash, 1998; Warren & Crompton, 1998) and *Alouatta* spp. (Milton, 1978). Erkert and Kappeler (2004) examined environmental controls of activity in *Propithecus verreauxi* in Kirindy, southwest Madagascar and found that although activity periods did decrease with decreasing hours of daylight, the pattern was not stable. The same effect has been found for *P. diadema* in this study, where hours of daylight and activity can differ seasonally by over three hours: activity in colder winter months was less than the respective decrease in day length. Given that these data do not cover days when activity is known to have extended into twilight, this difference is in reality even greater. In addition the time offset from sunrise to the start of activity increases proportionally more in winter than the offset between end of activity and sunset. However behavioural seasonality in the rainforest species, *P. diadema* does not appear to match that of the dry-forest species, *P. verreauxi*. Erkert and Kappeler (2004) found that duration of the activity period had a strong positive correlation with minimum temperature. However in this study, minimum temperature does not appear to be a controlling factor for activity duration. It might be hypothesised that the offset between sunrise and onset of activity in winter months, would be explicable if *P. diadema* needed a period of 'warming-up' before commencing activity after a cold night. For *P. diadema* maximum daily temperature proved a better predictor of activity time. Of course, if days were colder *P. diadema* would be expected to require a longer warming-up period following the night, regardless of the nocturnal minimum. Rainfall is also strongly correlated with activity time: increasing rainfall is accompanied by decreasing activity. It seems likely that in periods of heavy rain the extra expenditure of energy to keep warm requires that individuals move less to save energy.

As in the case of *P. diadema* the daily activity period of *I. indri* is correlated with day length. Once again this relationship is non-linear, with a difference of approximately three hours between the activity period and day length in summer and winter. The gap between day length and activity period widens in colder summer months. However *I. indri* achieves this decrease in activity duration by *increasing* the gap between sunrise and start of activity, and end of activity and sunset, almost evenly. Similarly to the case in *P. diadema* there is a strong correlation between activity time and maximum temperature. However contrary to the case in *P. diadema* there is no correlation between rainfall and duration of activity. This suggests that *I. indri* are either more efficient than *P. diadema* at maintaining their internal body temperature or have already decreased their activity period to its minimum and therefore must continue activity to meet their metabolic needs.

For *I. indri* there is no correlation between the daily duration of feeding and climatic factors, hours of daylight or hours of activity. This indicates that feeding is limited by internal metabolic requirements and is not affected by external factors. As hours of daylight vary seasonally, it can be said that there is no seasonal variation in the length of time spent feeding. Lack of seasonality in feeding times indicates either that although *I. indri* are less active in winter, their nutritional requirements are not diminished; *or*, that the quality of food decreases in winter, so that although their requirements decrease, they must spend the same length of time feeding to compensate for the lack of food quality.

Both travel and resting were found to correlate with external factors. The time spent resting each day is strongly correlated with maximum daily temperature, hours of activity and hours of daylight, and less strongly with minimum daily temperature. As all the external factors are linked it follows that as the hours of daylight and temperatures fall, the *I. indri* are active for a shorter period each day, but are less likely to rest within this period of activity. Travel time is strongly correlated with duration of daily activity, so that on days when *I. indri* are active for longer periods, they travel for longer. This indicates that in the colder winter months, when they are active for shorter periods of time, they travel less, in order to maintain feeding time at the same level.

The low-quality folivorous diet of *Lepilemur leucopus* (white-footed sportive lemur) has been linked with a decrease of travel and increase of rest in the colder season, where energy needs to be kept for warmth (Nash, 1989). For *P. diadema,* each of the three activity classes is correlated with environmental influences. As temperature and hours of daylight decrease, so does time spent travelling. This relationship is linked with the total time spent active: when the duration of the active period decreases so does travel time. The time that *P. diadema* spent resting during the day increased as temperatures fell. However time spent feeding showed a negative correlation with temperature, so that as temperatures fall, feeding time increases. This finding indicates that as temperatures fall, *P. diadema* travel less and rest more, in an effort to save energy. Despite this, they spend more time feeding. The latter finding suggests that the quality of their diet decreases in colder winter months, so that they have to spend longer feeding, for less energetic reward. *P. diadema* also took longer to become active after sunrise on winter mornings, which suggests that they need longer to return to their normal active body temperature.

This behaviour is similar to that found in *Colobus polykomos* who expended more energy by travelling further and feeding more during times of high energy food availability, while decreasing their energy expenditure by travelling less and resting more when such food was scarce (Dasilva, 1992).

I. indri and *P. diadema* thus appear to have very different activity strategies. *I. indri* maintain a lower quality diet all year, and survive the colder winter months by decreasing their overall period of activity, and thus travelling less. *P. diadema* maintain a higher quality diet, which results - in colder winter months - in *P. diadema* having to spend longer feeding and more time resting (either to aid digestion of lower quality foods or to save energy).

Large bodied folivores often spend long periods of time resting in order to digest leaves. Smith (1977) found a correlation between the proportion of leaves in the diet and percentage of time spent resting: longer rest periods were observed in more folivorous species. Folivorous *Alouatta palliata* (mantled howler monkey) in Panama spent long periods of time motionless compared to more frugivorous *Ateles geoffroyi* (Geoffroy's spider monkey), *Cebus capucinus* (white-throated capuchin) and *Saguinus geoffroyi* (red-crested tamarin).

H. g. griseus do not appear to substantially alter the amount of time spent feeding from season to season. However, in colder winter months they conserve energy by resting more and travelling less. The activity pattern seen in *H. g. griseus*, -- peaks of activity at dawn and dusk, with a resting period in the middle -- is a fairly common one among lemurs (Sussman, 1977). It has been hypothesised that this is connected with maximum daily temperature (Clutton-Brock & Harvey, 1977), however a similar pattern is observed in nocturnal prosimians (e.g. *Tarsius bancanus* [western tarsier]: Crompton & Andau, 1987; *Galago moholi* [northern lesser bushbaby] and *Otolemur crassicaudatus* [thick-tailed greater bushbaby]: Crompton, 1980). An alternative explanation is that mid-day rests are a requirement of food digestion. If an animal feeds on waking, it can then digest this food over a mid-day rest period, and spend the night digesting its afternoon feeding (Clutton-Brock & Harvey, 1977), this might especially be true for a low quality diet which requires a high degree of detoxification (Warren & Crompton, 1997b). The diet of *H. g. griseus* is high in cyanide and it appears that this cyanide is excreted, in part, by kidneys (Yamashita *et al.*, 2007). This process could require long periods of rest.

5.4.3. Comparison with Previous Studies

The percentage of time *I. indri* was found to spend in each activity in this study differs from previous work. Powzyk (1997) found *I. indri* travelled for only 3% of their activity period; in this study 13% of time was spent travelling. In this study 54% of *Indri*'s active period was spent feeding, compared to 42% in Powzyk's (1997). Pollock (1977) found that feeding comprised 39.2% and 36.6% of the total time of two groups at Analamazoatra, although this varied seasonally from 30 to 60%. Conversely in this study *I. indri* were found to spend less time resting, 33% of the total compared to 50% in Powzyk's.

Similarly, this study found *P. diadema* to spend more of the active period feeding (52% here compared to 42% in Powzyk and 36% in Irwin) and travelling (21% here compared to 6% in Powzyk) and less resting (27% here compared to 44% in Powzyk and 56% in Irwin) compared to previous studies (Irwin, 2006b; Powzyk, 1997). These differences are difficult to explain, especially as Powzyk (1997) worked in a similar area to the present study. It is possible that definitions of what constitutes each activity category (rest, travel, feed) vary between studies. Alternatively differences in lengths of each study could be acting as a bias against certain months. Activity data on both indriids in this study was collected from February to October, missing out many summer months. However as travel decreases and rest increases in winter months, it would be expected that this study would underestimate the importance of travel and over-estimate that of rest, which is the reverse of what is found. Both indriids additionally have smaller home ranges than in both other studies and it is possible that they deplete their resources at a quicker rate and therefore have to spend longer travelling and feeding on lower quality resources.

5.5. Summary

Hypothesis 5.1 held that: *I. indri* and *P. diadema* as larger bodied folivores will be diurnal; *H. g. griseus* as a much smaller folivore will be cathemeral.

Data from this study upheld the first part of hypothesis 5.1; *I. indri* and *P. diadema* were diurnal during the course of this study. The second part of this hypothesis is not upheld; *H. g. griseus* in Mantadia are not cathemeral. Their activity pattern would more correctly be termed crepuscular; a peak of activity at dawn and dusk and a lull mid-day.

Hypothesis 5.2 held that: *I. indri*, *P. diadema* and *H. g. griseus* will be more active in summer months (long hours of daylight) compared to winter months (short hours of daylight)

Hypothesis 5.2 was upheld for *I. indri* and *P. diadema* but not for *H. g. griseus*. The length of the daily active period in *I. indri* and *P. diadema* correlated with hours of daylight: they spent significantly longer active on days during the summer opposed to the winter. No correlation was observed between hours of daylight and active period for *H. g. griseus*.

Hypothesis 5.3 held that: the start and end of the active period will run parallel to sunrise and sunset for the diurnal *I. indri* and *P. diadema*

This hypothesis was upheld for *I. indri*: *I. indri* start their active period later in the morning and end it earlier in the evening in accordance with sunrise and sunset. It was not upheld for *P. diadema*; although they did alter the start and end of their active period with the progression of sunrise and sunset the difference between sunrise/sunset and start/end of activity is not constant.

Hypothesis 5.4 held that: for *I. indri*, *P. diadema* and *H. g. griseus* resting (during the active period) will increase in the austral winter, when availability of good-quality food should be relatively low, while travelling and indeed feeding will proportionately decrease.

For *I. indri* this hypothesis was rejected: length of daily feeding shows no correlation with daylight, while length of daily rest and travel periods decreases. This hypothesis can be rejected for *P. diadema*: the rest and travel periods during the active period decreases in winter while the feeding time increases. No correlation was found for rest, travel or feed periods with hours of daylight, hence the hypothesis is rejected. This hypothesis can in-part be rejected for *H. g. griseus*: feeding time did not alter seasonally, while rest and travel increased slightly during the austral winter.

Chapter 6 Feeding Behaviour

An understanding of diet is an essential component of a study of metabolic budgets. This chapter begins by reviewing the literature on metabolism and diet, with reference also to age/sex differences and spatial and temporal variation. Method, results and analysis for the diet and feeding behaviour observed ensue, in comparison with the literature on feeding behaviour and diet in the study species.

6.1 Introduction

6.1.1 Metabolism and Diet

Small mammals have large surface-to-mass ratios and hence high energetic requirements for thermoregulation. They therefore require foods that are high in energy such as insects and fruit (Mutschler, 2002). Folivory is not therefore usually seen in mammals weighing less than 1.5kg (Kay, 1984).While larger mammals have lower thermoregulatory costs, their costs for locomotion are absolutely larger; these requirements can however be met by bulkier, lower quality foods such as leaves as their gut volumes are relatively large. In accord with expectations from a relatively large body mass, the main dietary component of *I. indri* is immature leaves, so that this genus is commonly categorised as folivorous (Powzyk, 1996; Powzyk & Mowry, 2001; Britt *et al.*, 2002; Birkinshaw & Colquhoun, 2003); but fruit, flowers, galls, bark, mature leaves and new branches are also eaten (Powzyk, 1997). However, despite Powzyk's report that *P. diadema* are actually greater in mass than *I. indri*, and might therefore be expected to take a lower quality diet, *P. diadema* is classified by Birkinshaw and Colquhoun (2003) as a 'frugivore - graminivore' (*sic*). Graminivore in Birkinshaw and Colquhoun (2003) means grass-eater, and must be a typographical error, which should have read *granivore*. Nevertheless, Powzyk (1997) and Powzyk and Mowry (2001) report that while fruits, seeds, galls and flowers are also consumed, leaves dominate *P. diadema* diet.

However, *Avahi* spp. (woolly lemurs) and *Lepilemur* spp. (sportive lemurs) are both folivores, and all well below Kay's threshold. *Hapalemur* spp. are similarly well below the threshold, and despite this *Hapalemur* spp. have diets in which bamboos predominate, although Birkinshaw and Colquhoun (2003) classified *H. g.*

griseus as folivorous-frugivorous. One possible explanation for the common existence of folivores less than a kilogramme in mass in Madagascar is that lemurs appear to be hypometabolic (Daniels, 1984), i.e. that their basal metabolic rates (BMR) are lower than expected from Kleiber's relationship, an allometric scale where BMR in mammals is proportional to the two-thirds power of body weight (¾ ratio [Kleiber, 1947]). BMR is considered the minimum energetic cost of maintaining cells and organs ready for activity, defined as the 'rate of energy metabolism of a non-growing organism at rest under postabsorptive conditions [i.e. no digestion] in a thermoneutral environment' (Ricklefs *et al.*, 1996). Energy metabolism measured on a free-living animal is that of an *active* organism and is termed the 'field metabolic rate' (FMR [Ricklefs *et al.*, 1996]). The relationship between BMR and FMR can be considered the relationship between readiness and action (Ricklefs *et al.*, 1996). Koteja (1991) concluded that BMR is not a reliable index of energy expenditure in free ranging animals, however a relationship between BMR and FMR in mammals has been found by Ricklefs *et al.* (1996). Therefore measurements of 'BMR' conducted on wild animals, while valuable and necessary, should be treated with caution. Further, the validity of Kleiber's relationship is unclear as factors aside from body mass are known to affect BMR. McNab (1986) found that diet was an important influence on BMR in Eutheria (placental mammals); consumption of invertebrates, fruit and woody leaves requires a low metabolic rate, while consumption of vertebrates, herbs and nuts requires a high metabolic rate. Therefore, arboreal mammals who primarily consume leaves will have lower metabolic rates than suggested by Kleiber's rule (McNab, 1978; 1980). Despite this, a review by Ross (1992) found no definite link between BMR and diet within the primates. Da Silva *et al.* (2006) reviewed BMR literature to examine the validity of the ¾ allometric scaling. They found that the method of data collection and analysis affected scaling, so that a range of ⅔ to ¾ was found in mammals and birds. Body size of mammals was found to affect this ratio, whereby small mammals had ratios less than or approximately equal to ⅔, while larger mammals have ratios greater than or approximately equal to ¾. They further found that in deep torpor the metabolic rate of animals has approximately a scaling of 1.

If Kleiber's rule of a ¾ ratio between body mass and BMR is incorrect, especially for small arboreal folivores, the argument of lower-than-expected BMRs for lemurs may be wrong. However with no definitive answer, the idea of a low

BMR in lemurs will be discussed. Ross (1992) suggests that the nocturnal ancestral lemur had a relatively low BMR and that the extant diurnal lemurs have retained the ancestral condition. He proposes that this is either because there has been insufficient energetic diversity within the lemuroids to allow evolution of a higher BMR, or that conditions have not selected against a low BMR. This would imply that small bodied lemur species are pre-adapted to a folivorous diet (Ross, 1992). On the other hand reduction of BMR appears to alter an animal's tolerance to low-energy foods, allowing small bodied animals to be folivorous (Mutschler, 2002). Mutschler (2002) believes there must be reasons other than low BMR behind the ability of small bodied lemurs to exist on a folivorous diet, including perhaps the possession of specialized digestive tracts, which give a greater ability to digest dietary fibre, alongside behavioural adaptations. Not all workers agree that the ancestral condition was hypometabolic: it has been suggested that the ancestral lemur would have weighed some 2kg and would therefore have been too large to exhibit hypometabolism (Stankiewicz *et al.*, 2006; Masters *et al.*, 2007). Mutschler's (2002) claim that lemurs are hypometabolic is based on studies of only a few lemurs; but all those which have been studied so far studied do have lower BMRs than expected from Kleiber's ¾ scaling. Schmid and Ganzhorn (1996) investigated the resting metabolic rates of 17 wild *Lepilemur ruficaudatus* (red-tailed sportive lemur) in dry forest around Morondava, western Madagascar. Resting metabolic rates were 50% lower than that expected from Kleiber's rule, and metabolic rates while active were higher than at rest (Schmid & Ganzhorn, 1996). Daniels (1984) measured the BMR of captive *Eulemur fulvus* (common brown lemur) at a rate 28% lower than expected based on Kleiber for an animal of that mass.

6.1.2. Dietary Quality and Niche Differentiation

Clutton-Brock (1977a; 1977b) defined three qualitative differences affecting the selection of plant species as food: first an individual must chose food depending on its specific chemical content, which varies from food species to food species; secondly, individuals may try to avoid secondary compounds, for example tannins and alkaloids, unless they are adapted to detoxifying them; thirdly foods or other materials may be selected and ingested to facilitate digestion: ingested soil and clay may absorb secondary compounds.

Resource availability helps to determine intra-species and inter-species group size and spacing and sympatric species can avoid direct competition by having fundamentally different diets: e.g. folivorous versus frugivorous; or by feeding at different heights (Clutton-Brock, 1977b).

Both *I. indri* and *P diadema* are well above Kay's threshold and generally described as folivores (*I. indri*) or folivore-frugivores. But since they have a substantially overlapping range in body size and generally similar ('vertical clinging and leaping') locomotor repertoire we must expect niche differentiation to be quantitative, rather than fundamental. The following hypotheses may thus be proposed: **Hypothesis 6.1: the similar body size and locomotor repertoire of sympatric *I. indri* and *P. diadema* suggests that niche differentiation between *I. indri* and *P. diadema* occurs by adoption of quantitatively different diets** and it follows from this that we may expect (see Chapter 8) quantitative differences in stratum (see e.g. Crompton, 1984 and particularly Ganzhorn, 1989). **Hypothesis 6.2: *I. indri*, as proposed by Powzyk (1997) is a more specialized feeder on low quality food, and *P. diadema* a generalist, eating higher quality food** and **Hypothesis 6.3: as a more specialized feeder *I. indri* will have fewer and longer feeding bouts each day compared to *P. diadema* (Powzyk, 1997 [see also e.g. Crompton, 1984 for *Galago moholi* {southern lesser bushbaby} and *Otolemur crassicaudatus* {thick-tailed greater bushbaby}]).**

6.1.3 Age, Sex and Dietary Variation

Feeding behaviour can differ between ages and sexes within a species, influenced *inter alia* by differences in feeding location, species and plant parts eaten, and the overall time spent feeding. Lighter individuals such as sub-adults (Crompton, 1983) and in some taxa, females, may have access to thinner branches.

Further, demands of reproduction, pregnancy and lactation require females to feed for longer, or take better-quality food, than males, while dominance affects an individual's access to food resources. For example, dietary differences have been found to exist between the sexes in *H. g. griseus* (Tan, 1999; Grassi, 2002). Females eat a greater variety of food, possibly as a result of their increased reproductive needs, eating more fruit and more non-bamboo food (Grassi, 2002). Given the dietary constraints on all three species, we expect that: **Hypothesis 6.4: females of each species will take better-quality food from more diverse sources.**

6.1.4 Seasonal and Temporal Variation in Diet

Temporal differences are found diurnally and seasonally (Clutton-Brock, 1977b; Chapman *et al.*, 2002): diurnal variation can be observed in changes in heights used, the amount of time spent feeding and the choice of foods at different time of the day. Seasonal variation is related to resource availability and climate. Powzyk (1997) recorded mean monthly minima in Mantadia ranging from 10.1°C to 17.3°C and mean monthly maxima varying from 17.2°C to 30.1°C. Britt *et al.* (2002) found the diet of *I. indri* to be seasonal in Betampona, eastern Madagascar. Between April and May, and from September to November, mature leaves were the most commonly eaten food; these are periods when there were fewer young leaves. Fruit consumption increased in April and from July to September, which period also saw bark appear as an important component of diet. Flowers were most commonly eaten from April to June and in October, petioles being eaten mostly in September.

Since Madagascar is subject to particularly intense seasonality for the tropics (Kappeler, 2000a; Pochron & Wright, 2003), and the present study deals with three sympatric species at Mantadia, where past climatic records (Powzyk, 1997) show strong seasonality, and we have no reason to expect that the three subject species should respond differently to variation in dietary availability, we can propose: **Hypothesis 6.5: all three species will show strong seasonality in diet.**

6.2. Methods

6.2.1. Field Methods

Continuous focal animal sampling (Altmann, 1974) was conducted by Sabine Day, the aim being to follow a single individual throughout the daily observation period. If an individual was lost, observation continued on the physically closest alternative subject. Within-species data was pooled, so unless otherwise stated, analysis is independent of individual and time. The schedule of data collection (Table 6.1) by Day was part of a larger study of activity. The time at the start and end of each feeding bout was recorded as: hour; minute; seconds. The estimated height of subjects when feeding was recorded in metres, in consultation with Blanchard and guides. Plant species were identified with the help of the local guides and, when familiarity was achieved, were recorded by their Malagasy vernacular names. In cases where the name was not known, they were recorded as: plant, orchid, liana etc. Plant-parts consumed were recorded as either: young leaves, mature and young leaves, mature leaves, young fruit, old fruit, open flowers, flower buds, petioles, stem, twigs, galls, bark (Table 6.2) and the non-plant part of soil, not included in analysis of plant parts.

Table 6.1. Schedule of observations conducted by Day on feeding behaviour.

1	Date
2	Species and individual identification
3	Time at start of feeding
4	Time at end of feeding
5	Height (m)
6	Plant species
7	Plant part(s) consumed (Table 6.2)
8	Patch size

Table 6.2. Definition of plant parts used within this study.

Young leaves	Younger flexible leaves that are paler in colour.
Mature leaves	Older leaves that have lost their flexibility and are darker in colour.
Petioles	Stems which support the leaf blade
Young fruit	New whole fruit, still on tree
Old fruit	Old whole fruit, that has fallen to the ground
Galls	A swelling of plant tissue caused by an insect or fungus
Open flowers	Flowers which are mature and open to pollination
Flower buds	Unopened flowers
Stem	Fleshy stem, not including petiole
Twigs	Woody stems
Bark	Outer layer of bark, composed of the phloem and cortex.

Vernacular Malagasy names were compared to a listing supplied by ANGAP at the Parc National Andasibe Mantadia. This list recorded family and species for the Malagasy vernacular names, as well as endemic status, plant utilisation, location (Special Reserve or National Park), habitat (primary or secondary forest etc.) and type (tree, herbaceous, etc. [Appendix D1]). Where possible the species name was recorded, however some Malagasy vernacular names represent multiple species, so only generic and in some cases family names could be identified. Unfortunately not all Malagasy vernacular names could be identified to Linnean species names. Most of these have later been identified in consultation with Day and ANGAP guides, a few remaining un-identified. As vernacular names might refer to more than one species, all species counts must be viewed as a minimum.

6.2.2. Data Analysis

Simpson's diversity index was used to measure annual and monthly dietary diversity (Equation 6.1). This value depends on the number of species eaten, as well as accounting for the time spent on each; plant species eaten less do not affect diversity as greatly as commonly-consumed species (Simpson, 1949; Irwin, 2006b). This value ranges between 1 and the total number of species within the diet. Unknown 'plants' were treated as a single species, so the diversity index represents a minimum.

$$D = 1/\sum P_i^2$$

Equation 6.1. Simpson's diversity index (***D***), where P_i is the proportion of feeding time for each plant species consumed.

Dietary overlap was measured using Schoener's (1968) index (Equation 6.2), recommended by Abrams (1980) as the best method of calculating niche overlap. This index has been used to examine dietary overlap in animals as diverse as fish (Makhabu, 2005) and ruminants (Mysterud, 2000). Overlap varies between 0, indicating no overlap, and 1 indicating all food types used in equal proportions (Irwin, 2006b). Both monthly and yearly dietary profiles were constructed.

$$D = 1 - 0.5\sum |P_{ij} - P_{ik}|$$

Equation 6.2. Schoener's Index (1968 [***D***]), where P_{ij} is the proportional representation of food type '*i*' in the diet of species/group '*j*' and P_{ik} is the proportional representation of food type '*i*' in the diet of species/group '*k*'.

The Pearson-correlation coefficient (*r*) has been used to test for correlations between the above indices and hours of observations, significance is set at $p \leq 0.05$. The Mann-Whitney (*U*) test has been used to examine inter-specific differences between bouts. The Mann-Whitney test uses the median and is suitable for non-parametric samples where variables are independent (Kinnear & Gray, 2004). In the Mann-Whitney tests significance is met when $p \leq 0.05$.

6.3. Results

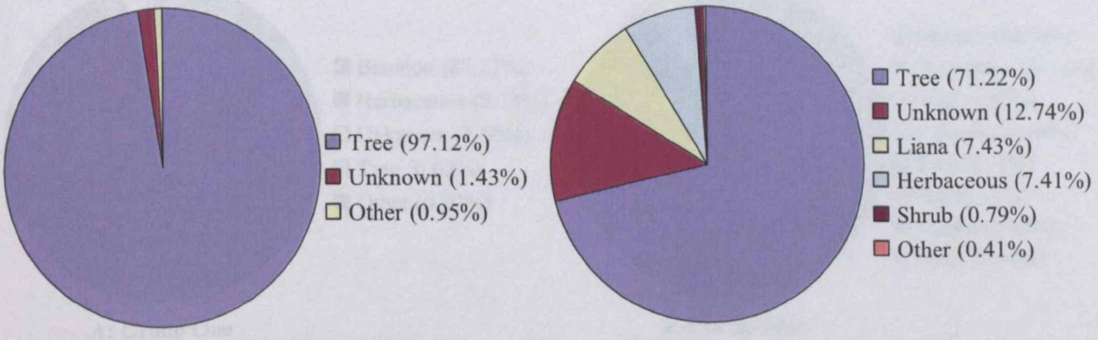
Over 250 hours of feeding data was collected between the three study species (Table 6.3).

Table 6.3. Number and time of feeding observations for *I. indri*, *P. diadema* and *H. g. griseus* Group One and Two.

	I. indri	*P. diadema*	*H. g. griseus*	
			One	**Two**
Total number of recorded feeding bouts	496	652	688	381
Total recorded feeding time (seconds)	266238	277406	217489	148047
Total recorded feeding time (hours)	74	77.1	60.4	41.1
Number of days of observation	22	21	17	11

6.3.1. Plant Type

Most of the total time *I. indri* were observed feeding, they were eating from trees (Figure 6.1). *P. diadema* spent the majority of the total observed feeding time eating from trees), lianas and herbaceous plants were quite commonly eaten.



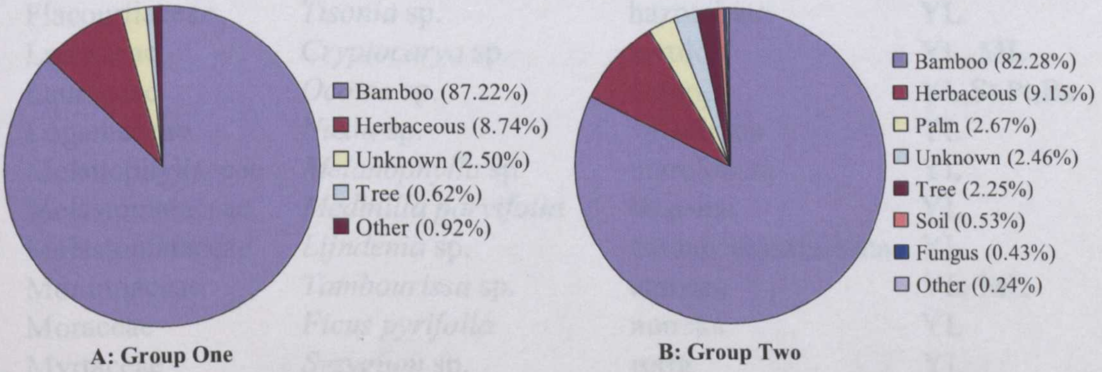
A: ***I. indri*** **B:** ***P. diadema***

Figure 6.1. A: Percentage of the total observed feeding time *I. indri* spent feeding on each plant type. Other: liana (0.85%); moss (0.07%); soil (0.04%). **B:** Percentage of the total observed feeding time *P. diadema* spent feeding on each plant type. Other: parasites (0.27%); orchids (0.07%); soil (0.04%); ferns (0.03%).

The percentage of time *P. diadema* spent feeding on non-tree plants varies monthly (Figure 6.2). They spent less time feeding from non-tree plants during winter months (June to August) compared to the summer months.

Figure 6.2. Percentage of time spent feeding on non-tree plant types (lianas, parasites, ferns, orchids, herbaceous and shrubs) compared to the time spent feeding on trees, for *P. diadema*.

Both groups of *H. g. griseus* spent most of the total observed feeding time feeding from bamboo (Figure 6.3). Following this both groups spent a similar period of time feeding on herbaceous plants; other categories each contributed less than 3% of feeding time.



A: Group One

B: Group Two

Figure 6.3. A: Percentage of the total observed feeding time *H. g. griseus* Group One spent feeding on each plant type. Other: orchids (0.13%); lianas (0.10%). **B:** Percentage of the total observed feeding time *H. g. griseus* Group Two spent feeding on each plant type. Other: liana (0.34%); fungus (0.27%); shrub (0.15%); grass (0.1%); soil (0.05%).

6.3.2. Plant Species

6.3.2.1. *Indri indri*

Over the study period *I. indri* were recorded as eating from a minimum of 37 different plant species (Table 6.4).

Table 6.4. Plant species consumed by *I. indri* in the present study, ranked alphabetically by Family.

Family	Species	Vernacular name	Parts consumed
Anacardiaceae	*Protorhus ditimena*	ditimena	YL
Annonaceae	*Xylopia flexuosa*	hazoambo	YL
Araliaceae	*Cuphocarpus* sp.	vantsilana	YL
Asteraceae	*Apodocephala angustifolia*	beaty	YL
Asteraceae		merampamelona	YL
Asteraceae	*Brachylaena perrieri*	merana	YL
Chlaenaceae	*Rhodolaena altivola*	fotona	YL
Clusiaceae		kijy	YL, Fl
Clusiaceae	*Symphonia fasciculata*	kijy bonaka	Fr
Clusiaceae	*Garcinia mangourensis*	kijy masina	YL
Clusiaceae	*Callophyllum milvum*	vintanona	YL
Combretaceae	*Terminalia tetrandra*	antafanala	YL
Cunoniaceae	*Weinmannia* sp.	lalona	YL
Erythroxylaceae	*Erythroxylum* sp.	menahihy	YL
Euphorbiaceae		hazondomohina	YL
Euphorbiaceae	*Macaranga* sp.	mankaranana	YL
Euphorbiaceae	*Uapaca densifolia*	voapaka	YL, Bu, Pt
Flacourtiaceae	*Tisonia* sp.	hazombato	YL
Lauraceae	*Cryptocarya* sp.	tavolo	YL, ML
Lauraceae	*Ocotea* sp.	varongy	YL,St,Pt,Ba
Loganiaceae	*Nuxia* sp.	valanirana	YL
Melanophyllaceae	*Melanophylla* sp.	marefolena	YL
Melastomataceae	*Medinilla parvifolia*	takasina	YL
Melastomataceae	*Lijndenia* sp.	tsimahamasatsokina	YL
Monimiaceae	*Tambourissa* sp.	ambora	YL, ML
Moraceae	*Ficus pyrifolia*	nonoka	YL
Myrtaceae	*Syzygium* sp.	rotra	YL
Pittosporaceae	*Pittosporum* sp.	hazombary	YL
Rubiaceae	*Anthirea borbonica*	malemiravana	YL
Sapindaceae	*Filicium* sp.	elatrangidina	YL
Sapindaceae	*Tinopsis* sp.	ramaindafa	YL
Sapindaceae	*Plagiocyphus jumellei*	volanary	YL
Sapotaceae	*Chrysophyllum boivinianum*	famelona	YL
Sapotaceae		nanto	YL
Sphaerosepalaceae	*Carallia brachiata*	farimamy	YL
		liana	YL, Bu
		lomotra (moss)	YL

YL: young leaves; ML: mature leaves; Bu: buds; Ba: bark; Fl: flowers; Fr: fruit.

The overwhelming majority (90.03%) of the total feeding time of *I. indri*, was spent feeding on ten plant species (Table 6.5).

Table 6.5. Top ten plant species consumed by *I. indri*, ranked by feeding time.

Family	Species	Plant part	Seconds feeding	Percent of feed time
Euphorbiaceae	*Uapaca densifolia*	YL, Bu, Pt	74563	28.15
Lauraceae	*Ocotea sp.*	YL, St, Pt, Ba	52761	19.92
Monimiaceae	*Tambourissa sp.*	YL, ML	29943	11.30
Lauraceae	*Cryptocarya sp.*	YL, ML	27985	10.56
Myrtaceae	*Syzygium sp.*	YL	19622	7.41
Erythroxylaceae	*Erythroxylum sp.*	YL	10663	4.03
Clusiaceae		YL, Fl	8353	3.15
Sapotaceae		YL	5355	2.02
Annonaceae	*Xylopia flexuosa*	YL	5316	2.01
Sapindaceae	*Tinopsis sp.*	YL	3936	1.49

YL: young leaves; ML: mature leaves; Bu: buds; Pt: petioles; St: stems; Ba: bark; Fl: flowers.

The total dietary diversity of plant species eaten by *I. indri* was calculated using Simpson's diversity index and found to be 7.12. There was monthly variation in the diversity index (Figure 6.4), with a low of 3.34 in May and a high of 6.15 in August. To insure that this apparent variation was real and not a consequence of variation in the number of monthly hours of observation, a Pearson correlation coefficient was calculated for the indices against hours of observation. This indicated no correlation (r [9] = 0.256, $p > 0.05$) suggesting that the variation in diversity index was a real phenomenon.

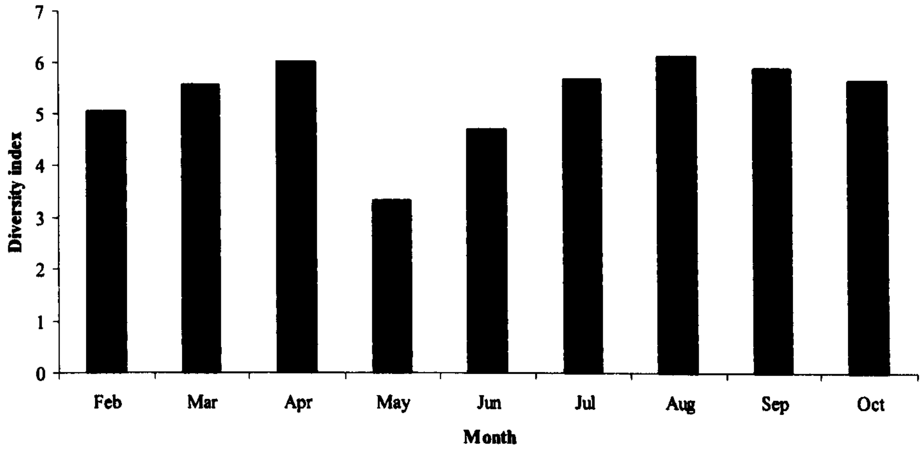


Figure 6.4. Monthly dietary diversity, using Simpson's diversity index, for *I. indri*.

I. indri ate from 23 known families out of a total of 104 listed by ANGAP at Park National Andasibe-Mantadia (Table 6.6).

Table 6.6. List of plant families eaten by *I. indri*, ranked by total feed time.

Family	Species	Total feed time		Young leaves		Other	
		Sec	%	Sec	%	Sec	%
Lauraceae	2	80746	30.49	62764	26.64	14311[a]	2.53
Euphorbiaceae	3	75327	28.45	73241	31.09	2086[b]	0.37
Monimiaceae	1	29943	11.31	28104	11.93	1839[c]	0.32
Myrtaceae*	1	19622	7.41	19622	8.33		
Clusiaceae	4	11279	4.26	4679	1.99	547162[d]	96.65
Erythroxylaceae	1	10663	4.03	10663	4.53		
Sapindaceae	3	6448	2.44	6448	2.74		
Unknown	4	6237	2.36	5526	2.35	711[e]	0.13
Sapotaceae*	2	5449	2.06	5449	2.31		
Annonaceae	1	5316	2.01	5316	2.26		
Moraceae	1	2665	1.01	2665	1.13		
Chlaenaceae*	1	1976	0.75	1976	0.84		
Cunoniaceae*	1	1752	0.66	1752	0.74		
Anacardiaceae*	1	1313	0.50	1303	0.55		
Flacourtiaceae	1	1181	0.45	1181	0.50		
Sphaerosepalaceae*	1	1160	0.44	1160	0.49		
Melastomataceae*	2	1027	0.39	1027	0.44		
Asteraceae	3	1020	0.39	1020	0.43		
Loganiaceae*	1	383	0.14	383	0.16		
Rubiaceae*	1	368	0.14	368	0.16		
Araliaceae	2	333	0.13	333	0.14		
Pittosporaceae*	1	295	0.11	295	0.13		
Melanophyllaceae*	1	180	0.07	180	0.08		
Combretaceae*	1	119	0.04	119	0.05		

Other: [a]Bark, mature leaves, stalks and petioles; [b]Petioles and buds; [c]mature leaves; [d]flowers, fruits; [e]buds. *Not recorded by Powzyk (1997).

6.3.2.2. *Propithecus diadema*

A minimum of 78 plant species were recorded as consumed by *P. diadema* (Table 6.7).

Table 6.7. Plant species consumed by *P. diadema* in the present study, ranked alphabetically by family.

Family	Species	Vernacular name	Parts consumed
Acanthaceae	*Hypoestes corymbosa*	beloalika	YL, ML
Acanthaceae	*Hypoestes* sp.	ravimabelatra	YL
Anacardiaceae	*Protorhus ditimena*	ditimena	YL
Anacardiaceae	*Micronychia* sp.	tsiramiramy	YL
Annonaceae	*Xylopia* sp.	hazoambo	YL
Aquifoliaceae	*Ilex mitis*	hazondrano	YL

Family	Species	Vernacular name	Parts consumed
Araliaceae	*Cussonia* sp.	voatsilana	YL
Aspleniaceae	*Asplenium nidus*	ampango	YL
Asteraceae	*Apodocephala angustifolia*	beaty	YL
Asteraceae	*Brachylaena* sp.	meramaintso	YL
Asteraceae	*Brachylaena perrieri*	merana	YL
Asteraceae	*Vernonia* sp.	sirambengy	YL
Bignoniaceae	*Phyllarthron* sp.	zahana	ML
Chlaenaceae	*Rhodolaena altivola*	fotona	YL
Clusiaceae	*Garcinia verrucosa*	kijim-boalavo	YL
Clusiaceae		kijy	YL
Clusiaceae	*Symphonia fasciculata*	kijy bonaka	YL
Combretaceae	*Terminalia tetrandra*	antafanala	YL
Cunoniaceae	*Weinmannia* sp.	lalona	YL
Erythroxylaceae	*Pleuroridgea* sp.	malambovay	YL, Fl
Erythroxylaceae	*Erythroxylum* sp.	menahihy	YL
Euphorbiaceae	*Blotia* sp.	fanjavala	YL
Euphorbiaceae	*Blotia oblongifolia*	fanjavala beravina	YL
Euphorbiaceae	*Blotia mimosoides*	fanjavala madinidravina	YL
Euphorbiaceae		hazondomohina	YL
Euphorbiaceae	*Macaranga* sp.	mankaranana	YL
Euphorbiaceae	*Uapaca densifolia*	voapaka	YL
Fabaceae	*Dallbergia* sp.	palissandre	YL, St
Fabaceae	*Albizzia gummifera*	volomborona	YL
Flacourtiaceae		menavahatra	YL
Icacinaceae	*Leptaulus* sp.	maintsoririnina	YL
Lauraceae		tavaratra	YL
Lauraceae	*Cryptocarya* sp.	tavolo	YL
Lauraceae	*Ocotea* sp.	varongy	YL
liana vine		liana	YL, St
Loranthaceae	*Bakerella clavata*	dongavelona	YL
Melastomataceae	*Medinilla parvifolia*	takasina	YL
Melastomataceae	*Lijndenia* sp.	tsimahamasatsokina	Fr
Monimiaceae	*Tambourissa* sp.	ambora	YL
Moraceae	*Stribulus obovata*	dipaty	YL
Moraceae	*Ficus pyrifolia*	nonoka	YL,ML,Fr
Moraceae	*Ficus* sp.	other nonoka	Fr
Myrsinaceae	*Oncosternon* sp.	hazontoho	YL
Myrsinaceae	*Maesa lanceolata*	radoka	YL
Myrtaceae	*Eugenia sakalavarum*	hazompasika	YL
Myrtaceae	*Eugenia emirnensis*	robary	YL
Myrtaceae	*Syzygium* sp.	rotra	YL, ML
Myrtaceae		rotra mena	YL
Pittosporaceae	*Pittosporum* sp.	hazombary	YL
Poaceae	*Poecilostachys festicaceus*	vilonala	YL

Family	**Species**	**Vernacular name**	**Parts consumed**
Proteaceae	*Dilobeia thouarsii*	vivaona	YL, ML
Rubiaceae	*Craterispermum laurinum*	hazomamy	YL
Rubiaceae	*Schismatoclada farahipensis*	hazoporetika	YL
Rubiaceae	*Anthirea borbonica*	malemiravana	YL, Fr
Rubiaceae	*Breonia sinensis*	molompangady	YL, Fl
Rubiaceae	*Canthium* sp.	pitsikahitra	YL
Rubiaceae	*Canthium* sp.	pitsikahitra oloina	YL
Rubiaceae	*Tricalysia albicaulis*	tsikafekafe	YL
Sapindaceae	*Filicium* sp.	elatrangidina	YL
Sapindaceae	*Allophylus cobbe*	karambito	YL
Sapindaceae	*Tinopsis* sp.	ramaindafa	YL
Sapindaceae	*Plagiocyphus jumellei*	volanary	YL
Sapotaceae	*Chrysophyllum boivinianum*	famelona	YL
Sapotaceae		nanto	YL, ML
Smilacaceae	*Smilax kraussiana*	fandrikataly	YL
Solanaceae	*Solanum auxicilatum*	bakobako	Fr
Stericuliaceae	*Dombeya* sp.	hafotra	YL
		anjananjana	YL
		fougeres	YL
		manitranefitra	YL
		molotrangaka	YL
		orchid	YL, St
		parasitic plant	Fl
		unknown plant	YL, Fr, St
		ramitisihaka	YL
		sakatairotrala	Fl
		tsingarivary	YL, ML, Fr, OF
		voroinampanga	YL

YL: young leaves; ML: mature leaves; Fr: fruit; OF: old fruit; Fl: Flowers; St: stem; Ba: bark.

72.64% of the total feeding time of *P. diadema* was spent feeding from 10 plant species (Table 6.8). A different 'top-ten' is found for plant parts (Table 6.9).

Table 6.8. Top ten plant species consumed by *P. diadema*, ranked by feeding time.

Family	Species	Parts eaten	Seconds feeding	Percent of feed time
Lauraceae	*Ocotea* sp.	YL, ML, Fr, OF	30134	11.07
Myrtaceae	*Syzygium* sp.	YL, ML, Ba	29412	10.80
		YL, St, Fr	27287	10.02
Sapotaceae		YL, ML	22373	8.22
		YL	20599	7.56
Loranthaceae	*Bakerella* sp.	YL	18476	6.78
Euphorbiaceae	*Uapaca* sp.	YL	15162	5.57
Clusiaceae		YL, Fr	14626	5.37
Melastomataceae	*Lijndenia* sp.	Fr, Bu	11480	4.22
Clusiaceae	*Symphonia fasciculata*	Fl	8278	3.04

YL: young leaves; ML: mature leaves; Fr: fruit; OF: old fruit; Ba: bark; St: stem; Bu: buds.

Table 6.9. Top ten plant food parts/plant species for *P. diadema*, ranked by time spent feeding.

Family	Species	Plant part	Seconds feeding	Percent of feed time
Myrtaceae	*Syzygium* sp	Young leaves	28728	11.00
		Young leaves	25689	9.83
Lauraceae	*Ocotea* sp.	Young leaves	23529	9.01
		Young leaves	20288	7.77
Sapotaceae		Young leaves	20281	7.76
Loranthaceae	*Bakerella* sp.	Young leaves	18476	7.07
Euphorbiaceae	*Uapaca* sp.	Young leaves	15162	5.80
Clusiaceae		Young leaves	13778	5.27
Melastomataceae	*Lijndenia* sp.	Fruit	11480	4.39
Lauraceae	*Cryptocarya* sp.	Young leaves	4808	1.84

P. diadema had a dietary diversity index of 16.08 with monthly variation, ranging from 3.27 in February to 10.96 in September. However the monthly indices were found to correlate with the number of hours of observations per month at the 0.05 level (r [9] = 0.705, $p < 0.05$) indicating that this is probably not a real phenomenon of seasonal change in dietary diversity. *P. diadema* ate from 32 known families (Figure 6.8).

Table 6.10. List of plant families eaten by *P. diadema*, ranked by total feed time.

Family	**Number species**	**Total feed time**		**Young leaves**		**Other**	
		Sec	**%**	**Sec**	**%**	**Sec**	**%**
Unknown	12	56352	22.78	53243	94.48	3109^{abg}	5.52
Lauraceae	3	37111	12.24	28596	77.06	8515^{bc}	22.94
Myrtaceae	4	35489	13.50	31537	88.86	3254^{bcg}	9.17
Clusiaceae	3	24116	6.41	14990	62.16	9126^{bg}	37.84
Sapotaceae	2	23980	9.37	21888	91.28	2092^{c}	8.72
Euphorbiaceae	6	20241	8.47	19799	97.82	442^{b}	2.18
Loranthaceae	1	18476	7.91	18476	100		
Melastomataceae	2	12959	0.63	1479	11.41	11480^{bd}	88.59
Sapindaceae	4	5108	2.19	5108	100		
Monimiaceae	1	4287	1.83	4287	100		
Rubiaceae	7	4114	1.71	3994	97.08	120^{bg}	2.92
Moraceae	3	4030	1.18	2759	68.46	1271^{bc}	31.54
Flacourtiaceae	1	3170	1.36	3170	100		
Aquifoliaceae	1	3150	1.35	3150	100		
Erythroxylaceae	2	2669	1.11	2590	97.04	79^{g}	2.96
Annonaceae	1	2597	0.99	2303	88.68	294^{e}	11.32
Pittosporaceae	1	2079	0.89	2079	100		
Anacardiaceae	2	1938	0.83	1938	100		
Proteaceae	1	1936	0.77	1790	92.46	146^{c}	7.54
Chlaenaceae*	1	1859	0.80	1859	100		
Asteraceae	3	1620	0.69	1620	100		
Araliaceae	1	1500	0.64	1500	100		
Acanthaceae	2	1352	0.48	1125	83.21	227^{c}	16.79
Fabaceae	1	1115	0.46	1070	95.96	45^{f}	4.04
Combretaceae*	1	1008	0.43	1008	100		
Poaceae*	1	726	0.31	726	100		
Icacinaceae*	1	520	0.22	520	100		
Cunoniaceae	1	460	0.20	460	100		
Myrsinaceae	2	445	0.19	445	100		
Smilacaceae*	1	138	0.00			138^{c}	100
Bignoniaceae*	1	112	0.00			112^{c}	100
Solanaceae	1	96	0.00			96^{b}	100
Stericuliaceae*	1	93	0.04	93	100		
Pteridophyte*	1	75	0.03	75	100		

Other: ^{a}stems; ^{b}fruit; ^{c}mature leaves; ^{d}buds; ^{e}galls; ^{f}stems; ^{g}flowers. *Not recorded by Powzyk (1997).

6.3.2.3. Comparison between *Indri indri* and *Propithecus diadema*

P. diadema ate food from more plant species than *I. indri* in all months (Figure 6.5), a statistically significant distinction ($U\,[18] = 7, p < 0.01$).

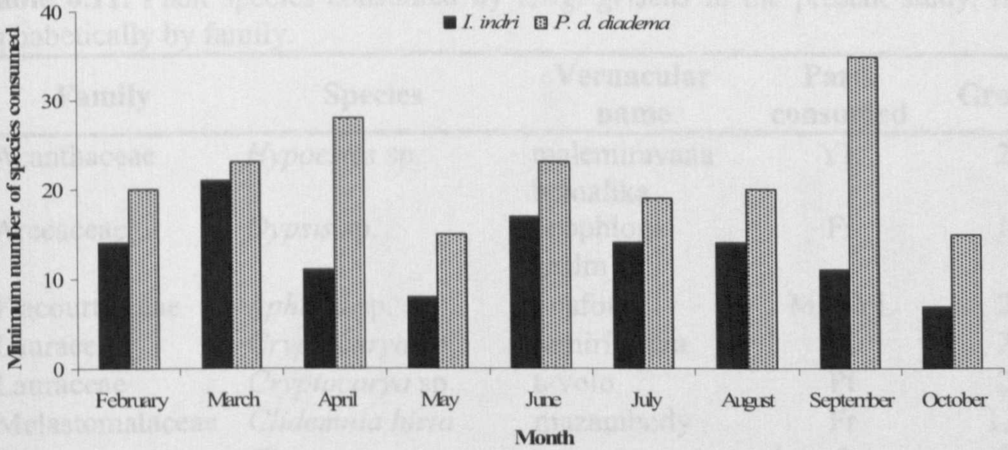


Figure 6.5. Comparison of the minimum number of plant species consumed each month by *I. indri* and *P. diadema*.

Calculation of Schoener's index indicated a dietary overlap of 0.42 in plant species consumed by *I. indri* and by *P. diadema*. When consumed plant parts were considered, the overlap dropped to 0.38. Monthly dietary overlaps were calculated using plant parts consumed (Figure 6.6), and this indicated that dietary overlap is higher in winter months, with a high of 0.53 in July, and lower in summer, with a low of 0.15 in April.

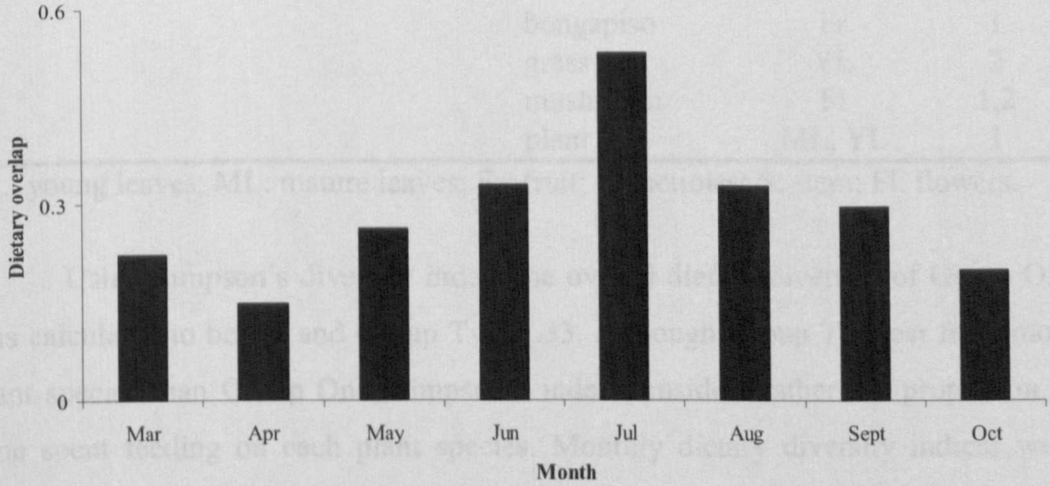


Figure 6.6. Monthly dietary overlap, measured using Schoener's index, between *I. indri* and *P. diadema*.

6.3.2.4. *Hapalemur griseus griseus*

H. g. griseus were recorded to consume parts from only 19 plant species (Table 6.11): Group One ate from 12 different species and Group Two from 14 species.

Table 6.11. Plant species consumed by *H. g. griseus* in the present study, ranked alphabetically by family.

Family	Species	Vernacular name	Parts consumed	Group
Acanthaceae	*Hypoestes* sp.	malemiravana beloalika	YL	2
Arecaceae	*Dypsis* sp.	neophloga (palm)	Fr	1
Flacourtiaceae	*Aphloia* sp.	voafotsy	ML, YL	2
Lauraceae	*Cryptocarya* sp.	ramiringitra	YL	2
Lauraceae	*Cryptocarya* sp.	tavolo	Pt	2
Melastomataceae	*Clidemnia hirta*	mazambody	Fr	1,2
Moraceae	*Ficus* sp.	voara montsana	?	2
Moraceae		voaroy	YL, ML	2
Orchidaceae		orchid	ML, Fl	1
Poaceae	*Cathariostachys madagascariensis*	giant bamboo	YL, S	1,2
Poaceae	*Poecilostachys festucaceus*	vilonala	YL	1,2
Poaceae	*Cephalostachyum* sp.	liana bamboo	YL, S	1,2
Stericuliaceae	*Dombeya* sp.	hafotra ramiringitra	ML, YL	1,2
Stericuliaceae	*Dombeya* sp.	long hafotra ramiringitra	ML, YL	1
		liana	Fr	2,1
		bongapiso	Fr	1
		grass	YL	2
		mushroom	Fl	1,2
		plant	ML, YL	1

YL: young leaves; ML: mature leaves; Fr: fruit; Pt: petioles; S: stem; Fl: flowers.

Using Simpson's diversity index, the overall dietary diversity of Group One was calculated to be 1.6 and Group Two 1.33. Although Group Two eat from more plant species than Group One, Simpson's index considers rather the proportion of time spent feeding on each plant species. Monthly dietary diversity indices were calculated for each group (Figure 6.7). Diversity values were checked for a correlation with the number of hours of observation each month, but no correlation was found (Group One: r [11] = -0.099, $p >$ 0.05ns; Group Two: r [6] = -0.356, $p >$ 0.05ns) indicating that the differences in dietary diversity are not artificial.

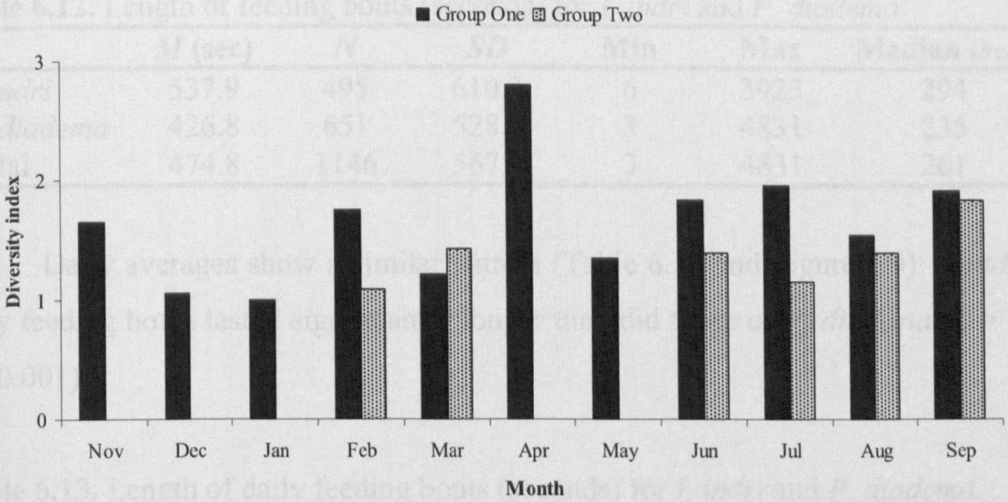


Figure 6.7. Monthly dietary diversity for Group One and Two *H. g. griseus*.

The dietary overlap for species between Group One and Two, calculated using Schoener's Index, was found to be 0.86. This only fell to 0.85 when plant parts consumed were considered. There was monthly variation in overlap considering plant part and species (Figure 6.8). A monthly high was observed in March of 0.86, while in September dietary overlap fell to 0.44.

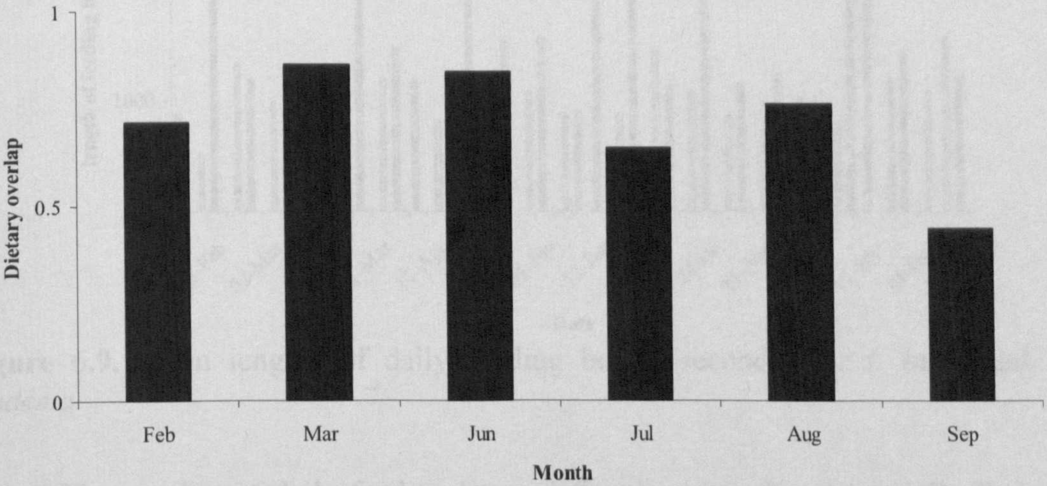


Figure 6.8. Monthly dietary overlap of *H. g. griseus* Group One and Two, using Schoener's Index.

6.3.3. Bout Length and Frequency

I. indri fed in single bouts, regardless of food item, for a median of 294 seconds and *P. diadema* for 235 seconds (Table 6.12), a significant difference ($U = 140052.5, p < 0.001$).

Table 6.12. Length of feeding bouts (seconds) for *I. indri* and *P. diadema*.

	***M* (sec)**	***N***	***SD***	**Min**	**Max**	**Median (sec)**
I. indri	537.9	495	610.3	6	3923	294
P. diadema	426.8	651	528.5	3	4831	235
Total	474.8	1146	567.7	3	4831	261

Daily averages show a similar pattern (Table 6.13 and Figure 6.9): *I. indri's* daily feeding bouts lasted significantly longer than did those of *P. diadema* ($U = 79$, $p < 0.001$).

Table 6.13. Length of daily feeding bouts (seconds) for *I. indri* and *P. diadema*.

	***M* (sec)**	***N***	***SD***	**Min**	**Max**	**Median (sec)**
I. indri	1507.8	20	587.5	848	2829	1234
P. diadema	997.7	20	245.7	531	1540	975.5
Total	1252.7	40	514.1	531	2829	1117

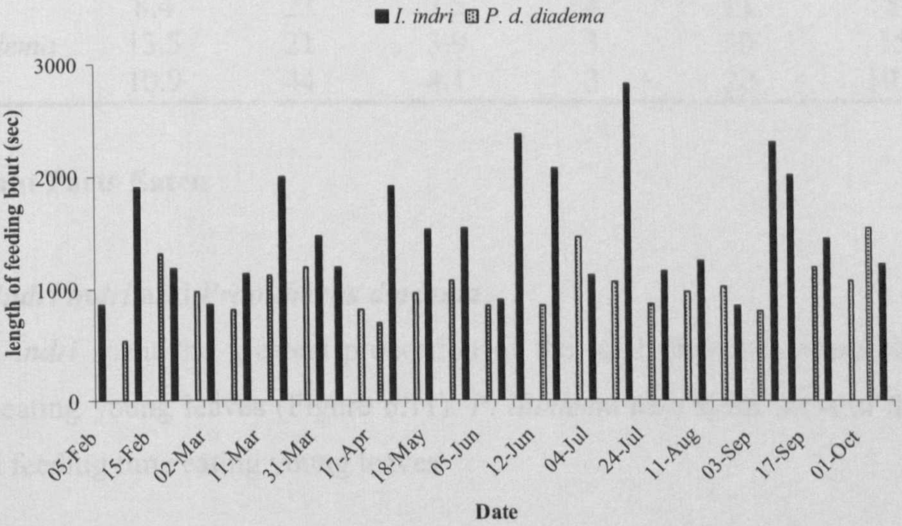


Figure 6.9. Mean lengths of daily feeding bouts (seconds) for *I. indri* and *P. diadema*.

The number of daily feeding bouts differs between *I. indri* and *P. diadema* (Figure 6.10). *P. diadema* had significantly more feeding bouts per day than *I. indri*. ($U = 63.5$, $p < 0.001$). *P. diadema* had a median of 15 feeding bouts on each day of observation, while *I. indri* had eight (Table 6.14). The number of daily bouts for *P. diadema* dropped in March as well as in June and July.

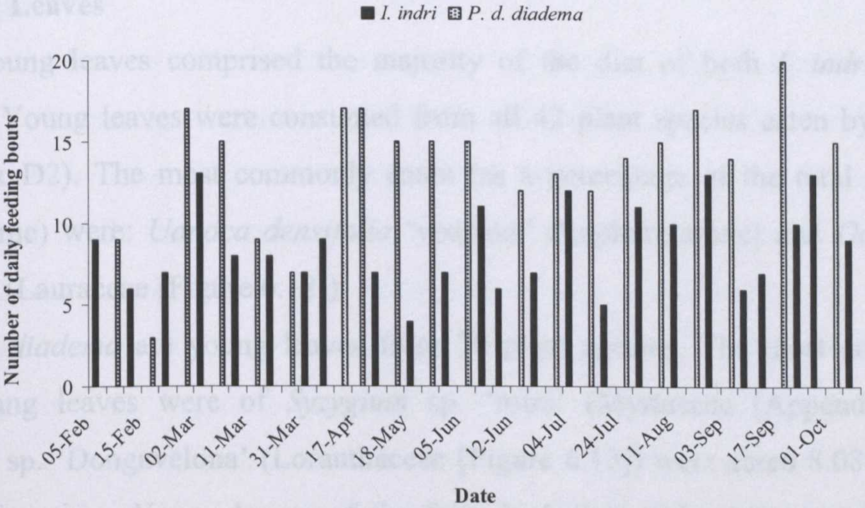


Figure 6.10. Total number of daily feeding bouts for *I. indri* and *P. diadema*.

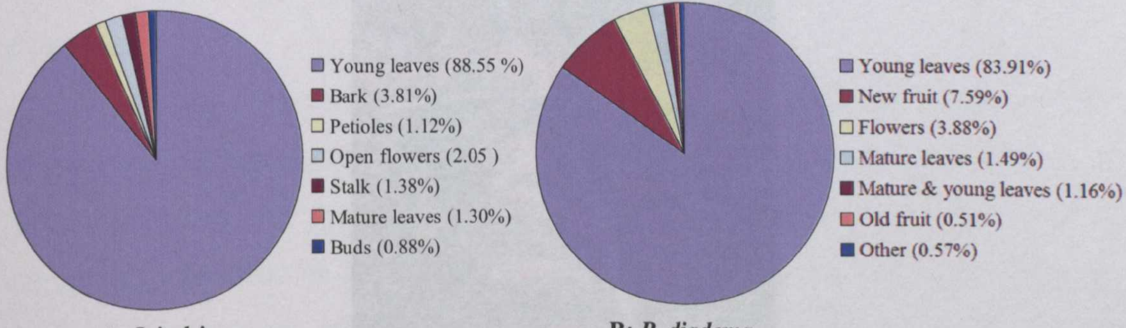
Table 6.14. Number of daily feeding bouts for *I. indri* and *P. diadema*.

	M	*N*	*SD*	Min	Max	Median
I. indri	8.4	23	2.5	4	13	8
P. diadema	13.5	21	3.9	3	20	15
Total	10.9	44	4.1	3	20	10.5

6.3.4. Plant Parts Eaten

6.3.4.1. *Indri indri* and *Propithecus diadema*

I. indri spent the greatest proportion of the total time they were observed feeding, eating young leaves (Figure 6.11). *P. diadema* also spent most of the total observed feeding time eating young leaves.



A: ***I. indri*** **B:** ***P. diadema***

Figure 6.11. A: Percentage of total feeding time *I. indri* spent feeding on each recorded plant part. **B:** Percentage of total feeding time *P. diadema* spent feeding on each recorded plant part. Other: bark (0.15%); stems (0.29%); galls (0.11%); buds (0.01%).

A. Young Leaves

Young leaves comprised the majority of the diet of both *I. indri* and *P. diadema*. Young leaves were consumed from all 42 plant species eaten by *I. indri* (Appendix D2). The most commonly eaten (as a percentage of the total recorded feeding time) were: *Uapaca densifolia* 'voapaka' (Euphorbiaceae) and *Ocotea* sp. 'varongy' (Lauraceae [Figure 6.12]).

P. diadema ate young leaves from 70 plant species. The most commonly eaten young leaves were of *Syzygium* sp. 'rotra' (Myrtaceae [Appendix D3]). *Bakerella* sp. 'Dongavelona' (Loranthaceae [Figure 6.13]) were eaten 8.08% of the total feeding time. Young leaves of the fern *Asplenium nidus* were consumed by male *P. diadema* in April and September.

Figure 6.12. *Ocotea* sp., 'varongy' (Lauraceae). Photograph: Mary Blanchard, 18 September 2005.

Figure 6.13. Hemiparasitic *Bakerella clavata* 'dongavelona' (Loranthaceae). Photograph: Mary Blanchard, 26 November 2004.

B. Tree Bark

Bark, from *Ocotea trichophleibia* 'varongy voara' (Lauraceae), was consumed by *I. indri* in August though October (Appendix D4). All individuals of *I. indri* were observed feeding on bark, and eleven bouts were recorded. When *I. indri* ate bark they would strip it using their mouths (Figure 6.14). In addition to feeding by quadrupedal suspension on a horizontal branch, they would eat bark by clinging, maintaining a vertical body posture on vertical supports. Not all individuals fed on bark at the same time; e.g. on 9 August 2005 the adult female was observed stripping bark from 'varongy', while the sub-adult female fed on petioles .

A male *P. diadema* was observed eating bark from 'rotra' a *Syzygium* species (Myrtaceae) on one occasion in September. Although the bark was only consumed on one occasion, *P. diadema* ate 'rotra' leaves monthly.

Figure 6.14. Male *I. indri* eating bark from *Ocotea trichophleibia*, 'varongy voara' (Lauraceae). Note the pale sections that have already been stripped. Photograph: Mary Blanchard, 23 September 2005.

C. Fruit

Only one species of fruit was consumed by *I. indri* at Mantadia 'kijy' (Clusiaceae) in February (Appendix D4). In contrast, *P. diadema* ate fruit from 10 different species over the study period (Appendix D5). *P. diadema* were observed eating old, fallen fruit on one occasion. The entire group ate old fruit from *Ocotea* sp. 'varongy' (Lauraceae), which had fallen to the forest floor. *P. diadema* collected and ate the fruit from the ground, picking it from amidst the leaf litter. Individuals were observed to climb down small-diameter verticals, before leaping from a height of 1 to 0.5m almost directly to the ground (covering a horizontal distance of less than

0.5m). After feeding they would leap over 2m horizontally and up to 4m vertically, onto medium-diameter verticals.

D. Flowers

In March and April *I. indri* ate flowers of *Symphonia fasciculata* 'kijy bonaka' (Clusiaceae [Figure 6.15]). In July and August they ate buds from *Uapaca densifolia* 'voapaka' (Euphorbiaceae [Appendix D4]). *P. diadema* were observed eating open flowers from six species (Appendix D5).

Figure 6.15. *Symphonia fasciculata*, 'Kijy bonaka' (Clusiaceae) flowers and buds, eaten by *I. indri* and *P. diadema*. Photographs: Mary Blanchard, 11 and 22 April 2005.

E. Other

I. indri ate mature leaves from only two species (Appendix D4). *P. diadema* fed on mature leaves of seven different species (Appendix D5). All *I. indri* were observed selectively eating leaf petioles (Appendix D4), allowing the remainder of the leaf to fall to the ground. Petioles were eaten from *Uapaca densifolia* 'voapaka' (Euphorbiaceae) and *Ocotea* sp. 'varongy' (Lauraceae). Petioles are also eaten selectively by *I. indri* at Betampona (R.H. Crompton pers. comm.). *P. diadema* were never observed selectively eating petioles, although they would consume them while eating young and mature leaves. In July, the adult male *I. indri* was observed feeding on stems of 'varongy', *Ocotea* sp. (Lauraceae [Appendix D4]) *P. diadema* ate stems from five different species (Appendix D5). The adult female *P. diadema* carrying her infant was observed eating galls, from *Xylopia* sp. 'hazoambo' (Annonaceae) once in July.

6.3.4.2. *Hapalemur griseus griseus*

Both groups of *H. g. griseus* were similar in the percentage of overall time spent feeding on each plant part (Figure 6.16). Most of the time for both groups was spent feeding on young leaves (82.5% and 84.37%), fruit was the second most popular food choice (9.48% and 7.89%),

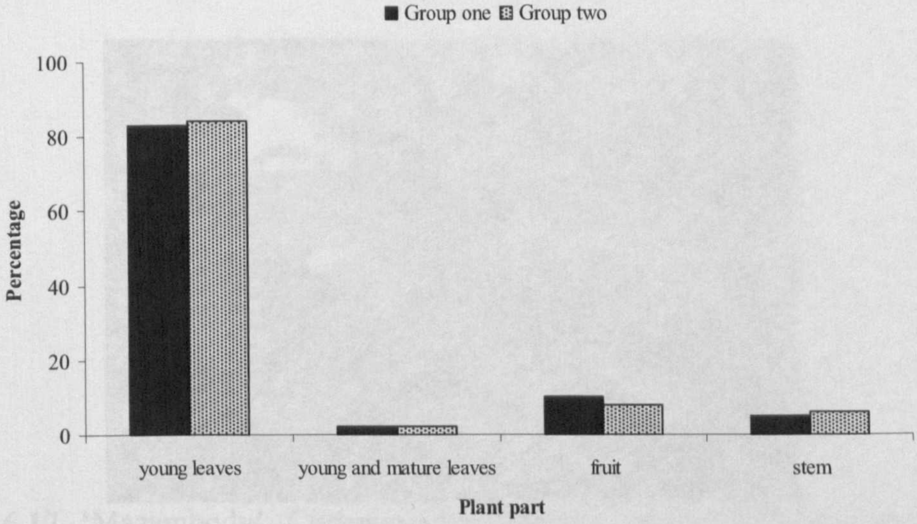


Figure 6.16. Percentage of total time spent feeding that all individuals of *H. g. griseus* spent on each plant part.

A. Young Leaves

Young leaves of *Cathariostachys madagascariensis*, giant bamboo, are the most commonly eaten food stuff for both groups of *H. g. griseus*, comprising 74.45% of the total diet of Group One and 80.52% of Group Two (Appendix D6 and D7).

The young leaves of *Cephalostachyum pierreri* (vine bamboo), are eaten by both groups, although the amounts eaten are very small. Group One ate young leaves of *C. pierreri* for 2.78% of their total feeding, and they comprised 1.27% of the total diet of Group Two. Group Two ate young leaves from a greater variety of non-bamboo sources than Group One, 1.60% compared to 0.75% compared to the total consumption of young leaves. Group One ate young leaves from two non-bamboo food sources, while Group Two ate from six.

B. Fruit

Fruit comprised 8.94% of the total diet of Group One and 7.86% of Group Two and was eaten throughout the year. Approximately half of the total fruit consumption for Group One and almost all for Group Two was from *Clidemia hirta* 'mazambody' (Melastomataceae [Figure 6.17]). 'Mazambody' was eaten from

February through to September (Appendix D6 and D7). Feeding on mazambody involved the entire group and lasted up to one hour, the group returning to feed on mazambody multiple times in the same day. Group One also ate fruit from *Dypsis* sp., a palm, and 'bongapiso', an unidentified plant. Group Two were never observed feeding from either of these plants.

Figure 6.17. 'Mazambody', *Clidemia hirta* (Melastomataceae).The fruit (edible to humans) is eaten by *H. g. griseus*. Juice from the leaves is used by local people to treat wounds. Photograph: Mary Blanchard, 04 April 2006.

C. Other

Both Group One and Group Two ate the stems of '*Cathariostachys madagascariensis* (giant bamboo) throughout the year (Appendix D6 and D7). Group One also ate stems from *Cephalostachyum pierreri* (vine bamboo). Both groups ate some plants where a combination of young and mature leaves tended to be taken. Young and mature leaves of *Dombeya* sp. 'hafotra ramiringitra' (Stericuliaceae), were a prominent food source for both groups (Appendix D6 and D7). A juvenile from Group One ate mature leaves from an orchid on two occasions (Appendix D6) and an infant from Group Two was observed eating petioles from *Cryptocarya* sp. 'tavolo' (Lauraceae). In September, a juvenile from Group One ate leaves and flower of an orchid.

6.3.5. Plant Parts Eaten Month by Month

6.3.5.1. *Indri indri* and *Propithecus diadema*

The diet of *I. indri* is generally far more conservative that *P. diadema*, as shown by their lower diversity index. In six of the nine study months *I. indri* ate more young leaves than *P. diadema*, however in three months (July, August and October) the reverse occurred (Figure 6.18). The breakdown of the 'other' can be seen in Figure 6.19

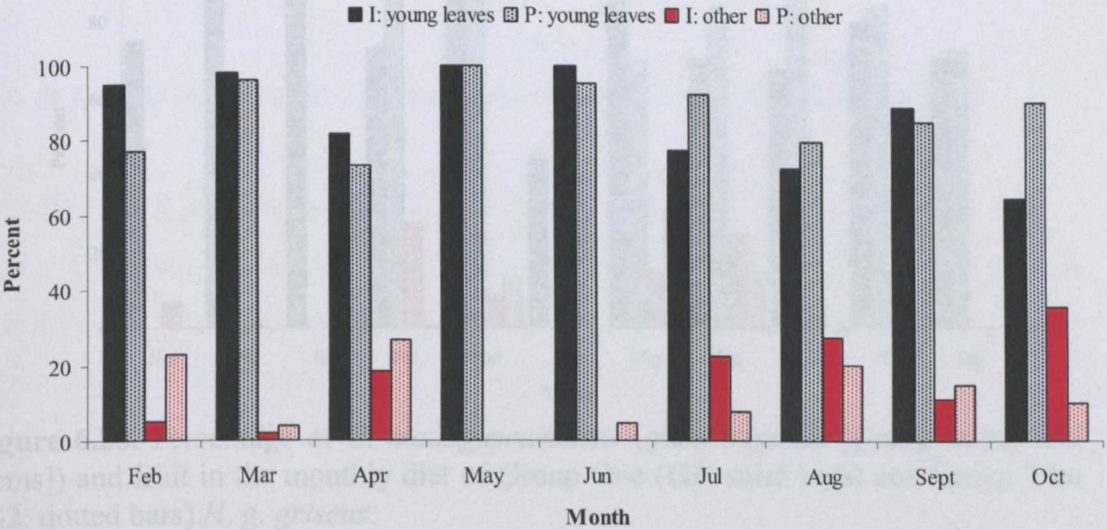


Figure 6.18. Percentage of young leaves and 'other' in the monthly diets (as a percent of total feeding time) for *I. indri* (**I**: solid bars) and *P. diadema* (**P**: dotted bars).

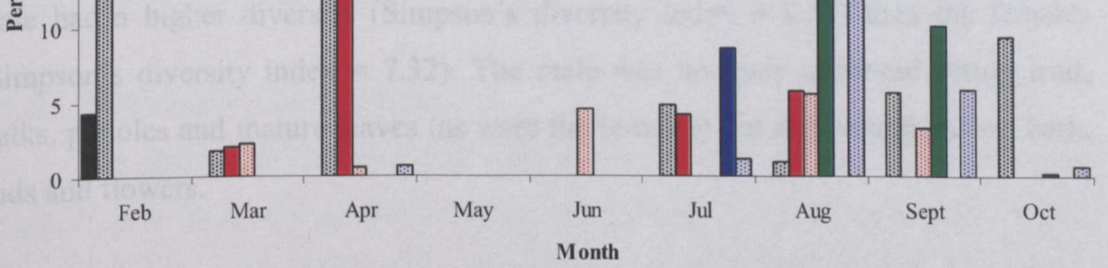


Figure 6.19. Proportion of fruit (old and new), flowers (open and buds), bark and mature leaves (including young leaf combinations) in the monthly diets of *I. indri* (**I**: solid bars) and *P. diadema* (**P**: dotted bars).

6.3.5.2. *Hapalemur griseus griseus*

The predominant food source throughout the entire study for both groups was *Cathariostachys madagascariensis* (giant bamboo); mainly young leaves with an addition of stem. Secondary to this was fruit. The proportion of fruit in the diet increased considerably from February to July (Figure 6.20).

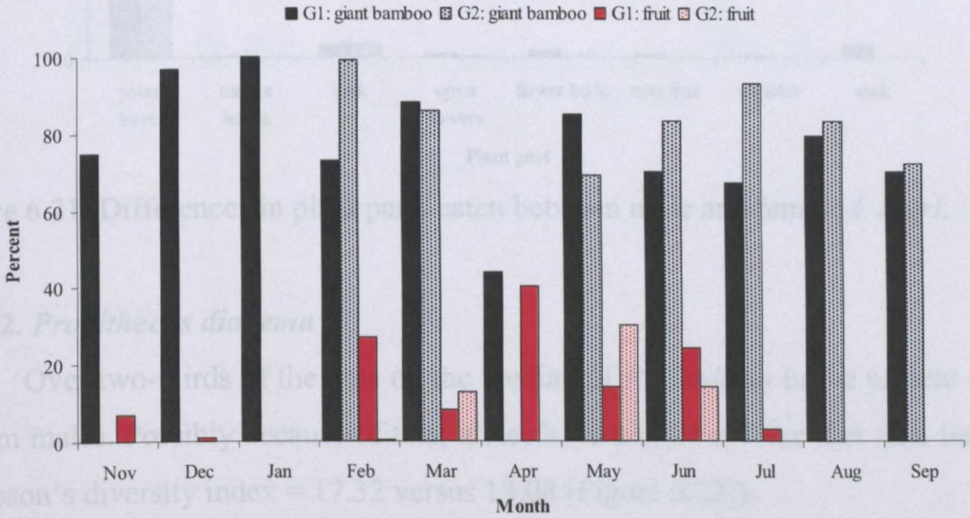


Figure 6.20. Percentage of *C. madagascariensis* (giant bamboo [young leaves and stems]) and fruit in the monthly diet of Group One (**G1**: solid bars) and Group Two (**G2**: dotted bars) *H. g. griseus*.

6.3.6. Sex Differences in Plant Parts Eaten

6.3.6.1. *Indri indri*

In the present study, for *I. indri*, it should be noted that findings for 'male' refer to the adult male, and for 'female' to a combination of the adult female with and without the infant, and the sub-adult female. The diet of the females is the most conservative (Figure 6.21). Dietary diversity was calculated for both sexes and the male had a higher diversity (Simpson's diversity index = 8.54) than the females (Simpson's diversity index = 7.32). The male was not only observed eating fruit, stalks, petioles and mature leaves (as were the females) but also young leaves, bark, buds and flowers.

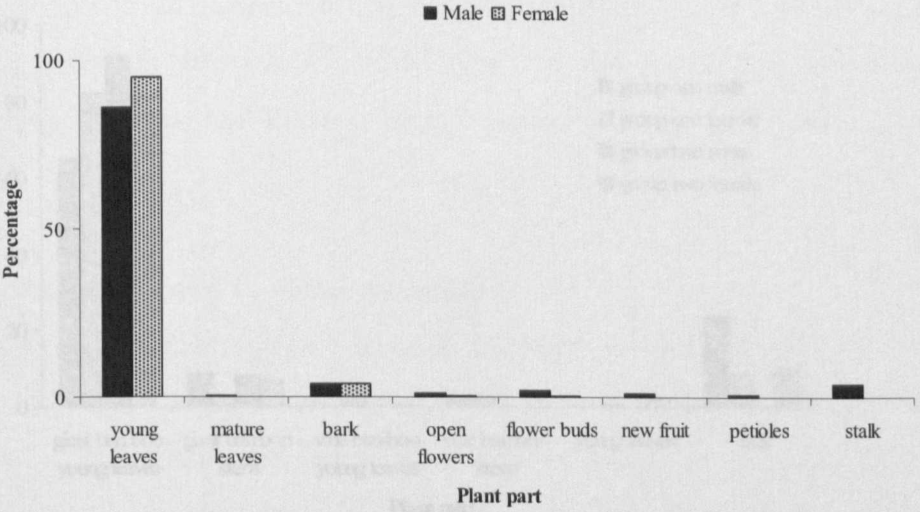


Figure 6.21. Differences in plant parts eaten between male and female *I. indri*.

6.3.6.2. *Propithecus diadema*

Over two-thirds of the data on the feeding of *P. diadema* in the present study is from males. Possibly because of this, males have a more diverse diet than females (Simpson's diversity index = 17.32 versus 13.08 [Figure 6.22]).

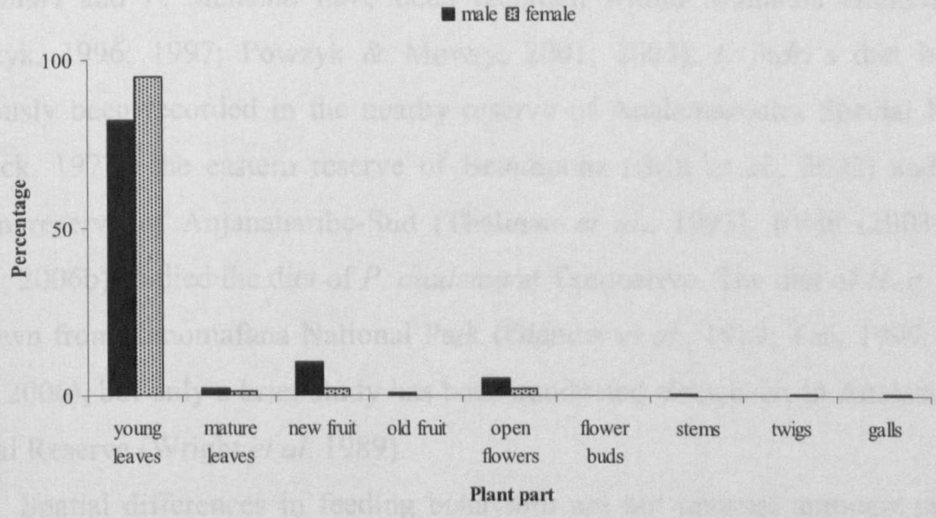


Figure 6.22. Differences in plant parts eaten between male and female *P. diadema*.

6.3.6.3. *Hapalemur griseus griseus*

It is difficult to compare data collected in the present study for male versus female *H. g. griseus* because more data exists for females than males. For Group One 74% of the data attributed to a known sex is for females and for Group Two 86%. Comparison of the sexes (Figure 6.23) shows no clear pattern. In detail, males appeared to eat from far fewer food sources than the females and be more reliant on the giant bamboo.

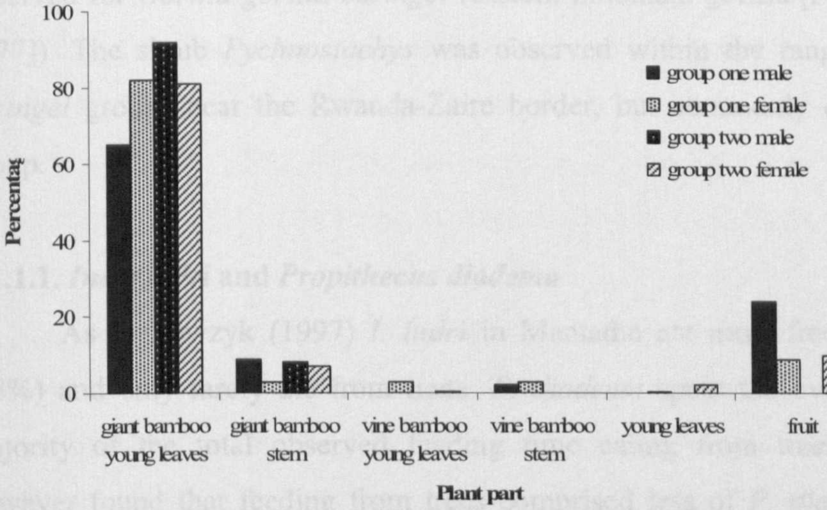


Figure 6.23. Differences between male and female *H. g. griseus*, in plant parts eaten.

6.4. Discussion

6.4.1 Dietary Overview and Comparisons with Previous Studies

Diets of all three species have been documented in previous studies. The diets of *I. indri* and *P. diadema* have been recorded within Mantadia National Park (Powzyk, 1996; 1997; Powzyk & Mowry, 2001; 2003). *I. indri*'s diet has also previously been recorded in the nearby reserve of Analamazoatra Special Reserve (Pollock, 1977), the eastern reserve of Betampona (Britt *et al.*, 2002) and north-eastern reserve of Anjanaharibe-Sud (Thalman *et al.*, 1993). Irwin (2003; 2005; 2006a; 2006b) studied the diet of *P. diadema* at Tsinjoarivo. The diet of *H. g. griseus* is known from Ranomafana National Park (Glander *et al.*, 1989; Tan, 1999; Grassi, 2002; 2006), but only a brief study has been conducted elsewhere, in Analamazoatra Special Reserve (Wright *et al.* 1989).

Spatial differences in feeding behaviour are not unusual amongst primates. The diet of *Procolobus badius* (western red colobus) in Kibale National Park, Uganda, exhibited sizeable intra-group and yearly variation (Chapman *et al.*, 2002). Time spent feeding on leaves increased from 56% in 1994 to 76% in 1998. Species and plant parts eaten was found to vary between *P. badius* groups in different forest types; dependence on young leaves varying up to 38%, even between groups with overlapping home ranges. Another species in Kibale, *Cercocebus albigena* (grey-cheeked mangabey), showed dietary differences to *C. albigena* in Uganda, independent of availability (Waser, 1977). Intra-specific dietary variation has been observed for *Gorilla gorilla beringei* (eastern mountain gorilla [Fossey & Harcourt, 1977]). The shrub *Pychnostachys* was observed within the ranges of three *G. g. beringei* groups near the Rwanda-Zaire border, but commonly eaten by only one group.

6.4.1.1. *Indri indri* and *Propithecus diadema*

As in Powzyk (1997) *I. indri* in Mantadia ate most frequently from trees (98%) and only rarely ate from liana. *P. diadema* spent the overwhelming (98%) majority of the total observed feeding time eating from trees. Powzyk (1997) however found that feeding from trees comprised less of *P. diadema*'s diet (79%) while lianas and herbaceous plants were quite commonly eaten.

Both *I. indri* and *P. diadema* were recorded eating from fewer plant species compared to Powzyk (1997). While *P. diadema* ate from 32 known families, rather than the 47 recorded by Powzyk (1997) in the present study eight families were recorded as eaten in this study but not by Powzyk. The overwhelming majority (90%) of the total feeding time of *I. indri*, was spent feeding on ten plant species and only three of these species overlap with the 'top-ten' found by Powzyk (1997). Although *I. indri* ate from a minimum of 37 different plant species, compared to 79 species observed by Powzyk (1997), in this study they ate from a wider range of families. In total there were six families utilised by *I. indri* in Powzyk's (1997) study but not recorded here and 12 from this study which are not recorded in Powzyk's. Powzyk (1997) noted differences between the diet of *I. indri* at Mantadia National Park and at Analamazoatra Special Reserve. Despite the same species-availability, *I. indri* in Analamazoatra appeared to eat from plants not eaten by *I. indri* in Mantadia National Park (Abraham, pers. comm. to Powzyk, 1997).

I. indri spent the greatest proportion of the total time they were observed feeding, eating young leaves (89%) agreeing with their classification as folivorous (Powzyk, 1996; Powzyk & Mowry, 2001; Britt *et al.*, 2002; Birkinshaw & Colquhoun, 2003). *P. diadema* are classified by Birkinshaw and Colquhoun (2003) as frugivorous-gra(mi)nivorous. However, while fruits, seeds, galls and flowers are also consumed, leaves dominate their diet (Powzyk, 1996; Powzyk & Mowry, 2001). However, in this study *P. diadema* spent most of the total observed feeding time eating young leaves (84%) and would more correctly be termed folivorous.

Young leaves of *Bakerella* sp. (small mistletoe [Loranthaceae]) were eaten by *P. diadema* for 8% of the total feeding time. Irwin (2003; 2005; 2006a; 2006b) found that the hemiparasite *Bakerella* sp. was a year-round staple of *P. diadema* living in fragmented forest in Tsinjoarivo, consumption accounting for 30 to 60% of the total feeding time, while groups living in continuous forest relied on it primarily during winter months.

Young leaves of the fern *Asplenium nidus* were consumed by male *P. diadema* in April and September. *P. diadema* is one of only three known lemur species that utilises ferns as food (Birkinshaw & Colquhoun, 2003). Simmen *et al.* (1999) suggests this is a reflection of the unusually high tolerance of *Propithecus* spp. to tannins, as fern fronds are rich in tannins (May, 1978).

Only flowers were eaten from parasitic plants. Similarly a study in Tsinjoarivo, eastern Madagascar, observed *P. diadema* eating the inflorescences of two subterranean parasitic plants: *Langsdorffia* sp. (Balanophoraceae) and *Cytinus* sp. (Cytinaceae [Irwin *et al.*, 2007]). These 'flowers' are found hidden in leaf litter and Irwin *et al.* (2007) suggest that *P. diadema* were using olfactory cues to locate food items. Inflorescences of *Langsdorffia* sp. were eaten by *P. diadema* elsewhere in Mantadia (Powzyk, 1997) although this behaviour was not observed in this study.

A higher degree of overlap between the two indriids was found compared to Powzyk (1997). In this study overlap, calculated by Schoener's Index, was 0.42, while Powzyk (1997) found a value of 0.12. While even the maximum value of monthly overlap in this study (0.53 in July) falls short of the 0.6 significance value suggested by Scrimgeour and Winterbourn (1987), the difference between the two studies is of note. This compares with an overlap of 0.69 between *Saguinus mystax* (moustached tamarin) and *Saguinus fuscicollis* (saddle-backed tamarin) forming mixed-species groups (Heymann & Buchanan-Smith, 2000).

There are a number of explanations as to the dietary differences found between this study and Powzyk's (1997). Home ranges in the present study (Chapter 7) were smaller than those recorded by Powzyk (1997) and it is possible that there were fewer plant species available in individual ranges. Unfortunately no data was collected on plant species availability with which to test this. Alternatively the shorter period of observations has discounted feeding from October through December. It is again possible that differences are simply spatial differences between groups.

6.4.1.2. *Hapalemur griseus griseus*

H. g. griseus have the most diverse diets of all bamboo lemurs (Tan, 1999). Although the diet of *H. g. griseus* was found to be about three-quarters comprised of giant bamboo, the diet of *H. g. griseus* in this study was found to be adaptable; both study groups of *H. g. griseus* exploited the fruit of *C. hirta*, a plant introduced to Madagascar less than 100 years ago (Binggeli, 2003), just as from site to site the literature shows it is variable. Ad-hoc personal observations on non-study groups of *H. g. griseus* in Mantadia indicated that groups living further from the miner's road in primary forest most commonly ate from vine bamboo. A study conducted by Tan (1999), at Ranomafana National Park, found that *H. g. griseus* ate from four bamboo species: *C. madagascariensis* (73% of all feeding records), *C.* cf. *perrieri*, *C.* cf. *viguieri* and *Nastus elongatus* (Tan, 1999). They also ate other bamboo and grasses (16%), non-bamboo foliage, predominantly lianas (4%), fruit (5%), and other items (3%), percentages referring to the proportion of total feeding records. However at a different location in Ranomafana Grassi (2002) found that a single species, *Cephalostachyum pierreri* (vine bamboo), comprised 68% of *H. g. griseus's* diet. and Glander *et al.* (1989) and Wright *et al.* (1989) recorded *H. g. griseus* feeding on leaf bases, blades and vine pith of *C.* cf. *perrieri*, which is found throughout the forest from the ground up to 15m (Grassi, 2002). Overdorff *et al.* (1997), also working in Ranomafana, calculated that 89% of *H. g. griseus* diet was comprised of the new growth of two species of liana bamboo combined with *C. pierreri.*

Although *H. g. griseus* has a dependence on bamboo throughout its range, the predominant species is clearly subject to variation. But the choice is not neutral in its consequences: at Tan's site in Ranomafana (Tan, 1999), and in this study, the main food was *Cathariostachys madagascariensis* (giant bamboo). A concentration on this species may be more problematic than a concentration on vine bamboo *Cephalostachyum* cf. *pierreri.* All growing parts of *C. madagascariensis* have been found to contain high levels of cyanide while low amounts of cyanide are found in *Cephalostachyum* cf. *perrieri* (Yamashita *et al.*, 2007); almost all urine samples from *Hapalemur* spp. contained cyanide, suggesting dietary cyanide was being absorbed by the gastrointestinal tract and, at least in part, excreted by the kidneys. A specialization on bamboo is not unique to *Hapalemur* (bamboo lemurs) and *Prolemur* (greater bamboo lemurs) even among primates. Faecal samples of

Rhinopithecus bieti (black-and-white snub-nosed monkey), in the southern part of its range, were 59% comprised of bamboo leaves (Yang & Zhao, 2001).

However, the specialized bamboo diet of *H. g. griseus* coincides with a highly efficient digestive tract (Campbell *et al.*, 2004). Experimental studies suggest that *H. g. griseus* have a long (30 hours) gut transit time allowing them to digest a high proportion of ingested fibre (Campbell *et al.*, 2004). Total digested dietary fibre was found to be 62% (of ingested fibre), higher than the other lemur species studied (*Varecia variegata* [black-and-white ruffed lemur]: 20%, *Eulemur fulvus*: 28%, *Propithecus coquereli* [Coquerel's sifaka]: 53% [Campbell *et al.*, 2004]).

Dietary variation between different populations appears to characterise species that have relatively wide distributions and an ability to live in disturbed and fragmented forest. In Argentina *Cebus apella* (tufted capuchin) is able to adapt its diet to local conditions, utilising leaves of bromeliads when food resources are low (Brown & Zunino, 1990). In French Guyana flooding of a forest for a hydro-electric dam caused trees to lose their leaves: *Alouatta seniculus* (red howler monkey) responded to this challenge by eating from trees from which they would not usually eat (de Thoisy & Richard-Hansen, 1997).

The predominant difference in the plant types consumed by *H. g. griseus* Groups One and Two is that only Group One were observed eating fruit from palms and Group Two ate fruit from shrubs. It is possible they were utilising alternate resources within their home ranges, although there is no information to prove this. Grassi (2006) found differences between diets of adjoining *H. g. griseus* groups, suggesting a link to varying availability of plant species.

6.4.2. Foraging Strategies of *Indri indri* and *Propithecus diadema*

I. indri ate in significantly longer single bouts than *P. diadema*, similarly to the findings of Powzyk and Mowry (2001), while *P. diadema* had significantly more daily feeding bouts. The increased length spent in each bout results in decreased travel time for *I. indri* (Chapter 5). Overall both species spent a similar proportion of the day feeding (approximately 44%). Both *I. indri* and *P. diadema* fed most on young leaves, however *I. indri* are more conservative in their choice of plant parts and are far less likely than *P. diadema* to consume fruit or flowers.

This indicates that both species have adopted different feeding strategies. *I. indri* has a less diverse diet, spending longer periods of time in one location (i.e.

longer giving-up times) feeding on a small number of resources. The energy they conserve from not travelling long distances between food sources might be expected to allow them to survive on a lower quality diet, and this tends to be confirmed by *I. indri* lower consumption of fruit and flowers and consumption of some bark. *P. diadema* have a broader diet and are more selective in their choice of food, being prepared to travel further to find specific food items. They will expend more energy travelling between foods, and must in turn eat a higher quality to satisfy their metabolic needs. Powzyk (1997) and Powzyk and Mowry (2001) found that the alkaloid content of plants consumed by *P. diadema* was higher than *I. indri* and hypothesises that this is the basis of niche separation. Indeed, Ganzhorn (1989) found that species feeding at similar heights choose food based on different plant chemistry. But in the present study the two species fed at significantly different heights, and the factor of stratum must also be taken into consideration.

6.4.3. Sex and Age Differentiation in Diet within Species

Pollock (1977) found that male *I. indri* in Analamazoatra Special Reserve spent less time feeding than females. Powzyk reported no sex differences in the time spent feeding by *I. indri* on bark, flowers, fruits, galls and mature leaves in Mantadia National Park, although females spent more time feeding on immature leaves (Powzyk, 1996). Powzyk (1977) also found that males eat more fruits and less shoots than did adult females and their young.

Powzyk (1996) reported no sex differences in the total number of daily feeding bouts, but females spent slightly longer feeding than males. No sex differences were observed in the frequency of feeding on immature leaves, mature leaves, fruit, galls and immature fern fronds, but females did consume more flowers (Powzyk, 1996).

In the present study, the diet of the females is the most conservative, the male not only being observed eating fruit, stalks, petioles and mature leaves (as were the females) but also young leaves, bark, buds and flowers. This is the opposite of what could have been expected, since females are assumed to have a higher nutritional requirement due to reproduction. However, the result must be evaluated with reference to a bias towards the male in observation time, which may also be responsible for the increased diversity observed in male *P. diadema* compared to females.

Data for male *H. g. griseus* was more abundant than for females. but males appeared to eat from far fewer food sources than the females and be more reliant on the giant bamboo, in accordance with findings from both Tan (1999) and Grassi (2002), that females eat a greater variety of food, possibly as a result of their increased reproductive needs, eating more fruit and more non-bamboo food (Grassi, 2002).

6.4.4. Seasonal Variation

P. diadema maintained a more diverse diet, measured by Simpson's diversity index, than *I. indri*, less dominated by young leaves and containing more alternative foods, throughout most of the study, except July and August. Further, dietary overlap calculated by Schoener's index, peaked during July (0.53) and was at its lowest during April (0.15). July was the coldest month, so energetic requirements of maintaining body temperature would be expected to be at their highest. Although there is no phenological data available from this study, it might be expected that July and August are months with low food availability, given that decreasing temperatures and the austral 'winter' began in April. Powzyk (1997) examined phenology within Mantadia in 1993 and 1994 and found that while young leaves were available year round, flowers decreased in availability during April through July, whereas fruit increased in abundance in July and August.

These findings are in opposition to those of dietary overlap found elsewhere, where overlap *decreases* during lean periods (Smith *et al.*, 1978; Schulter, 1981; Schoener, 1982). It has been suggested that this is due to niche separation being most important when food is scarce; if food is plentiful it is less important to eat different thing (Peres, 1996). This pattern has been observed for mixed-associations of *Ateles geoffroyi* (Geoffroy's spider monkey) and *Alouatta palliata* (mantled howler monkey) in Costa Rica (Chapman, 1988). This could suggest that food availability during July and August is in fact higher than during April. Unfortunately the lack of phenological data, prevents a test of this assumption.

In the present study, fruit was consumed primarily by *P. diadema* and, contrary to what one would expect from Powzyk's (1997) findings of peak availability, was consumed primarily in February, April and October. *I. indri* ate flowers in April and July, similar to Britt and colleagues' (2002) findings in Betampona where they were consumed from April to June. Relative peaks of consumption of high energy fruit and flowers, in both *P. diadema* and *I. indri* during the austral summer suggest that they are utilising the best resources available at that time.

However both species also show a peak in alternate, non-young-leaf, food resources from July to August, when mature leaves and bark - both low energy resources - become utilised. As in Britt *et al.* (2002) bark was consumed by *I. indri* towards the end of the austral winter. This seasonal bias is similar to that seen in other primate species which consume bark in the absence of more nutritive food (Izawa, 1971; Jones & Sabater Pi, 1971; Nishida, 1972; Casimir, 1975; Nishida, 1976; Goodall, 1977; Hladik, 1977; Rodman, 1977; Rogers *et al.*, 1990; Watanuki & Nakayama, 1993; Yamagiwa *et al.*, 1994; Watanuki *et al.*, 1994; Yamakoshi, 1998).

If young leaf availability does not decrease in the austral winter (Powzyk, 1997), why do both indriids utilise low energy resources in colder months? Ganzhorn (1992) found a correlation between rainfall and leaf chemistry in Madagascar: increased rainfall correlates with decreased leaf quality. The explanation for this was that increased rainfall leads to increased cloud cover, reducing irradiance and limiting photosynthesis and thus decreasing leaf quality. Therefore although young leaves could be available to *I. indri* and *P. diadema* during colder, cloudier, wetter winter months leaf quality is liable to decrease.

This may explain *I. indri*'s feeding from bark and mature leaves. However, *P. diadema* also utilised a low quality diet in winter. Powzyk's (1997) found that even during winter months *P. diadema* searched for and ate fruit on every day sampled even if the travelling required was substantial. In the present study this phenomenon was not observed. Unfortunately there is little evidence which might suggest a reason for this. However, it is possible that the smaller home range size determined in the present study (Chapter 7) has acted as a limiter on fruit availability in the study group's home range.

This seasonal shift in diet can help explain the seasonal differences in activity. Both *P. diadema* and *I. indri* are anatomical folivores (Hill, 1953). However *I. indri*, having a comparatively longer midgut (Hladik, 1978), will be better adapted to digestion of complex carbohydrates (leaves), while *P. diadema*, with a comparatively longer small intestine, are more efficient at digesting simple sugars and fats (fruit). The mid-gut specialism of indriids (and *Hapalemur* spp.) requires symbiotic gut flora (protozoan and bacterial) to ferment fibre and make available nutrients (Hladik, 1978). This process requires long periods of rest as digestion will slow down or stop during movement (Smith, 1977). *P. diadema* will therefore be less able to digest low quality food, explaining its increased rest time during winter when its dietary quality decreases.

According to Powzyk and Mowry (2001) no alkaloids were found in any plant part eaten by *I. indri*. However, *I. indri* have been observed both previously (Pollock, 1975; Britt *et al.*, 2002), and in this study, eating earth. The highest frequency of this phenomenon coincided with the peak in mature leaf consumption (April to May and September to November [Britt *et al.*, 2002)]. This lead Britt *et al.* (2002) to suggest that earth could aid in neutralising secondary chemicals, such as tannins, present in mature leaves.

Overdorff *et al.* (1997) found that consumption of foods eaten by *H. g. griseus* varied seasonally: mature leaves were eaten each month, but only during the wet season did the Ranomafana *H. g. griseus* include small percentages of fruit (0.4%), fungus (0.5%), mushrooms (1.4%), leaf petioles (0.6%), flowers (0.4%) and new leaves (0.3% [percentages from the total proportion of scan samples]). Overdorff *et al.* (1997) found a seasonal trend in dietary diversity: the highest diversity being observed at the end of the dry season in August and September. The predominant food source throughout the entire study for both groups was *Cathariostachys madagascariensis*; mainly young leaves with an addition of stem. Secondary to this was fruit. The proportion of fruit in the diet increased considerably from February to July.

6.5. Summary

<u>Hypothesis 6.1</u> held that: niche differentiation between *I. indri* and *P. diadema* occurs by adoption of quantitatively different diets.

This hypothesis is not upheld; Schoener's index gives a dietary overlap of 0.42 (equivalent to 42%), ranging from 0.15 in April to 0.53 in July. This indicates that up to 50% of specific diets overlap; considerably more than the maximum 0.12 (equivalent to 12%) overlap found by Powzyk (1997).

Hypothesis 6.2 held that: *I. indri*, as proposed by Powzyk (1997) is a more specialized feeder on low quality food, and *P. diadema* a generalist, eating higher quality food.

This is partially upheld; *P. diadema* did have a more diverse diet compared to *I. indri*.

Hypothesis 6.3 held that: as a more specialized feeder *I. indri* will have fewer and longer feeding bouts each day compared to *P. diadema* (Powzyk, 1997 [and see also e.g. Crompton, 1984 for *Galago moholi* and *Otolemur crassicaudatus*]).

This hypothesis is upheld; the mean length of feeding bouts for *I. indri* was 1508 seconds, for *P. diadema* it is 998 seconds. *I. indri* had a mean of 8 feeding bouts per day, compared to a mean of 14 bouts per day for *P. diadema*.

Hypothesis 6.4 held that: females of each species will take better-quality food from more diverse sources.

This hypothesis is not upheld for *I. indri* or *P. diadema*: observations show that males have a more diverse diet. However this result could be attributed to sampling bias. The hypothesis is however upheld for *H. g. griseus*: females have the more diverse diet.

Hypothesis 6.5 held that: if all three species will show strong seasonality in diet.

This hypothesis is upheld; each species relied on young leaves, but used other resources as and when they were available.

Chapter 7 Ranging Behaviour

A home range is defined as an area in which an individual or group moves, feeds and rests (Burt, 1943; Oates, 1987; Harris *et al.*, 1990) and knowledge of ranging behaviour is therefore relevant to factors such as energy budgets, food availability and mode of locomotion as well as to social organisation, which is outside the scope of this thesis. This chapter discusses basic concepts of home range and daily path length before reviewing published home range and daily path length estimates for the study species. An overview of radio-tracking and GPS (global positioning satellite) techniques, and methods of determining home range, is included. Finally, home ranges and daily path lengths determined within this study are reported and discussed.

7.1 Introduction

There are two dominant features determining home range: body size and diet (Milton & May, 1976; Harvey & Clutton-Brock, 1981). Larger animals tend to have larger home ranges, and specialist feeders tend to have larger home ranges than generalists of a similar body weight (Harvey & Clutton-Brock, 1981). Fruit distributions are patchier than those of leaves, so frugivores tend to have larger home ranges than folivores (Sussman, 1977). Habitat differences can also lead to intraspecific variation (Oates, 1987). Home ranges may or may not be defended, but those that are defended are termed territories (Burt, 1943). Grant *et al.* (1992) compared the sizes of defended and undefended home ranges of primates, carnivores and ungulates. Size differences were seen in carnivores and ungulates, but not in primates. Kaufmann (1962) introduced the related concept of 'core areas' of home ranges. Core areas are those used more than expected compared to a uniform distribution of activity (Kaufmann, 1962). Preferential use of certain areas of a home range may be due to patchy distribution of food and rest sites (Dixon & Chapman, 1980; Crompton & Andau, 1986). Daily path lengths, as well as home range can exhibit seasonal variation. In *Varecia variegata variegata* (black-and-white ruffed lemur [Morland, 1993]) and *Varecia rubra* (red-ruffed lemur [Rigamonti, 1993]) path lengths are significantly shorter in winter than in summer. Path-lengths are also known to vary intra-specifically, partially dependent on group size and intra-group competition. Stevenson and Castellanos (2000) found daily path lengths dependent on group size in *Lagothrix lagotricha* (woolly monkey) in Colombia. Given the above, we propose that: **Hypothesis 7.1: Following Sussman (1977) since *P. diadema* are more frugivorous they will have the largest home range. All other things being equal, the more folivorous *I. indri* and *H. g. griseus* will have smaller home ranges; but solely on a body size basis the expectation is that *I. indri* will have a larger home range than *H. g. griseus*** and **Hypothesis 7.2: Following Warren and Crompton (1997b) *P. diadema* as a more selective feeder will use a larger proportion of its home range daily and monthly,** and therefore: **Hypothesis 7.3: *P. diadema* will have longer daily path lengths than *I. indri*.**

From results in the activity chapter, *I. indri* and *P. diadema* travel less during the austral winter and it is thus expected that: **Hypothesis 7.4: Daily path lengths in *I. indri* and *P. diadema* will be shorter in the austral winter** and **Hypothesis 7.5: Since *H. g. griseus* are seasonally frugivorous they will be expected to have longer daily path lengths and monthly home ranges in the season when fruit is most commonly consumed.**

7.2 Methods of Tracking, Positioning and Home Range Determination

Calculation of home range and daily path lengths requires the ability to locate and follow the individual or group, and then to log and map their position through time. Prior to deciding which methods are to be used, it is important to consider the social and grouping structure of the study species. If the study species forms socially-cohesive groups, then any member of the group can be independently studied, and results combined for analysis. If animals within a group travel separately, ranges must be calculated for each individual. The likelihood of seasonal changes mean that the most accurate home ranges are those that are calculated from data covering at least a year. Comparison between studies can be difficult when methods are not stated and different methods of analysis used (Boulanger & White, 1990; Kool & Croft, 1992).

At the start of any study in a new area it is beneficial, if not essential, to cut trails. The most efficient system for mapping is to cut trails in a grid, ensuring that they encompass the home ranges of the study species. The trail system must then be mapped, preferably including major features (rivers, topography etc.). This is not only necessary for mapping, but as an aid to movement in dense forest. Crompton and Andau (1987) used a grid based system of trails for determining ranging behaviour of *Tarsius bancanus* (western tarsier). A 50m grid of trails was marked at 10m intervals, and while trail tagging was usually sufficient in untouched primary forest, trail cutting was a requirement in dense secondary forest (Crompton & Andau, 1987). Cutting trails can be detrimental to the environment and the benefit of trails must be weighed against the environmental destruction. Trails were not required in the primary forest at Ampijoroa, where Warren and Crompton (1997a; 1997b) marked out a grid system using nylon forestry flagging tape (Warren, 1997; Warren & Crompton, 1997a; 1997b).

7.2.1. Locating and Tracking Animals in the Field

Conducting observations on wild primates involves two things, the capability to first find and then follow individuals and groups. There are a variety of options for finding and tracking, from simple eyes-and-ears based approaches, to sophisticated satellite-tracking techniques.

7.2.1.1. Eyes and Ears

The traditional, and most basic, method of finding and tracking wild animals is to locate and follow them using sight and sound. For species such as *I. indri* which make regular, loud, territorial calls the observer can wait for calls, and attempt to locate individuals from the direction. Alternatively an observer can walk around the known home range of a group until the animals are spotted. This is of course most applicable when groups have small home ranges and are diurnal.

7.2.1.2. Radio-Tracking

Radio-tracking is a useful tool when tracking cryptic diurnal animals and especially valuable when following nocturnal species. One approach is simply to use it to find the initial location of the group/individual, behaviour and position then being observed directly (Harris *et al.*, 1990). This method is most efficient for animals which live in the open and are therefore easy to visually track (Harris *et al.*, 1990). It requires individuals to be caught and fitted with radio-tracking collars. As capture could result in death of subjects, the necessity of radio-tracking must always be assessed.

There are two other methods of radio-tracking, continuous and discontinuous (Harris *et al.*, 1990). Continuous radio-tracking allows daily travel routes to be mapped, taking radio fixes at regular intervals, usually between 5 to 15 minutes (Harris *et al.*, 1990). This is especially useful for assessing any differential use of subunits of home range and for examining small-scale habitat selection (Harris *et al.*, 1990). Radio-tracking can be used to study interactions between individuals and the effects of weather, luminosity and other local factors on animals (Harris *et al.*, 1990). The difficulty is that observers are required to keep the animal within sight over long periods of time, which can be difficult with quick moving animals, difficult terrain and dense habitat (Harris *et al.*, 1990)

In discontinuous radio-tracking, animals are located at discrete or random time intervals (Harris *et al.*, 1990). Useful for determining home range size, this can allow a large number of groups or solitary individuals to be studied simultaneously (Harris *et al.*, 1990).

Radio-tracking has limitations and constraints. In a perfect system, constraints are signal range and life span of batteries (Lance & Watson, 1980). In practice, limitations are many; cost, breakages and malfunctions, difficulty of field repairs and replacements, restrictions on size and weight of transmitters which are necessary to reduce their potential energetic cost, increased vulnerability to predators or other harm to the animal and even the potential for fieldwork to become based around radio-tracking to the detriment of all else (Lance & Watson, 1980).

Radio-tracking becomes most helpful when studying nocturnal species. Zinner *et al.* (2003) for example determined home ranges of nocturnal *Lepilemur ruficaudatus* (red-tailed sportive lemur) by radio tracking: individual *L. ruficaudatus* were tracked for two hours, and locations recorded every 15 minutes by tagging. Discontinuous sampling was also used, to determine position of all *L. ruficaudatus* in the study. Crompton and Andau (1987) used radio-transmitters to track *Tarsius bancanus*, tagging trees every 5 minutes. Tags were relocated the following day, and each tag position mapped in relation to a 50m trail system. Gursky (1998) used a similar method to track *Tarsius spectrum* (spectral tarsier), tagging every 15 minutes with time, data and individual.

7.2.1.3. Satellite Tracking

Satellite tracking systems using systems such as the Global Positioning System (GPS) and Advanced Research and Global Observation Satellite (Argos) are becoming more widely used in studies involving animal tracking. As with radio-tracking, individuals must be captured and units attached. Satellite tracking has up to now largely been confined to large animals which roam over large distances, due to size constraints of the transmitting units and price. Interference from geographical features makes satellite systems especially problematic in a rainforest environment.

A major difference between Argos and GPS is that Argos transmits locations back to a base station, while GPS records positions on the receiver, requiring the retrieval of the receiver if it is mounted on the subject animal (Rodgers, 2001). Argos can also be used to transmit GPS data, removing the necessity of retrieving receiver units (Rodgers, 2001; Jay & Garner, 2003), and giving additional, although less accurate, Argos positions along with those from the GPS (Jay & Garner, 2003). Alternatively radio links can allow retrieval of GPS information (Rodgers, 2001; Jay & Garner, 2003). GPS collars used on *Alces alces* (moose) and *Canis lupus* (wolf) have used both on-animal datalogging and downloading via radio-transmission at set times (Zimmermann & Dötterer, 2001).

7.2.1.3.1. GPS

It is important to understand how GPS works, in order to appreciate its uses and limitations. Since 1995 there has been a full compliment of 24 NAVSTAR (Navigation System with Time and Ranging) geosynchronous satellites orbiting the earth (Wilkie, 1989; Moen *et al.*, 1996; Phillips *et al.*, 1998; Dominy & Duncan, 2001). Satellites are maintained by the United States Department of Defence and signals broadcast free of charge (D'Eon, 1995). Satellites circle the earth in 20,200km circular orbits, with a twelve hour period (Wilkie, 1989). Six planes inclined at 55° to each other each have three dedicated satellites (Wilkie, 1989; Dominy & Duncan, 2001). This allows a direct line-of-sight navigational signal from at least four satellites anywhere on the globe (Wilkie, 1989; Dominy & Duncan, 2001). Despite this world-wide coverage, some areas will not be able to view the four satellites necessary for good fixes at all times (Phillips *et al.*, 1998).

Satellites transmit positional information and time from atomic clocks (D'Eon, 1995; Dominy & Duncan, 2001) at a 'coarse acquisition' frequency of

1575.42MHz (Wilkie, 1989; Rempel *et al.*, 1995). Twice a day the United States Department of Defence ground station monitors each satellite's altitude, position and speed, sending back corrections where necessary (D'Eon, 1995).

Until 2000, 95% of positions were correct within 100m (D'Eon, 1995; Rempel *et al.*, 1995; Moen *et al.*, 1996; Dominy & Duncan, 2001; Jay & Garner, 2003). This was because of a deliberate error (selective availability) introduced by the US military (D'Eon, 1995; Dominy & Duncan, 2001). In 1996 a presidential directive suspended this error with effect 2 May 2000 (Dominy & Duncan, 2001; Rodgers, 2001). Since this time GPS should be accurate to within 10 to 30m, and even less with differential correction (Dominy & Duncan, 2001; Rodgers, 2001). The error in altitude calculations is approximately twice that for latitude or longitude (D'Eon, 1995).

GPS receivers contain an antenna, quartz clock and triangulation software (D'Eon, 1995; Dominy & Duncan, 2001). Locations are determined by the time lag between the radio signal (travelling at 299,460km/sec) being sent from the satellite and arriving at the receiver (Wilkie, 1989; Dominy & Duncan, 2001).

The amount of positional error caused by the geometry of the satellites with respect to each other and to the receiver is indicated by the Positional Dilution of Position (PDOP [Figure 7.1] [D'Eon, 1995]) which is comparable to the dimensional position. A complete 3-dimensional (3-D) position (latitude, longitude and altitude) low PDOP value, requires four satellite fixes (Wilkie, 1989; D'Eon, 1995; Rempel *et al.*, 1995). With a three-satellite fix, a 2-dimensional (2-D [latitude and longitude]) and high PDOP position is obtainable, but altitude must be known from either a separate hand-held device or internal altimeter (Wilkie, 1989; D'Eon, 1995; Rempel *et al.*, 1995). Fixes from two satellites are only possible when altitude is known and an external caesium 5.119155MHz frequency standard is connected to determine clock bias (Wilkie, 1989).

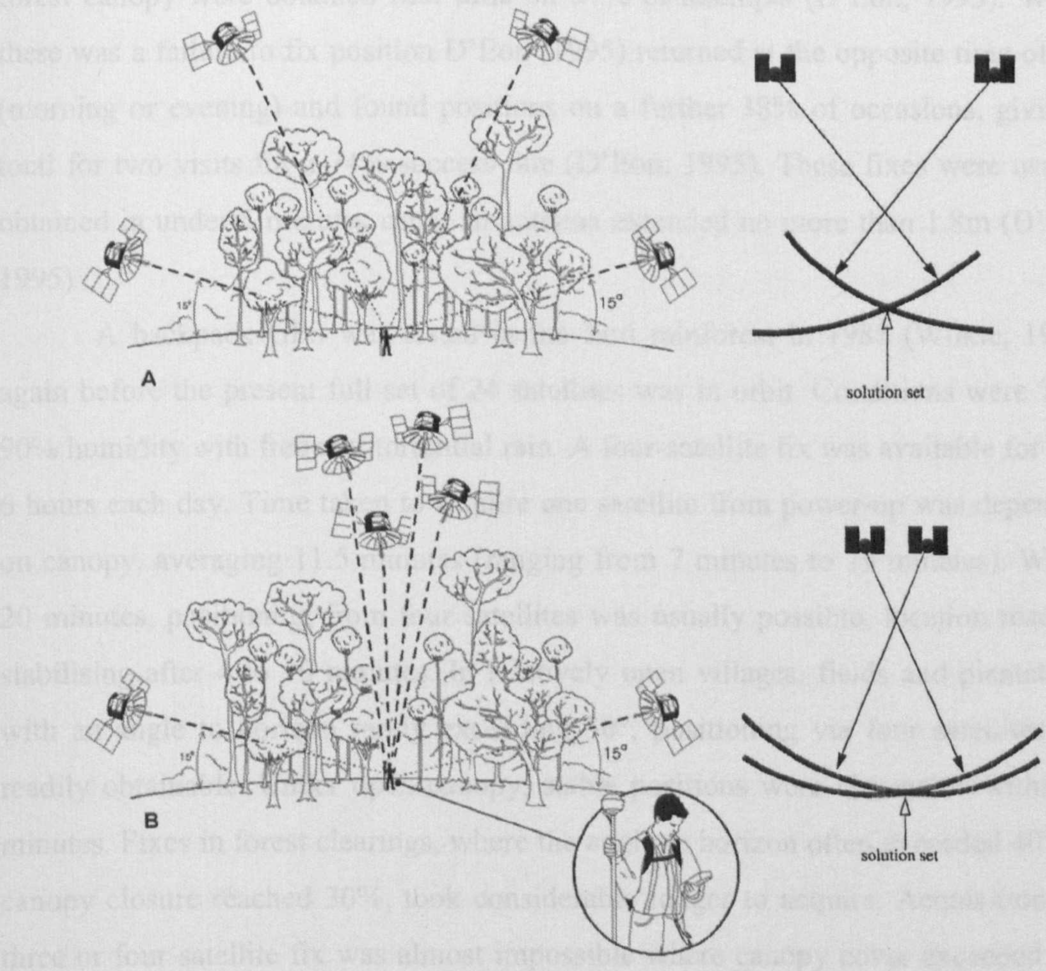


Figure 7.1. GPS and forest canopy interference, adapted from Dominy and Duncan (2001) and D'Eon (1995). **A:** Data collection is made impossible with forest cover, despite good satellite coverage, which would otherwise lead to good geometry and low PDOP. **B:** Only 4 of 6 satellites are usable due to forest cover. This leads to poor geometry and high PDOP, resulting in a low accuracy of positioning.

Obtaining a position in a forest is complicated as line of sight access to available satellites is decreased (Petersen, 1990). The time required for obtaining a fix can rise from 5 minutes in open country to over an hour in forest (Petersen, 1990). Satellites lower in the horizon are better for obtaining accurate fixes (D'Eon, 1995), but when there is tree cover most information will come from directly above, and satellites higher than 70° above the horizon do not provide useful positioning data (Wilkie, 1989). A frequency of 1,575.42MHz translates to a wavelength of around 20cm, capable of penetrating some, but not all forest canopies (Rempel *et al.*, 1995).

D'Eon (1995) studied accuracy of a hand-held GPS in a Canadian forest in 1992 (before all the 24 satellites presently functioning were in orbit). Positions under forest canopy were obtained first time on 57% of attempts (D'Eon, 1995). Where there was a failure to fix position D'Eon (1995) returned at the opposite time of day (morning or evening) and found positions on a further 38% of occasions, giving a total for two visits for a 74% success rate (D'Eon, 1995). These fixes were usually obtained in under 5 minutes using an antenna extended no more than 1.8m (D'Eon, 1995).

A backpack GPS was tested in the Ituri rainforest in 1988 (Wilkie, 1989), again before the present full set of 24 satellites was in orbit. Conditions were 70 to 90% humidity with frequent torrential rain. A four-satellite fix was available for only 6 hours each day. Time taken to acquire one satellite from power-up was dependent on canopy, averaging 11.5 minutes (ranging from 7 minutes to 79 minutes). Within 20 minutes, positioning from four satellites was usually possible, location readings stabilising after 4 to 10 minutes. In relatively open villages, fields and plantations, with an angle to horizon rarely exceeding 30°, positioning via four satellites was readily obtainable. Under open canopy, stable positions were obtainable within 25 minutes. Fixes in forest clearings, where the angle to horizon often exceeded 40° and canopy closure reached 30%, took considerable longer to acquire. Acquisition of a three or four satellite fix was almost impossible where canopy cover exceeded 30% and the angle to horizon exceeded 50°. However once locations were obtained they could be maintained even when passing through thick vegetation. The signal was initially lost, but new positions were obtainable within 5 minutes of reaching an open area (Wilkie, 1989).

Differences have been found between acquisition rates in temperate and tropical forests (Phillips *et al.*, 1998). Phillips *et al.* (1998) used the same GPS in both temperate (Ohio, USA) and tropical (Costa Rica and Trinidad) forests, comparing results. Their GPS could track up to eight satellites and had a typical accuracy of 30m. Acquisition rates in temperate forest were 97%, while in tropical forests this dropped to just 34%. They calculated that to acquire readings in tropical forest on at least 75% of occasions, canopy cover must not exceed 20%. However, Phillips *et al.* (1998) found no correlation between acquisition time and density of forest cover, suggesting that acquisition is an all or nothing phenomenon. Differences between temperate and tropical forest acquisition rates have been attributed to thickness of the canopy and wetness of the environment. Phillips *et al.* (1998) state that recreational GPS does not provide accurate locations in tropical rainforest.

A backpack GPS was trialled by Dominy and Duncan (2001) in the Kibale rainforest in Uganda from April to July 1999, after all satellites were in orbit. Kibale is moist evergreen forest to lowland tropical rainforest, trees mostly ranging in height from 25 to 40m, although some reach 50m (Dominy & Duncan, 2001). Dominy and Duncan had complete failure in obtaining accurate positions under forest canopy, for although four satellites were found, they were too high over the horizon to obtain accurate positions (Figure 1B). Dominy and Duncan (2001) ended up climbing trees to remove the effect of signal interference and at a height of 25 to 30m accurate positioning was possible, although it could take 10 to 15 minutes. They suggest that an antenna on a telescoping pole could replace the need to climb trees, but problems arrive from difficulties controlling and balancing a long pole and potential damage to the antenna and cable from vegetation. In addition the line antenna used by Dominy and Duncan (2001) could not exceed 30m without an inline repeater.

Nest sites of *Pan troglodytes verus* (West African chimpanzee) in Senegal were mapped using GPS (Pruetz *et al.*, 2002) and locations of *Papio cynocephalus* (yellow baboon) in Tanzania were found using GPS (Pochron, 2001). In Bwindi, Goldsmith (2000) used GPS to map *Gorilla gorilla beringei* (eastern mountain gorilla) nest sites. GPS has been successfully used to map *Alouatta palliata* (mantled howler monkey) positions in tropical forest in Ecuador (Charlat *et al.*, 2000). Ranging behaviour of *Eulemur rufus* (red-fronted brown lemur) was calculated using GPS, positions being taken every 30 minutes (Scholz & Kappeler, 2004).

Initial studies using datalogging GPS tracking collars have begun on *Macaca fuscata* (Japanese macaque [Sprague *et al.*, 2004]). A collar weighing 189g (Televilt) was used on a 7.2kg female *M. fuscata*. This collar was programmed to record a GPS position every hour on the hour, broadcast a radio signal from 08:00 to 17:00 and drop off when the battery was depleted. The collar worked for 9 days. Sprague *et al.* (2004) found the collar produced useful information, despite acquiring fixes on only 20% of occasions under forest canopy. Their main problem was the requirement for a high number of fixes and small size, leading to a low overall period of collection time (9 days [Sprague *et al.*, 2004]).

7.2.2. Positioning Animals within their Environment

7.2.2.1. Recording Positions on the Ground

The simplest method of initially recording an individual's position is to use flagging tape. While observing *Tarsius bancanus* positions were recorded every five minutes by tagging trees with brightly coloured flagging tape (Crompton & Andau, 1987). If following multiple animals during one period flagging should be numbered consecutively, including date, species and group. This method was also used for *Avahi occidentalis* (western woolly lemur) and *Lepilemur edwardsi* ([Milne Edward's sportive lemur] Warren, 1994; Warren & Crompton, 1997b). The interval between flagging locations will depend on how far and frequently the study species travels.

7.2.2.2. Mapping Known Positions Using Compass and Tape

Positions of flagging tape must at a later date be mapped. The traditional method is to use a compass and tape measure (Oates, 1977; Warren, 1994). In Crompton and Andau's (1987) study, the position of each tag was recorded in respect to a pre-defined grid system, positions calculated by taking a compass bearing and measurement from a known point on the grid of paths.

7.2.2.3. Mapping Known Positions Using GPS

GPS can not only be used for animal tracking in units attached to the animal, but simple hand held receivers can be utilised to plot locations of groups, either during follows, or subsequently to aid in locating tags. However, as many of the same problems apply as when attaching GPS units to animals. This method was used by Irwin (2006b), who recorded 3D positions at sleep and feeding trees.

7.2.3. Mathematical Methods of Determining Home Range

Once positions have been acquired in the field and mapped the data must be analysed to allow range sizes to be statistically or otherwise calculated. Each method of analysing the data will give a different result due to the methods' underlying assumptions and the results cannot often legitimately be compared (Boulanger & White, 1990). If ranging behaviour is strongly seasonal, home ranges described by season may be more appropriate than ranges covering a whole year (Harris *et al.*, 1990). Choice of method is very important as different methods will give different results. Some are better at producing a core area, but others at representing the total home range. Harris *et al.* (1990) suggest that results from two different methods should be given used to eliminate error, and that one of these should probably be the commonly-used minimum convex polygon method (below) to allow comparisons between studies. Accordingly, this thesis uses both a modified convex polygon and grid-cell method.

7.2.3.1. Minimum Convex Polygons: 'Taut String Method'

The 'taut string line method' or minimum convex polygon method, places a line around all the outer known positions of an individual, or a given set of animals., The total enclosed area is then calculated (Altmann & Altmann, 1970; Harris *et al.*, 1990; Kool & Croft, 1992). This is a non-statistical method, and the assumption is made that all areas within the outer limits are used by members of the group or individual (Harris *et al.*, 1990; Kool & Croft, 1992). This is not necessarily the case and can lead to overestimation of home range (Harris *et al.*, 1990; Kool & Croft, 1992). There is also no weighting of areas used most frequently (Harris *et al.*, 1990). The benefits of this method are that it can be used where the number of data points is low and that as a consequence of the popularity of this approach it is possible to compare data from different studies (Harris *et al.*, 1990). However, larger sample sizes lead to larger estimated home range (Boulanger & White, 1990). This method was used to determine home range size of *Avahi occidentalis* and *Lepilemur edwardsi* by Warren and Crompton (1997b).

7.2.3.2. Grid Cells

The use of grid cells is another non-statistical method (Harris *et al.*, 1990). The area used is divided into squares (for example 0.25ha) and the number of squares entered by the group or individual are added together to find the home range (Butynski, 1990; Kool & Croft, 1992). Pollock's (1977) study of *I. indri* at Analamazoatra used 50m quadrats and Crompton and Andau (1987) used 20m quadrats. This method has problems where individuals or groups of animals use only part of each quadrat and it can again lead to overestimates of home range (Kool & Croft, 1992).

7.3. Study Methods

7.3.1 Field Methods

At the start of the study it was decided that a grid system of trails was neither practical nor necessary, given a demonstrated ability of the handheld GPS to locate positions satisfactorily in the study site. To facilitate easy and quick movement of observers throughout the study area, main trails were however cut extending up and over hill ridges. These were tagged and numbered at 10m intervals; gaps determined using a tape measure. This was to allow observers to gain familiarity with the area and as a quick reference during observations. Initially three trails were cut: 'Indri', 'Props' and 'Hapa'.

During observations of all species Day or Blanchard tagged trees in the immediate vicinity of the group under observation every 5 minutes. Tags were consecutively numbered together with date, species and group if required. During periods of inactivity, either from resting or feeding, only one tag was used, but records were kept of the length of time spent at the tag.

The following day, or on the first day subsequently possible, tag positions were recorded using a handheld GPS. It was not possible to record GPS positions during observations as fixes could take too long during bouts of locomotion. From the outset of the study until August 2005 a Garmin GPSmap 76S was used, and following this a Garmin GPSmap 60CS with an internal barometer. The tag number and time of tag deployment were recorded along with the southings and eastings (latitude and longitude), accuracy (in metres), 'D'- whether a three-dimensional or two-dimensional fix, and in certain cases height (in metres [Table 7.1]).

The GPS was turned on at the first tag to obtain an initial position. If the first tag was in a valley the GPS unit was first positioned on a ridge above. The GPS unit was held at around head height to obtain the best accuracy possible. If accuracy was low, the position was recorded but the tag left in the field, to try and obtain a better accuracy at a later date.

Table 7.1. Summary of data collection schedule for position data.

1	Tag number
2	Time
3	South
4	East
5	Accuracy (metres)
6	3 or 2 D
7	Height (metres)
8	Notes

Raw data in excel files was transferred into tab-delimited text files and imported into GPS Utility Version 4.20.9.

7.3.2. Methods of Determining Home Range

Ranging data from this study was input into the software GPS Utility (GPS Utility Ltd. Version 4.20.9 www.gpsu.co.uk) and plotted against known trails. The minimum-convex-polygon method was used to determine home ranges to allow easy comparison with older studies. This resulted in small ranges compared to the literature for all study species. It was hypothesised that this was due to data points being collected by a hand-held GPS and not by the traditional 'tape measure and compass', therefore not taking into account elevation. GPS Utility does not take height into account, only horizontal position, so a routine, purpose-written in MATLAB by Dr. T. Pataky (Appendix E1), was used to enable elevation to be taken into consideration where known.

In addition grid cells were calculated using a grid of 0.01 seconds (equivalent to 0.018km), resulting in squares of 0.033ha. These were calculated using an Excel macro written by Mr. Paolo Caravaggi (Appendix E2).

7.3.3. Statistical Methods

The Mann-Whitney (*U*) test has been used to examine inter-specific differences. The Mann-Whitney test uses the median not the mean (Kinnear & Gray, 2004). This test is suitable for non-parametric samples, where variables are independent. In the Mann-Whitney tests significance is met when $p \leq 0.05$. The Pearson correlation coefficient (r) is used to test for correlations between observation days and ranging, significance is met when $p \leq 0.05$.

7.4. Results

7.4.1 Home Range

The position of the home ranges of the four study groups is plotted relative to trails and the road in Figure 7.2. Group One (red) and Two (green) *H. g. griseus* home ranges are adjacent to the miners' road on the west of the study area. The ranges of *P. diadema* (yellow) and *I. indri* (blue) overlap only slightly.

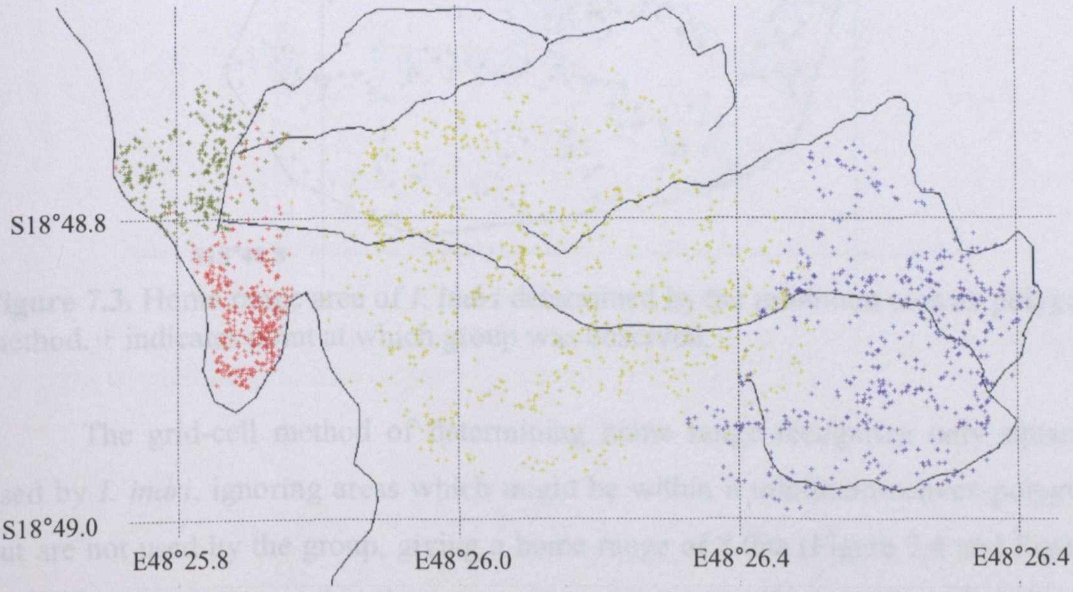


Figure 7.2. Map of study area with road and trails showing the home ranges of each study species. + *H. g. griseus* Group One, + *H. g. griseus* Group Two, + *P. diadema* and + *I. indri*.

7.4.1.1. *Indri indri*

The home range of *I. indri* (Figure 7.3) in this study was calculated using the minimum-convex-polygon method as 13.2ha, smaller than any other previously recorded. This increased to only 13.3ha when the MATLAB routine was used to take elevation into account.

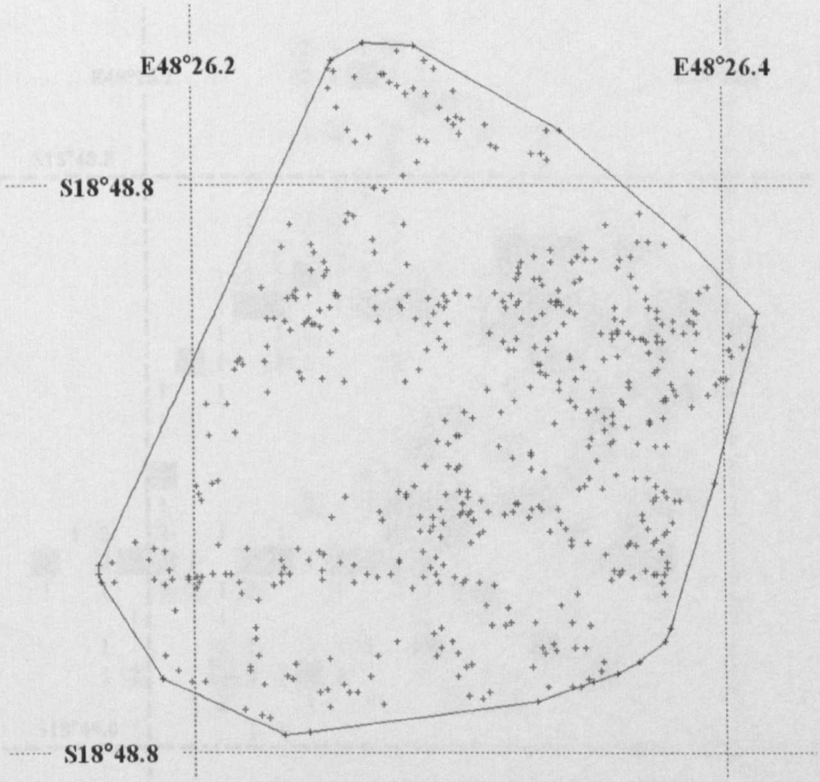


Figure 7.3. Home range area of *I. indri* determined by the minimum convex polygon method. + indicates point at which group was observed.

The grid-cell method of determining home range recognises only squares used by *I. indri*, ignoring areas which might be within a minimum-convex-polygon but are not used by the group, giving a home range of 8.0ha (Figure 7.4 and Figure 7.5). The plot indicates that there are many areas, centrally located in their home range which they do not appear to utilise. Grid-cell plots also indicate density of marker points, and for analysing these two different methods were used. The first examines frequency of usage, where each tag was only counted once, independent of the length of time the group remained there (Figure 7.4). The second (Figure 7.5) examines density using temporal data, and each 5 minute period the group remained at each tag is counted. These two plots both suggest that *I. indri* spend a large amount of time in very small areas of their home range.

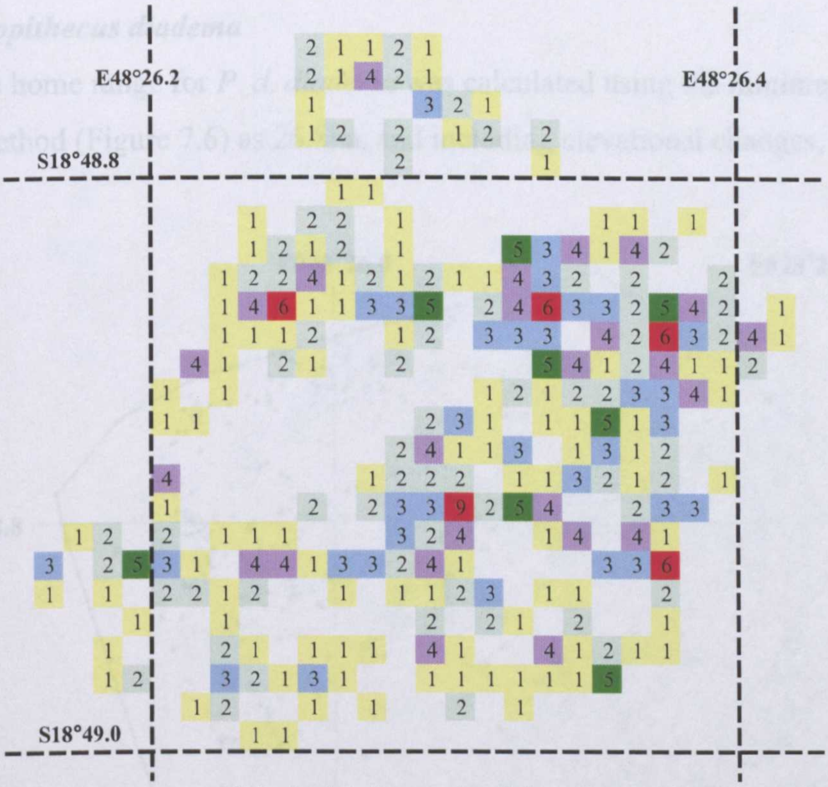


Figure 7.4. Home range of *I. indri* determined by the grid-cell method. Density calculated by frequency, where numbers and colours indicate number of tags recorded in each square. Each square represents 0.033ha. *N* = 518.

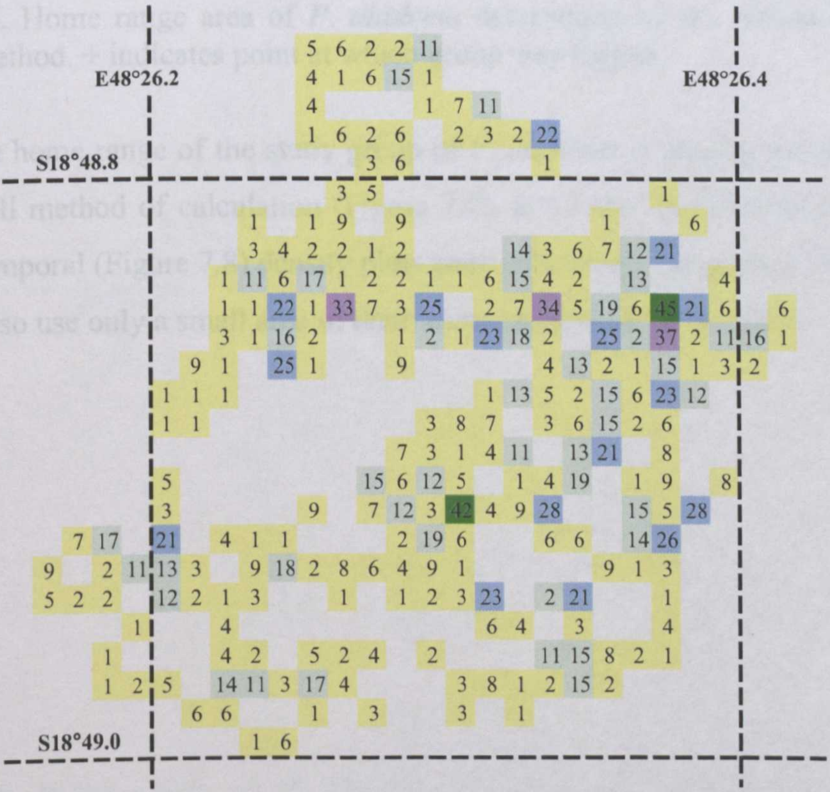


Figure 7.5. Home range of *I. indri* determined by the grid-cell method. With temporal density, where numbers and colours represents the number of 5-minutes periods recorded in each square. Each square represents 0.033ha. *N* = 2090.

5.4.1.2. *Propithecus diadema*

The home range for *P. d. diadema* was calculated using the minimum-convex polygon method (Figure 7.6) as 26.8ha, and including elevational changes, 27.0ha.

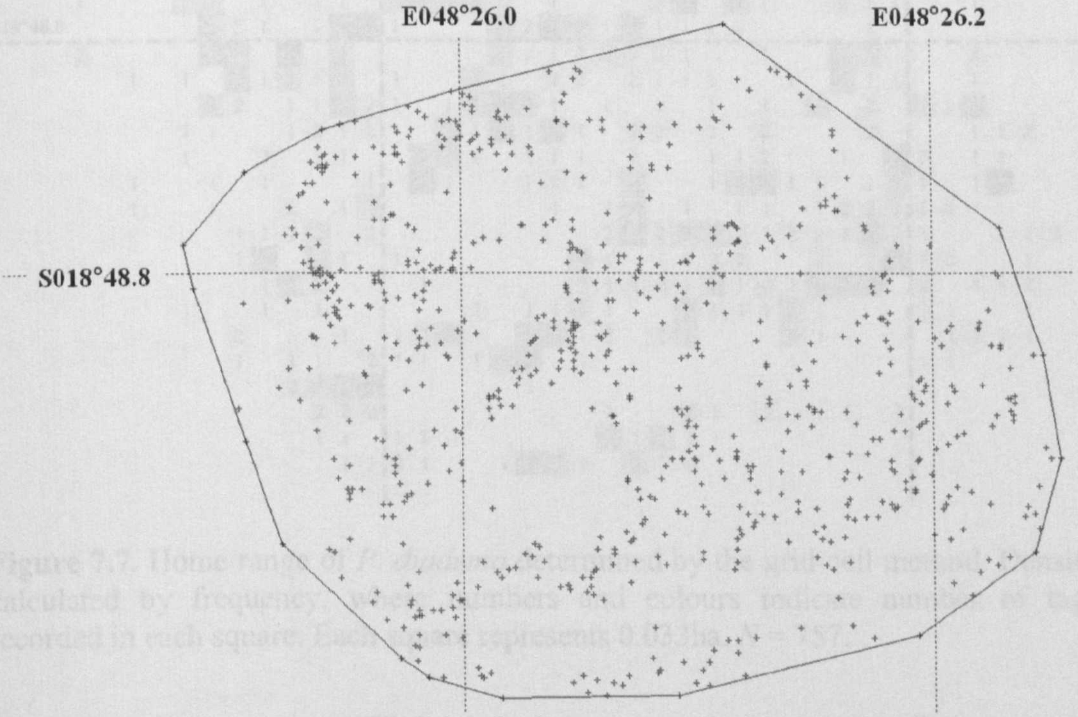


Figure 7.6. Home range area of *P. diadema* determined by the minimum convex polygon method. + indicates point at which group was tagged.

The home range of the study group of *P. diadema* is smaller yet when using the grid-cell method of calculation (Figure 7.7), at 12.8ha. Both frequency (Figure 7.7) and temporal (Figure 7.8) density plots were calculated. These plots show that *P. diadema* also use only a small area of their home range most of the time.

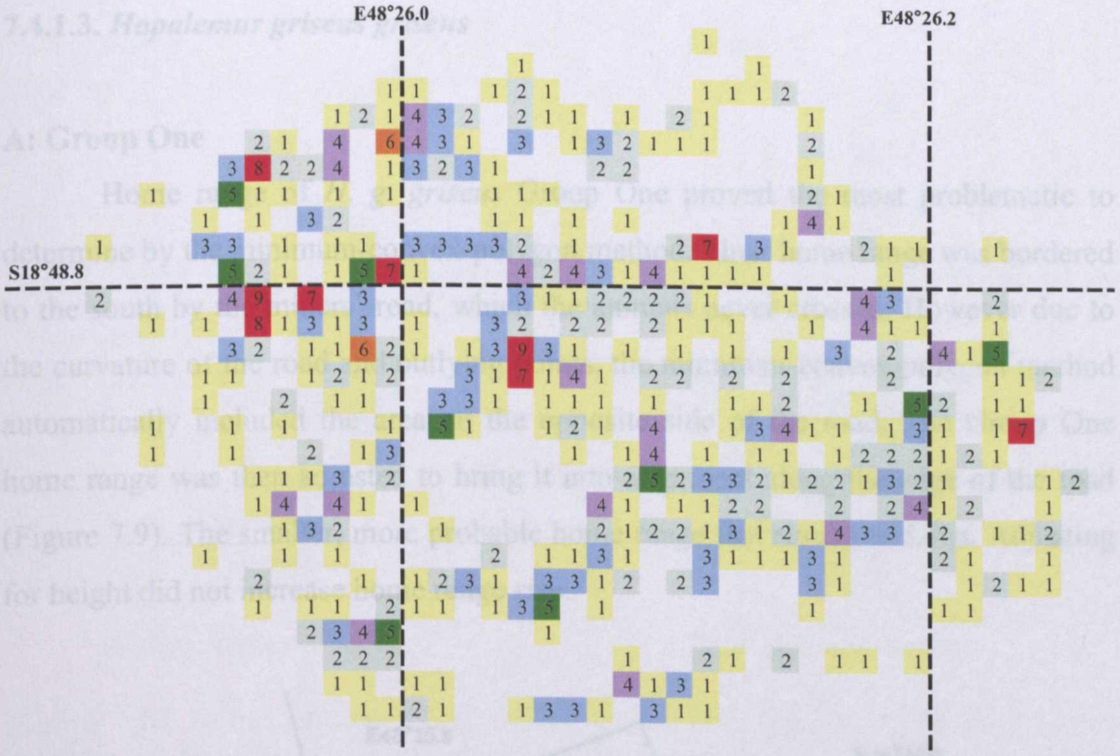


Figure 7.7. Home range of *P. diadema* determined by the grid-cell method. Density calculated by frequency, where numbers and colours indicate number of tags recorded in each square. Each square represents 0.033ha. *N* = 757.

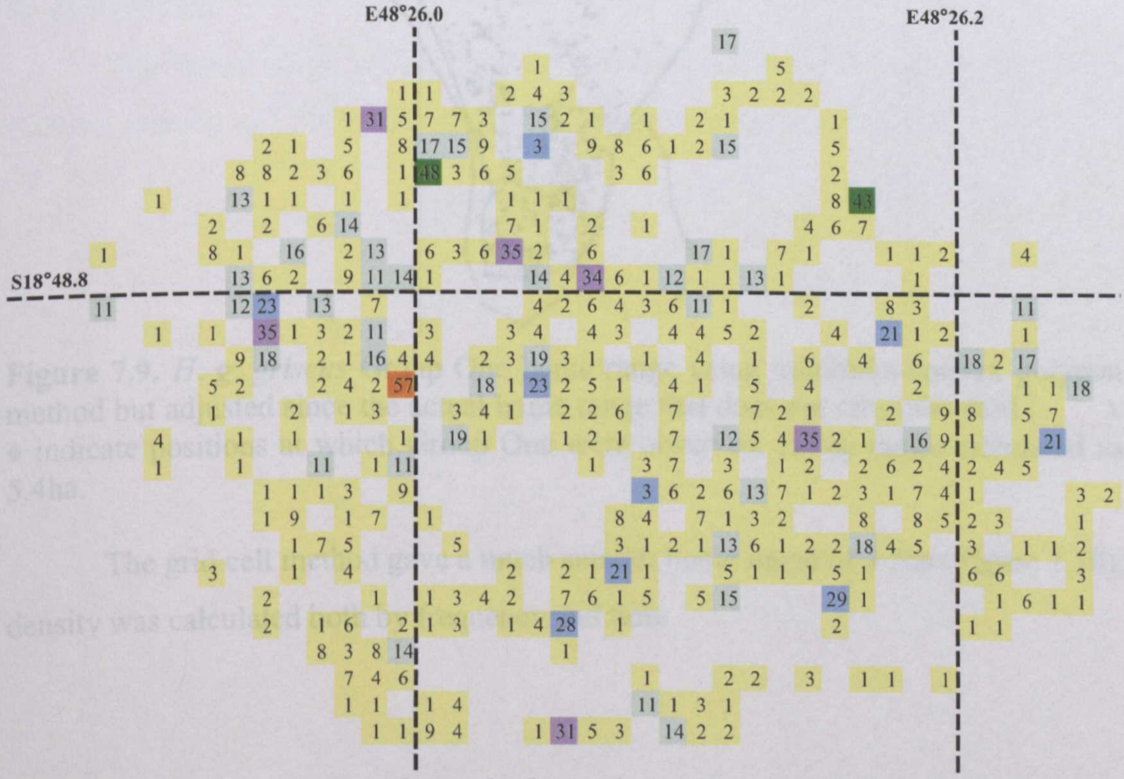


Figure 7.8. Home range of *P. diadema* determined by the grid-cell method. Temporal density, where numbers and colours represent the number of 5-minute periods recorded in each square. Each square represents 0.033ha. *N* = 2296.

7.4.1.3. *Hapalemur griseus griseus*

A: Group One

Home range of *H. g. griseus* Group One proved the most problematic to determine by the minimum-convex-polygon method. Their home range was bordered to the south by the miners' road, which the animals never crossed. However due to the curvature of the road and outlying points, the minimum-convex-polygon method automatically included the area on the opposite side of the road, The Group One home range was then adjusted to bring it into alignment along the edge of the road (Figure 7.9). The smaller, more probable home range that results is 5.4ha. Adjusting for height did not increase home range size.

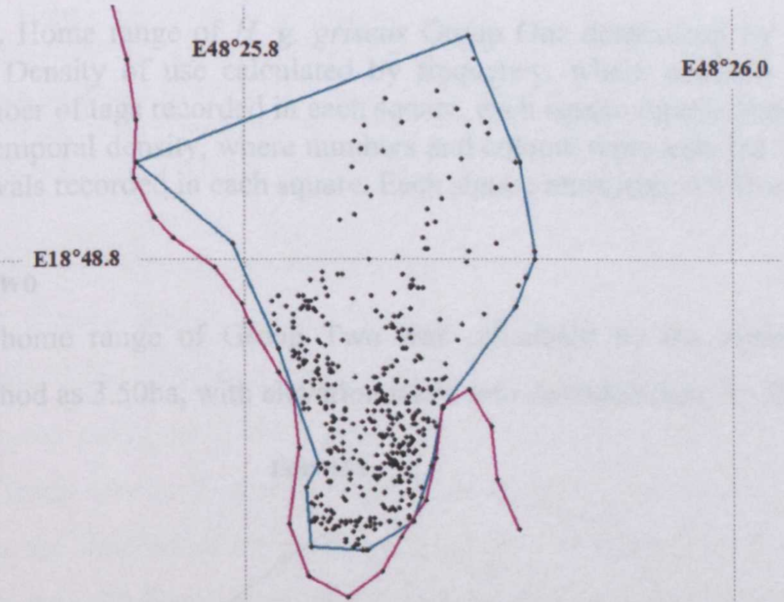
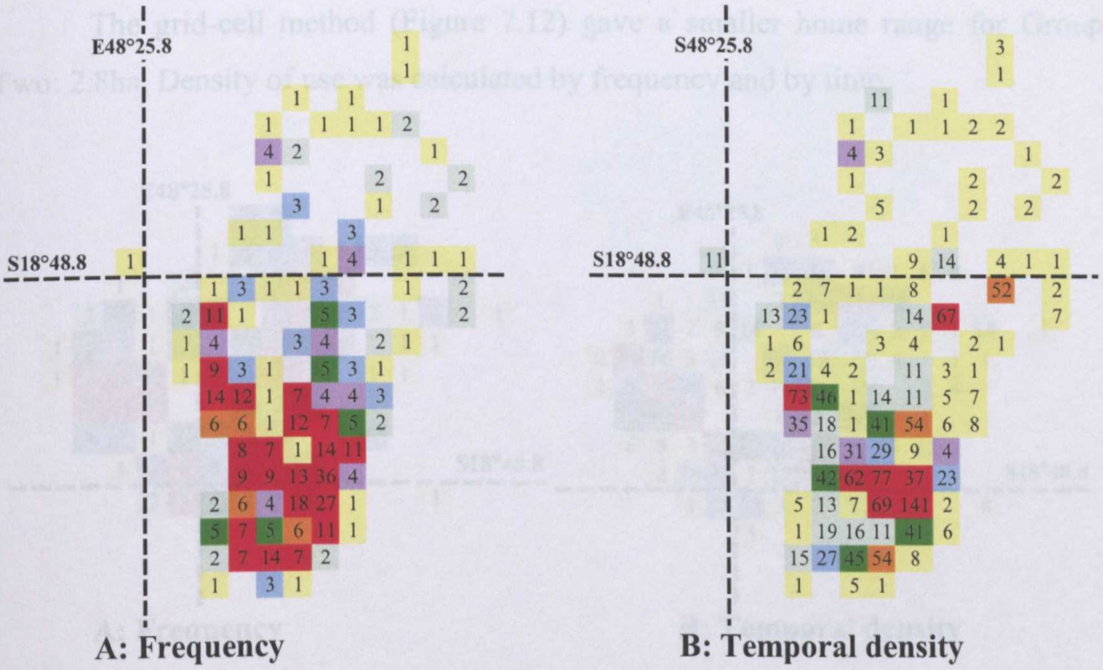


Figure 7.9. *H. g. griseus* Group One home range using minimum-convex polygon method but adjusted since the actual home range that does not cross the road (____). ♦ indicate positions at which Group One were observed. Home range calculated as 5.4ha.

The grid cell method gave a much smaller home range of 3.2ha (Figure 7.10), density was calculated both by frequency and time.



A: Frequency

B: Temporal density

Figure 7.10. Home range of *H. g. griseus* Group One determined by the grid-cell method. **A:** Density of use calculated by frequency, where numbers and colours indicate number of tags recorded in each square, each square representing 0.033ha. *N* = 498. **B:** Temporal density, where numbers and colours represents the number of 5-minute intervals recorded in each square. Each square represents 0.033ha. *N* = 2106.

B: Group Two

The home range of Group Two was calculated by the minimum-convex polygon method as 3.50ha, with elevation taken into consideration: 3.52ha.

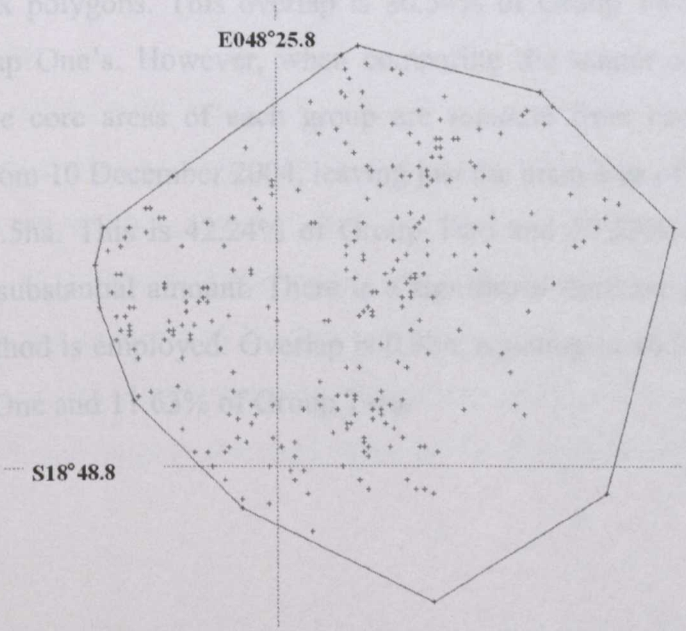
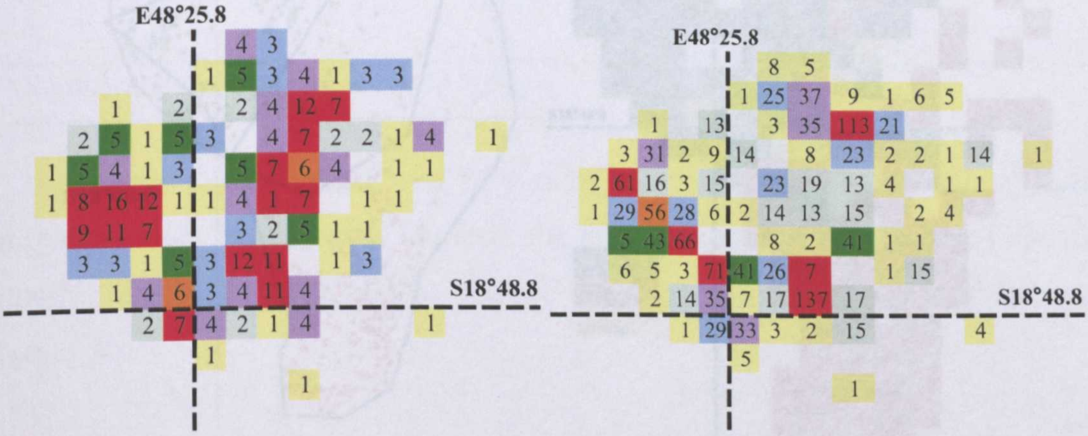


Figure 7.11. Home range area of *H. g. griseus* Group Two determined by the minimum convex polygon method. + signs indicate each point at which group was tagged. Home range is 3.5ha.

The grid-cell method (Figure 7.12) gave a smaller home range for Group Two: 2.8ha, Density of use was calculated by frequency and by time.

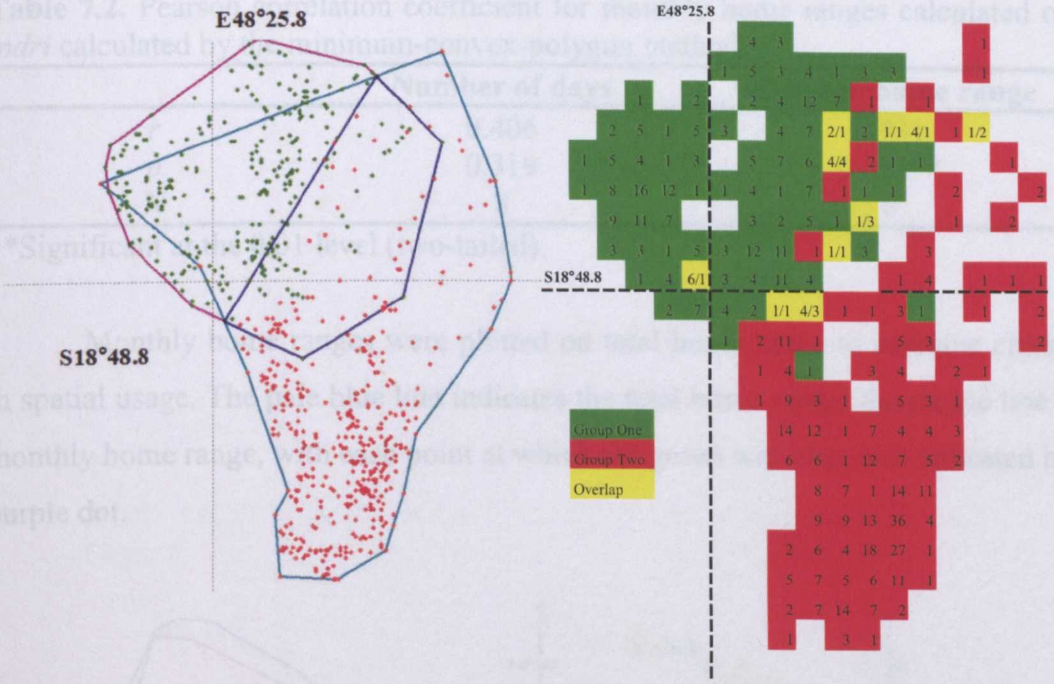


A: Frequency **B: Temporal density**

Figure 7.12. Home range of H. g. griseus Group Two determined by the grid-cell method. **A:** Density calculated by frequency, where numbers and colours indicate number of tags recorded in each square. Each square represents 0.033ha. N = 329. **B:** Temporal density, where numbers and colours represents the number of 5 minutes recorded in each square, each square represents 0.033ha. N = 1505.

C: Overlap between Group One and Group Two

There is considerable overlap between Group One and Group Two *H. g. griseus* (Figure 7.13). The two groups share 2.8ha of territory as calculated by minimum-convex polygons. This overlap is 80.54% of Group Two's territory and 52.49% of Group One's. However, when comparing the scatter of positions it is apparent that the core areas of each group are separate from each other. If one discounts data from 10 December 2004, leaving just the main area of shared territory, the overlap is 1.5ha. This is 42.24% of Group Two and 27.53% of Group One's territory, still a substantial amount. There is a significant decrease in overlap when the grid-cell method is employed. Overlap is 0.3ha, equating to 10.31% of the home range of Group One and 11.63% of Group Two.



A: MCP **B: Grid-cell**

Figure 7.13. Overlap between Group One and Two *H. g. griseus*. **A:** Minimum-convex polygon (MCP) overlap (____) of Group One (____ & +) and Group Two (____ & +). Total overlap is 1.5ha. **B:** Grid-cell method, numbers indicate number of times group was recorded in each square; each square represents 0.033ha. Where both groups occupied the same square, value for Group Two is given first.

7.4.2. Monthly Home Ranges

7.4.2.1. *Indri indri*

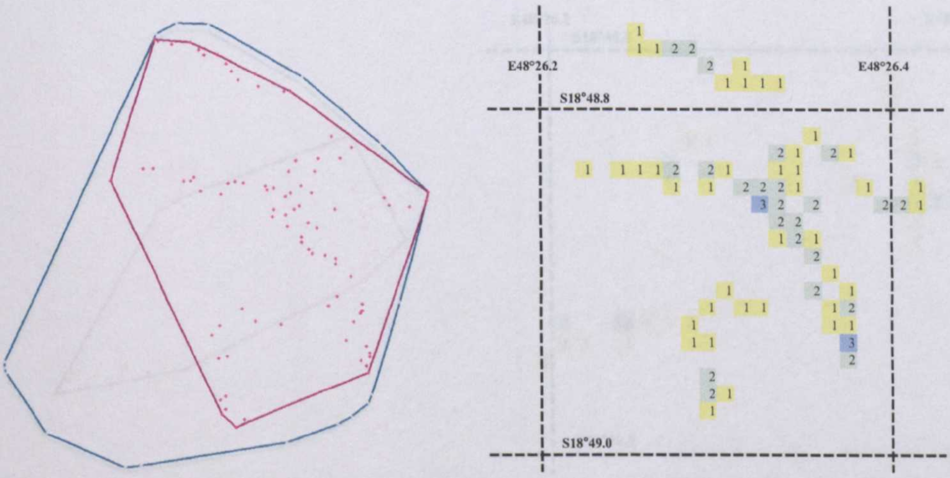
Monthly ranges were calculated using both the minimum-convex polygon and grid-cell methods, but excluding the month of October for which there was only one day of observation. There was, as would be expected, a strong correlation at the 0.01 level ($r = 0.931$) between home range size calculated by both methods (Table 7.2). Monthly ranges determined by the minimum-convex-polygon method (Table 7.2) were not correlated with the number of observation days each month ($r = 0.406$) and neither were home ranges calculated by the grid-cell approach ($r\ [8] = 0.537$, $p >$ 0.05ns).

Table 7.2. Pearson correlation coefficient for monthly home ranges calculated of *I. indri* calculated by the minimum-convex-polygon method.

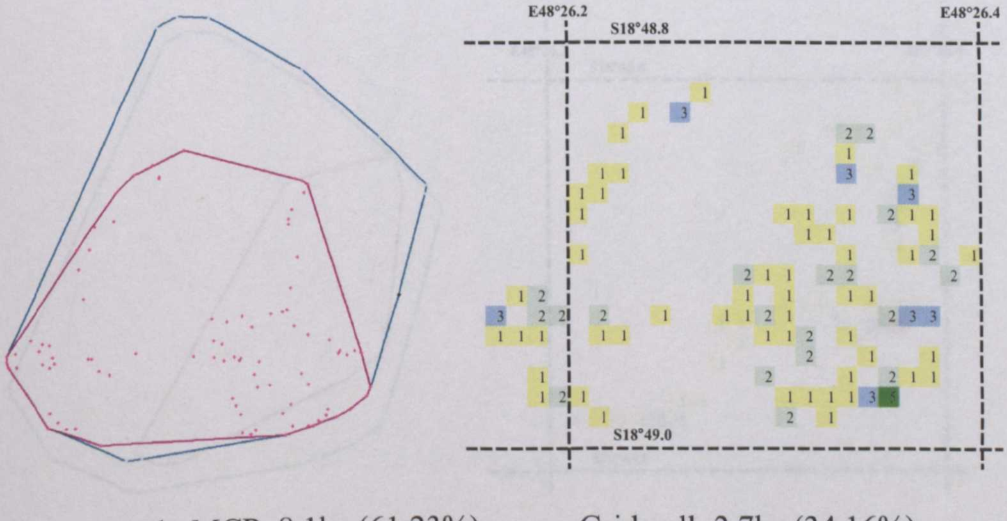
	Number of days	**Grid cell home range**
r	0.406	0.931
p	0.319	0.001**
N	8	8

**Significant at the 0.01 level (two-tailed).

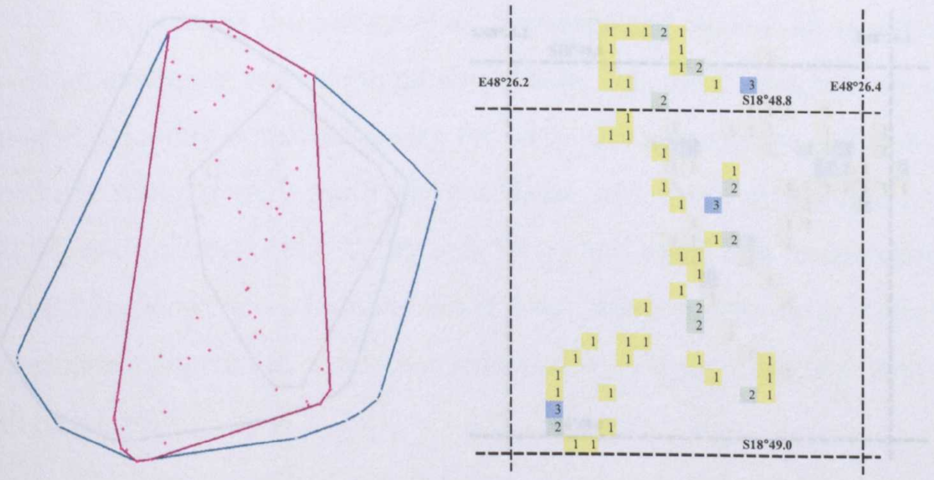
Monthly home ranges were plotted on total home range to examine changes in spatial usage. The pale blue line indicates the total home range, the purple line the monthly home range, with each point at which the group was observed indicated by a purple dot.



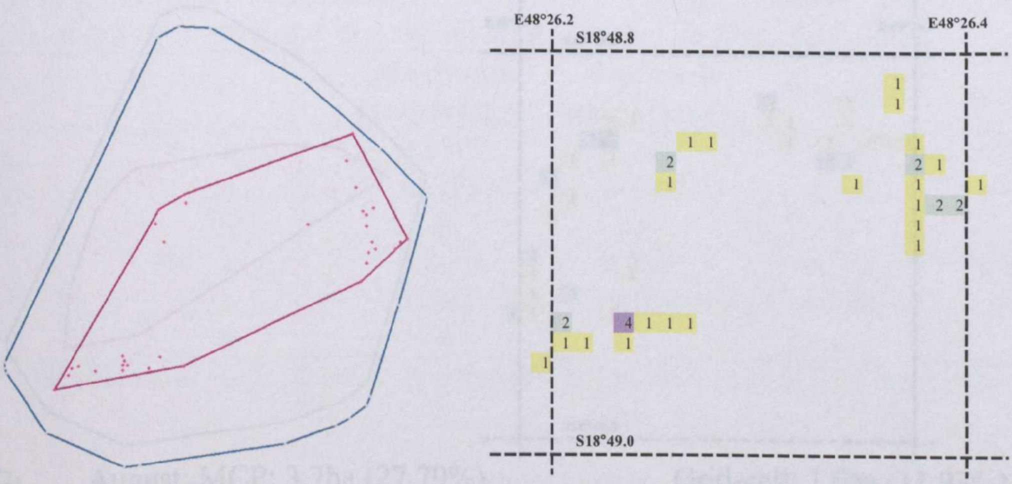
A: February: MCP: 8.0ha (60.73%) Grid-cell: 2.1ha (26.75%)
Days: 3 *N* = 92.



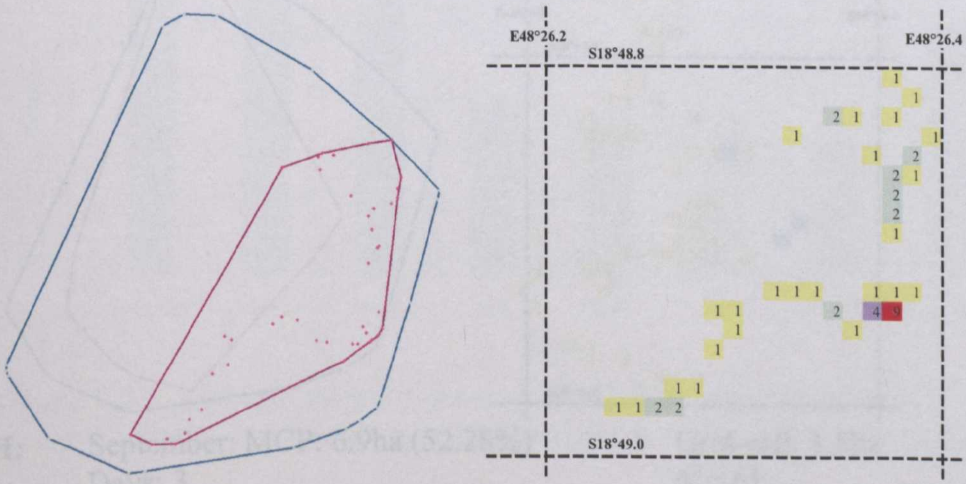
B: March: MCP: 8.1ha (61.23%) Grid-cell: 2.7ha (34.16%)
Days: 4 *N* = 121.



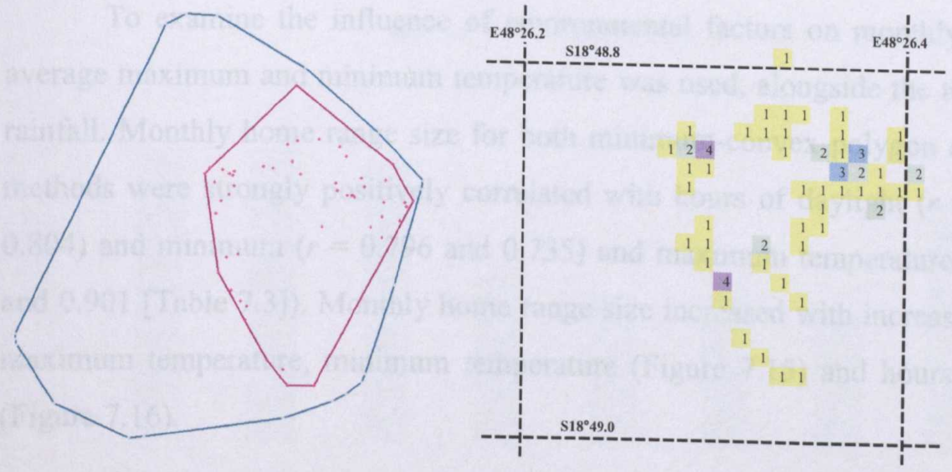
C: April: MCP: 7.7ha (57.96%) Grid-cell: 1.7ha (21.40%)
Days: 3 $N = 67$.



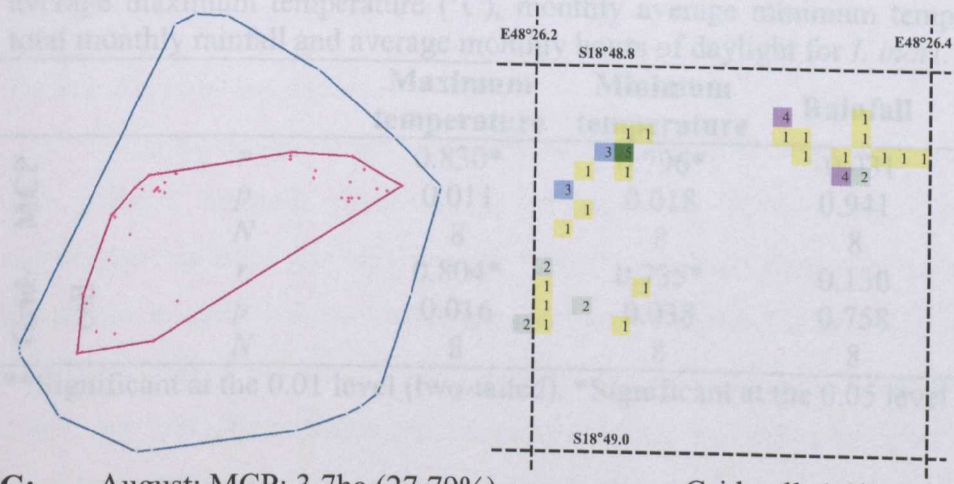
D: May: MCP: 4.7ha (35.47%) Grid-cell: 0.8ha (10.70%)
Days: 2 $N = 34$.



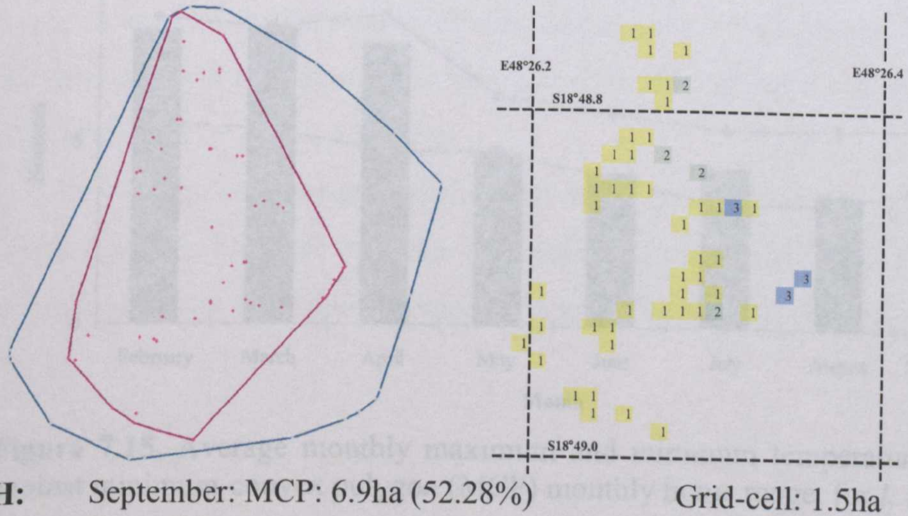
E: June: MCP: 4.2ha (31.70%) Grid-cell: 1.1ha (13.99%)
Days: 3 $N = 53$.



F: July: MCP: 4.3ha (32.84%) Grid-cell: 1.7ha (21.40%)
Days: 4 $N = 68$.



G: August: MCP: 3.7ha (27.79%) Grid-cell: 1.0ha (11.93%)
Days: 2 $N = 47$.



H: September: MCP: 6.9ha (52.28%) Grid-cell: 1.5ha
Days: 3 $N = 61$.

Figure 7.14. Monthly home ranges (_____) using the minimum-convex-polygon (MCP) method for *I. indri* plotted on the total home range (_____), ● representing points at which the group were observed. Grid-cell plots show frequency of observations. Percentages are of total MCP home range.

To examine the influence of environmental factors on monthly range size, average maximum and minimum temperature was used, alongside the total monthly rainfall. Monthly home range size for both minimum-convex polygon and grid-cell methods were strongly positively correlated with hours of daylight (r = 0.830 and 0.804) and minimum (r = 0.796 and 0.735) and maximum temperatures (r = 0.824 and 0.901 [Table 7.3]). Monthly home range size increased with increasing monthly maximum temperature, minimum temperature (Figure 7.15) and hours of daylight (Figure 7.16).

Table 7.3. Pearson correlation coefficients for monthly home range, as determined by the minimum-convex polygon (MCP) and grid-cell methods against monthly average maximum temperature (°C), monthly average minimum temperature (°C), total monthly rainfall and average monthly hours of daylight for *I. indri*.

		Maximum temperature	**Minimum temperature**	**Rainfall**	**Daylight**
MCP	*r*	0.830*	0.796*	-0.031	0.824
	p	0.011	0.018	0.941	0.012
	N	8	8	8	8
Grid-cell	*r*	0.804*	0.735*	0.130	0.901**
	p	0.016	0.038	0.758	0.002
	N	8	8	8	8

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

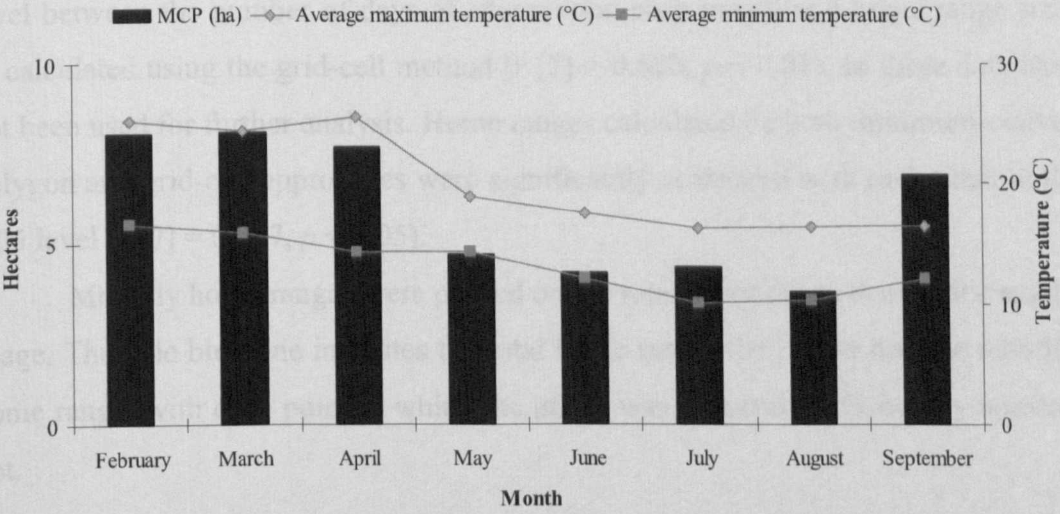


Figure 7.15. Average monthly maximum and minimum temperature (°C), plotted against minimum-convex polygon (MCP) monthly home range, for *I. indri* (2005).

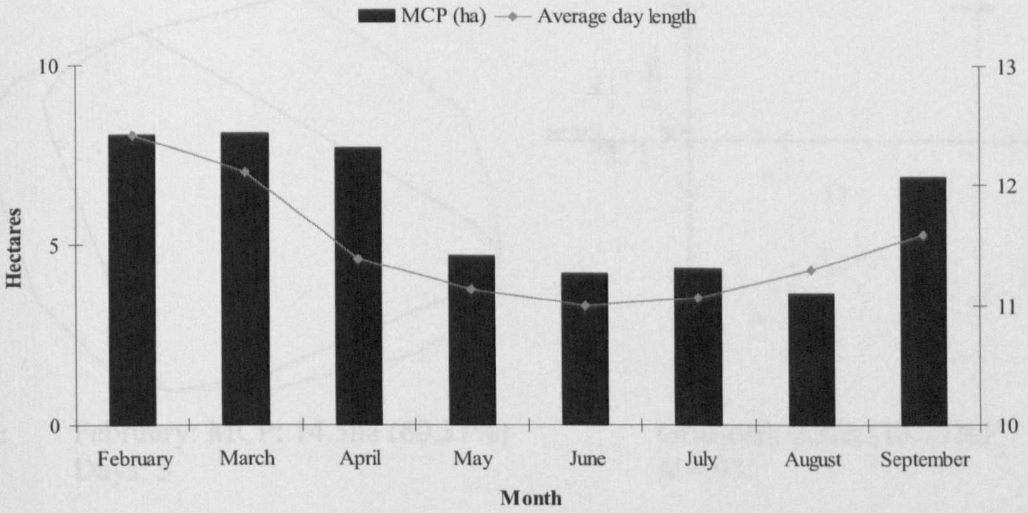
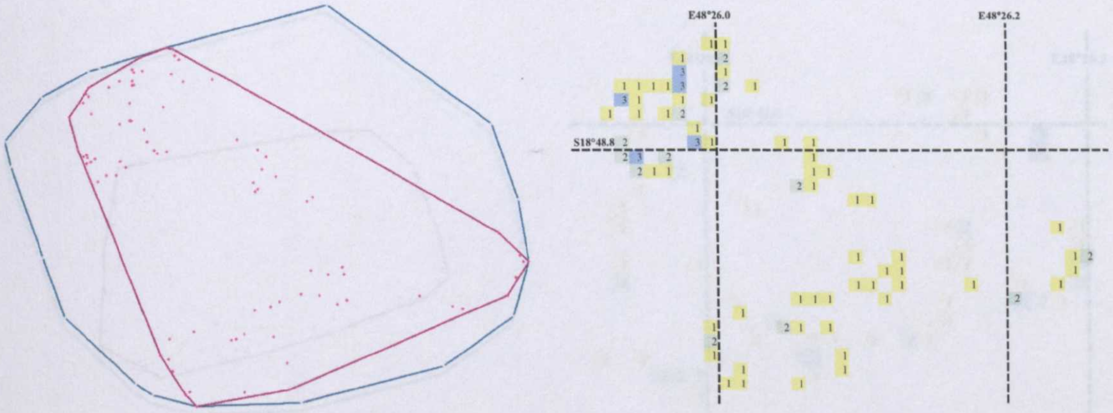


Figure 7.16. Average monthly day length, plotted against minimum-convex polygon (MCP) monthly home range, for *I. indri* (2005).

7.4.2.2. *Propithecus diadema*

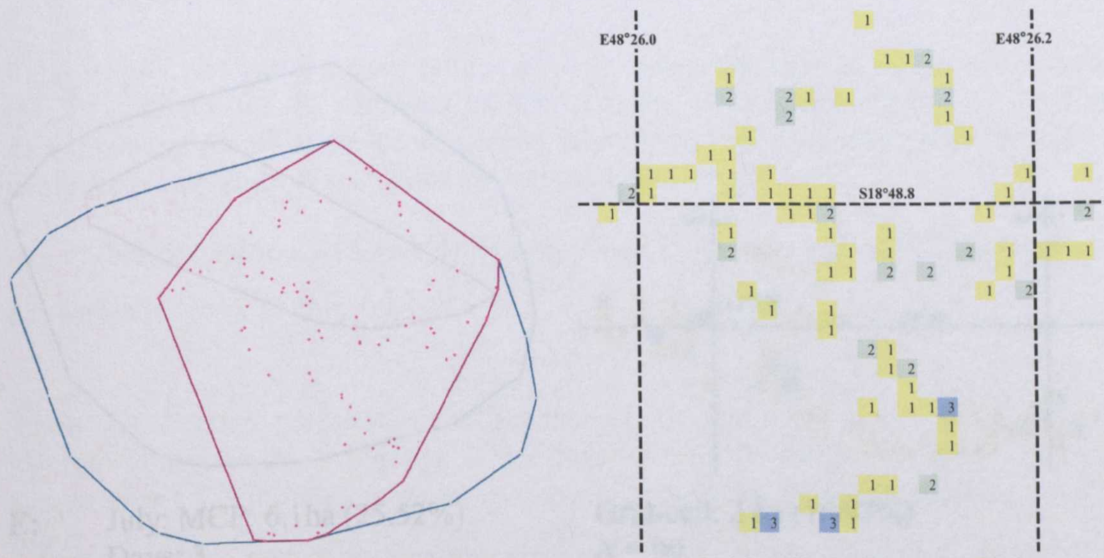
Monthly home ranges were calculated using both minimum-convex-polygon and grid-cell methods. The months of May and October were removed from calculations as there was only one day's worth of observation each and ranges were correlated at the 0.01 level with the number of days of observation for both the minimum-convex polygon (r [9] = 0.847, $p < 0.01$) and grid cell methods (r [9] = 0.861, $p < 0.01$). Even following this removal, there was still a correlation at the 0.01 level between the number of days of observation each month and home range sizes as calculated using the grid-cell method (r [7] = 0.880, $p < 0.01$), so these data have not been used for further analysis. Home ranges calculated by both minimum-convex polygon and grid-cell approaches were significantly correlated with each other at the 0.05 level (r [7] = 0.857, $p < 0.05$).

Monthly home ranges were plotted on the total home range to examine spatial usage. The pale blue line indicates the total home range, the purple line the monthly home range, with each point at which the group was observed indicated by a purple dot.



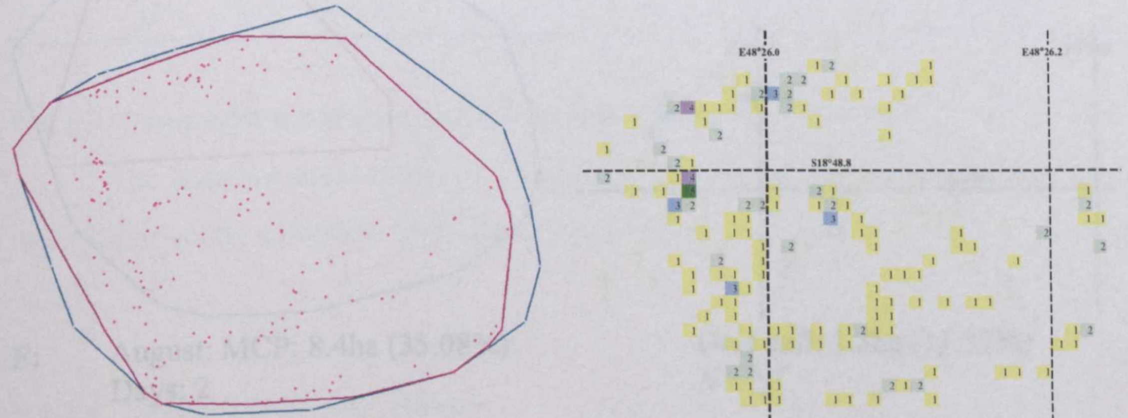
A: February: MCP: 14.5ha (60.37%)
Days: 3

Grid-cell: 2.3ha (18.25%)
N = 93.



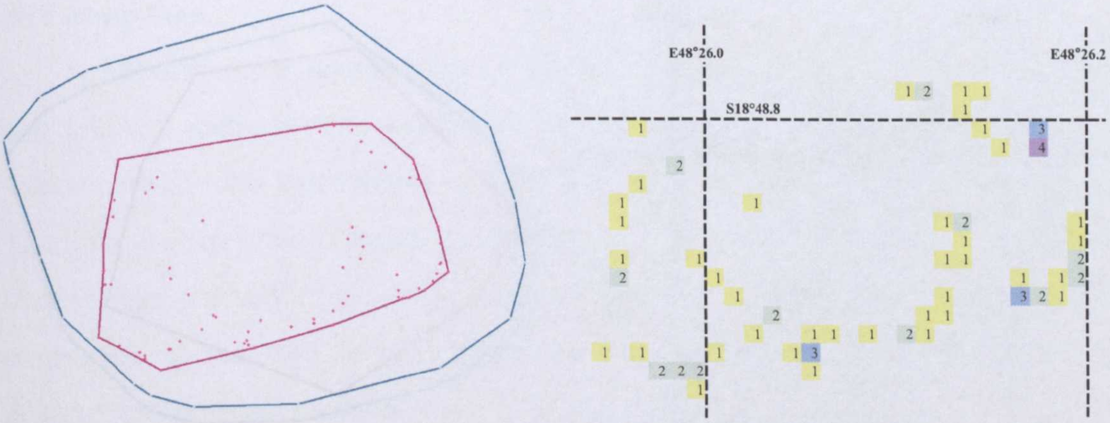
B: March: MCP: 13.4ha (55.92%)
Days: 3

Grid-cell: 2.6ha (20.57%)
N = 101.

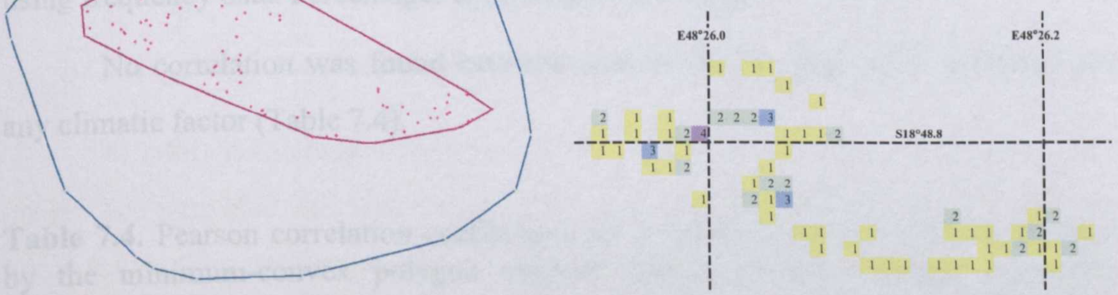


C: April: MCP: 21.1ha (88.08%)
Days: 4

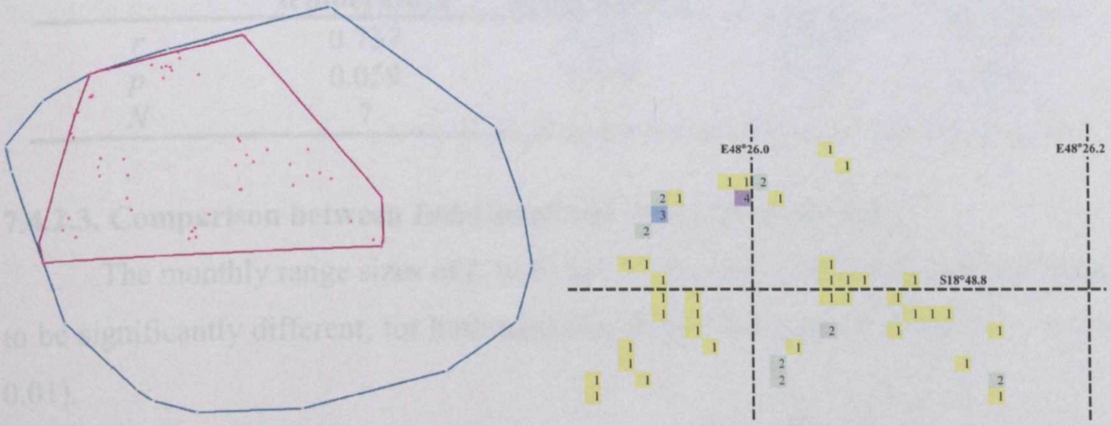
Grid-cell: 4.6ha (35.99%)
N = 186.



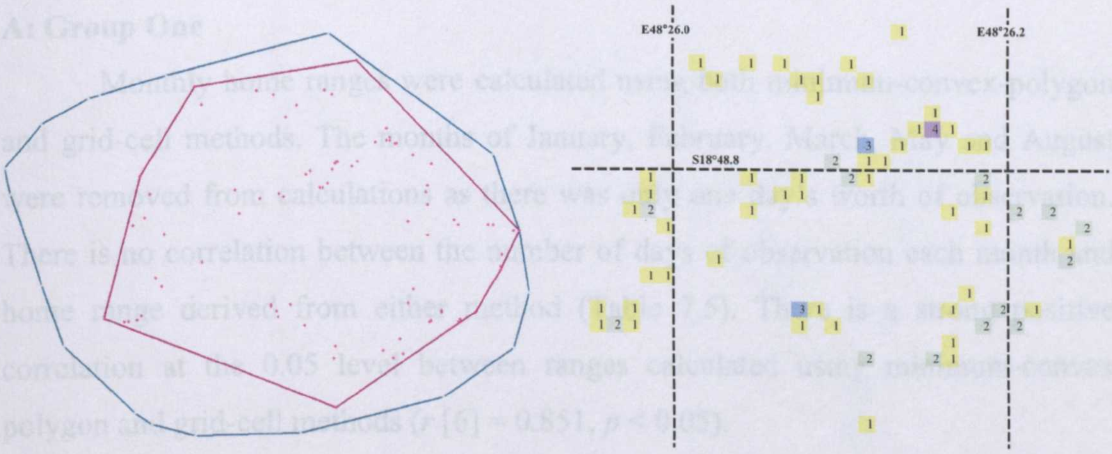
D: June: MCP: 9.9ha (41.53%) Grid-cell: 1.8ha (13.88%)
Days: 3 *N* = 76.



E: July: MCP: 6.1ha (25.52%) Grid-cell: 2.ha (16.97%)
Days: 3 *N* = 90.



F: August: MCP: 8.4ha (35.08%) Grid-cell: 1.5ha (11.57%)
Days: 2 *N* = 57.



G: September: MCP: 14.6ha (61.19%) Grid-cell: 2.1ha (16.71%)
Days: 3 $N = 86$.

Figure 7.17. Monthly home ranges (——) using the minimum-convex-polygon (MCP) method for *P. diadema* plotted on the total home range (——) with ●representing points at which the group were observed. Grid-cells were calculated using frequency data. Percentages are of total home range.

No correlation was found between monthly home range of *P. diadema* and any climatic factor (Table 7.4).

Table 7.4. Pearson correlation coefficients for monthly home range, as determined by the minimum-convex polygon method against monthly average maximum temperature (°C), monthly average minimum temperature (°C), total monthly rainfall (mm) and average monthly hours of daylight for *P. diadema*.

	Maximum temperature	**Minimum temperature**	**Rainfall**	**Daylight**
r	0.737	0.658	-0.589	0.411
p	0.059	0.108	0.165	0.360
N	7	7	7	7

7.4.2.3. Comparison between *Indri indri* and *Propithecus diadema*

The monthly range sizes of *I. indri* and *P. diadema* were compared and found to be significantly different, for both methods of size determination (U [15] = 4, $p < 0.01$).

7.4.2.4. *Hapalemur griseus griseus*

No significant difference was found between the monthly range sizes, using both methods, of Group One and Two (U [11] = 12, $p > 0.05$ns).

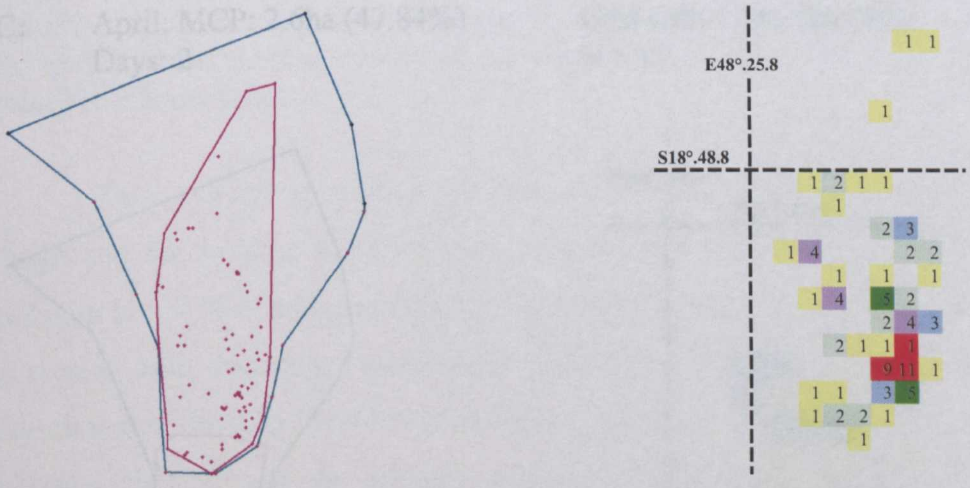
A: Group One

Monthly home ranges were calculated using both minimum-convex-polygon and grid-cell methods. The months of January, February, March, May and August were removed from calculations as there was only one day's worth of observation. There is no correlation between the number of days of observation each month and home range derived from either method (Table 7.5). There is a strong positive correlation at the 0.05 level between ranges calculated using minimum-convex polygon and grid-cell methods ($r\,[6] = 0.851$, $p < 0.05$).

Table 7.5. Pearson correlation coefficients for number of observation days each month with home range derived from minimum-convex polygons (MCP) and grid-cell for *H. g. griseus* Group One.

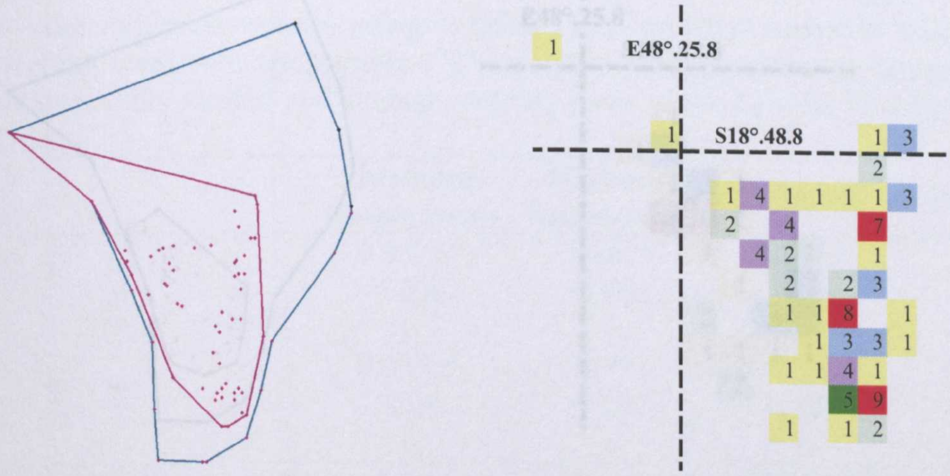
	MCP	Grid-Cell
r	0.217	0.295
p	0.679	0.570
N	6	6

Monthly home ranges were plotted on the total home range to examine spatial usage. The pale blue line indicates the total home range, the purple line the monthly home range, with each point at which the group was observed indicated by a purple dot. It does appear that from November through April the group uses the larger part of its home range, while from June to September the group uses a smaller area in the far south (bottom of the chart) of their home range.

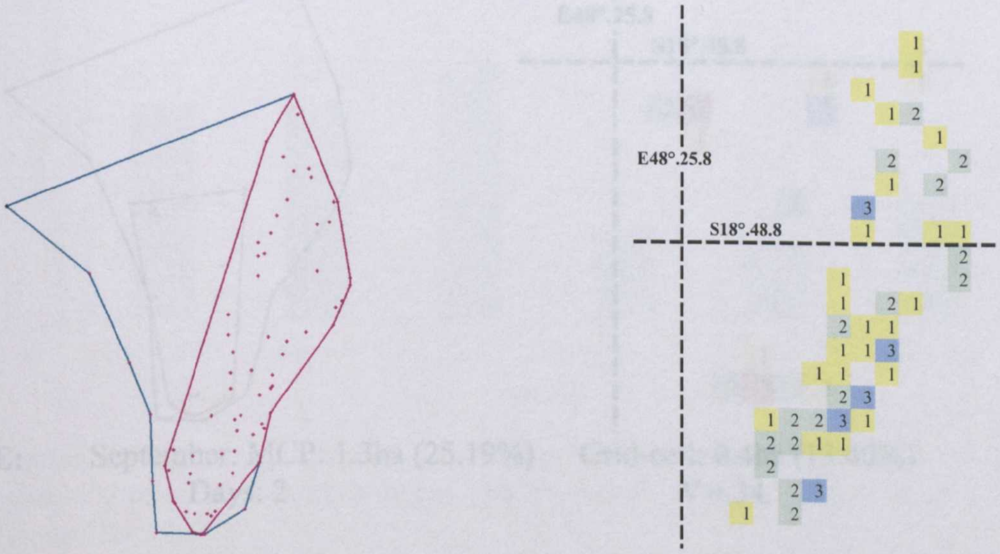


A: November: MCP: 2.1ha (39.83%)
Days: 3

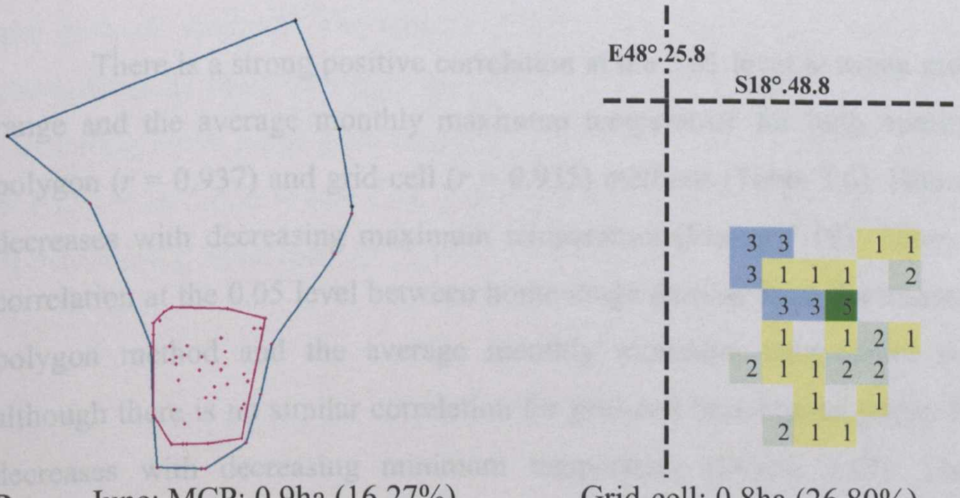
Grid-cell: 1.3ha (41.24%)
$N = 99$.



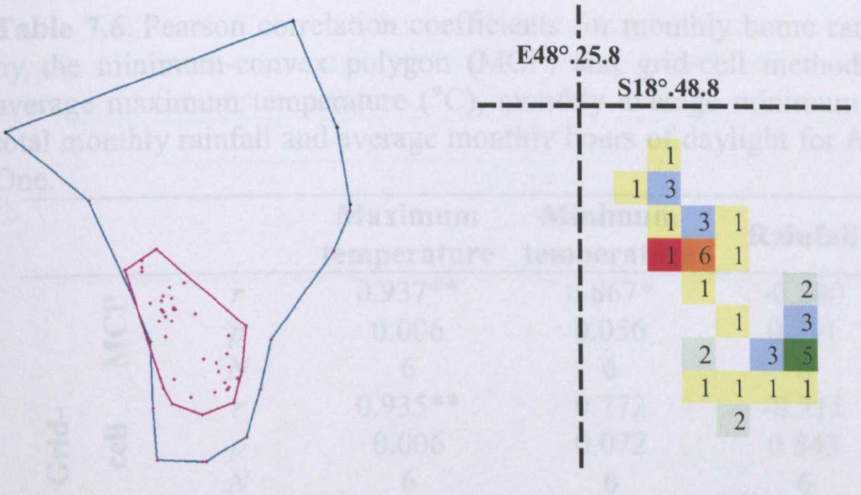
B: December: MCP: 2.1ha (39.57%) Grid-cell: 1.3ha (39.18%)
Days: 4 *N* = 91.



C: April: MCP: 2.6ha (47.84%) Grid-cell: 1.5ha (46.39%)
Days: 2 *N* = 71.



D: June: MCP: 0.9ha (16.27%) Grid-cell: 0.8ha (26.80%)
Days: 2 *N* = 46.



E: July: MCP: 0.8ha (15.12%) Grid-cell: 0.7ha (21.65%)
Days: 3 $N = 50$.

E: September: MCP: 1.3ha (25.19%) Grid-cell: 0.4ha (13.40%)
Days: 2 $N = 34$.

Figure 7.18. Monthly home ranges (___) using the minimum-convex-polygon (MCP) method for *H. g. griseus* Group One plotted on the total home range (___), for months when there is more than one day of observation only. Percentages are of total MCP home range.

There is a strong positive correlation at the 0.01 level between monthly home range and the average monthly maximum temperature for both minimum-convex polygon ($r = 0.937$) and grid-cell ($r = 0.935$) methods (Table 7.6). Home range size decreases with decreasing maximum temperature (Figure 7.19). There is a strong correlation at the 0.05 level between home range derived from the minimum-convex polygon method and the average monthly minimum temperature (r = 0.867), although there is no similar correlation for grid-cell based home range. Home range decreases with decreasing minimum temperature (Figure 7.19). There are no correlations between home range and either rainfall or the hours of daylight.

Table 7.6. Pearson correlation coefficients for monthly home range, as determined by the minimum-convex polygon (MCP) and grid-cell methods against monthly average maximum temperature (°C), monthly average minimum temperature (°C), total monthly rainfall and average monthly hours of daylight for *H. g. griseus* Group One.

		Maximum temperature	Minimum temperature	Rainfall	Daylight
MCP	*r*	0.937**	0.867*	-0.280	0.610
	p	0.006	0.056	0.591	0.348
	N	6	6	6	6
Grid-cell	*r*	0.935**	0.772	-0.315	0.499
	p	0.006	0.072	0.543	0.313
	N	6	6	6	6

**Significant at the 0.01 level (two-tailed) *Significant at the 0.05 level (two-tailed)

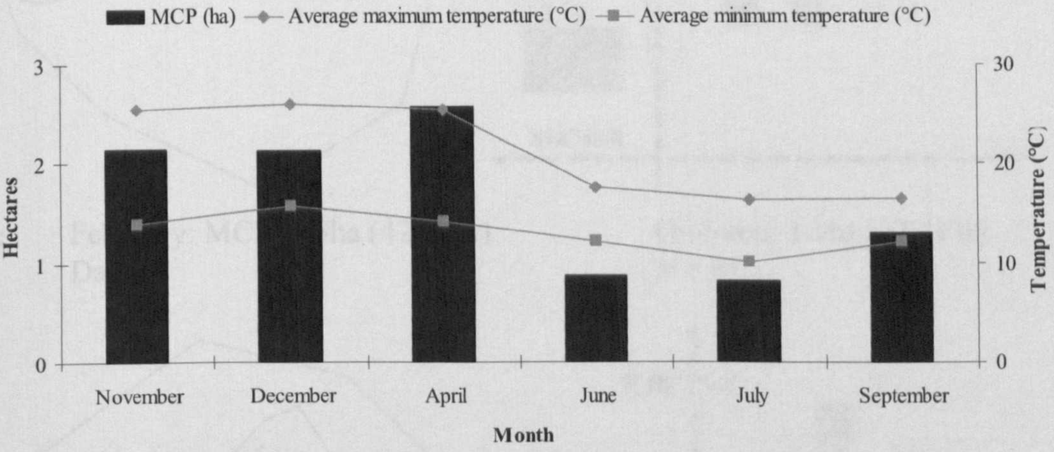


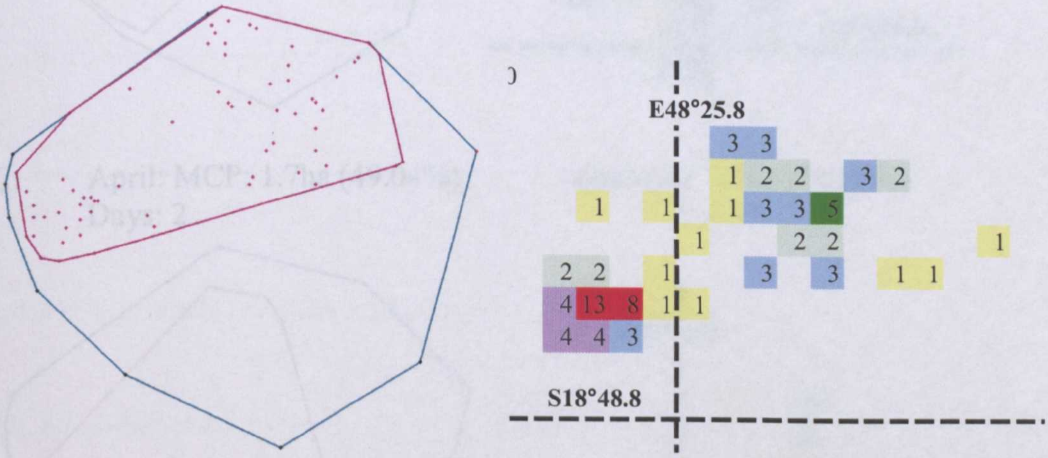
Figure 7.19. Average monthly maximum and minimum temperature (°C), plotted against minimum-convex polygon (MCP) monthly home range, for *H. g. griseus* Group One (2005).

B: Group Two

Monthly home ranges were calculated using both minimum-convex-polygon and grid-cell methods. The months of May, July and August were removed from calculations as there was only one days worth of observation. Neither method of calculating home range gave monthly home range sizes correlated with the number of daily observation (Table 7.7). There was no correlation between the two methods of determining home range (r [5] = 0.179, $p > 0.05$ns).

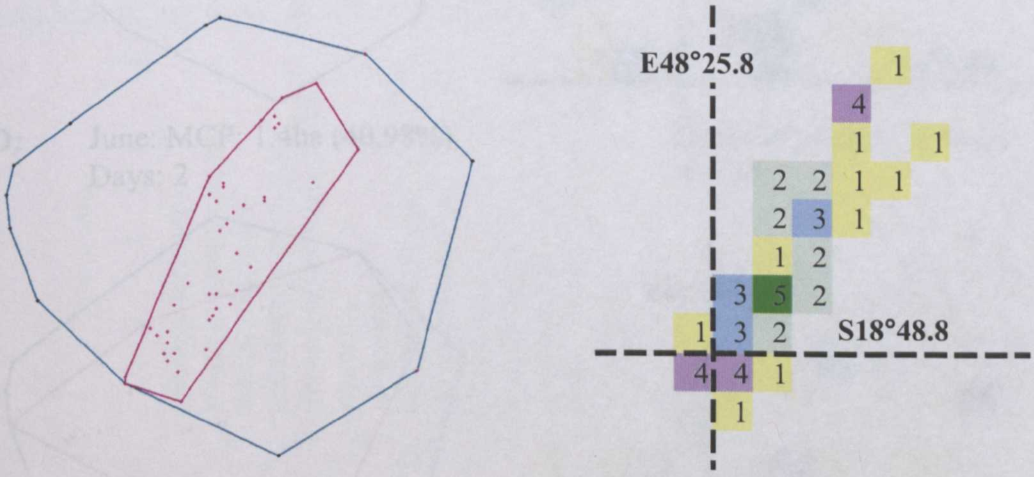
Table 7.7. Pearson correlation coefficients for number of observation days each month with home range derived from minimum-convex polygon (MCP) method and grid-cell method for *H. g. griseus* Group Two.

	MCP	Grid-Cell
r	0.068	0.664
p	0.914	0.221
N	5	5



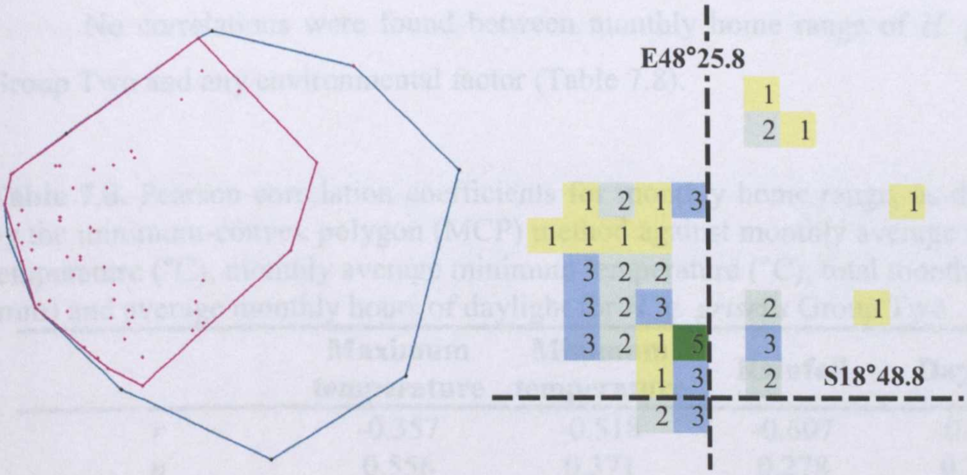
A: February: MCP: 1.5ha (42.87%) Days: 3

Grid-cell: 1.1ha (37.21%) *N* = 87.

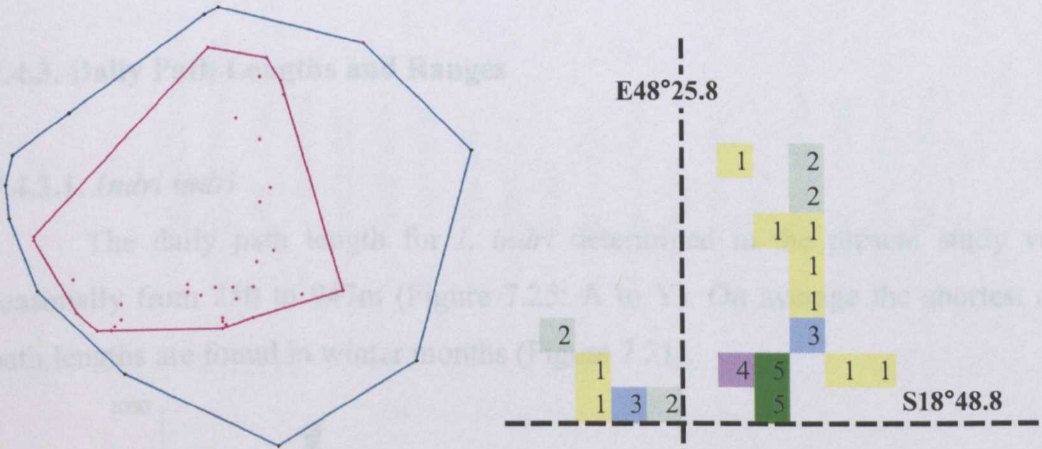


B: March: MCP: 0.8ha (21.43%) Days: 2

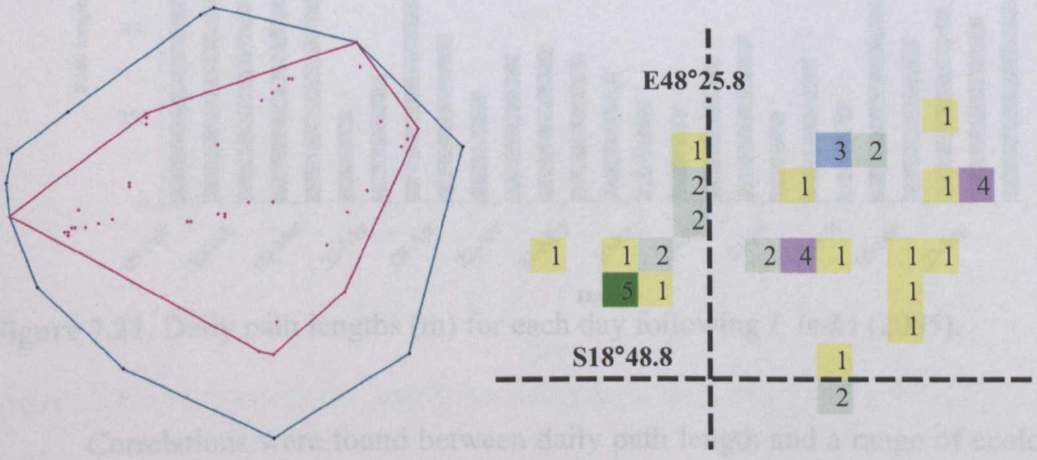
Grid-cell: 0.8ha (26.74%) *N* = 49.



C: April: MCP: 1.7ha (49.04%) Grid-cell: 1.0ha (34.88%)
Days: 2 *N* = 59.



D: June: MCP: 1.4ha (40.98%) Grid-cell: 0.6ha (20.93%)
Days: 2 *N* = 37.



E: September: MCP: 1.8ha (52.67%) Grid-cell: 0.8ha (26.74%)
Days: 2 *N* = 41.

Figure 7.20. Monthly home ranges (——) using the minimum-convex-polygon (MCP) method for *H. g. griseus* Group Two plotted on the total home range (——), for months when there is more than one day of observation. Percentages are of total home range.

No correlations were found between monthly home range of *H. g. griseus* Group Two and any environmental factor (Table 7.8).

Table 7.8. Pearson correlation coefficients for monthly home range, as determined by the minimum-convex polygon (MCP) method against monthly average maximum temperature (°C), monthly average minimum temperature (°C), total monthly rainfall (mm) and average monthly hours of daylight for *H. g. griseus* Group Two.

	Maximum temperature	**Minimum temperature**	**Rainfall**	**Daylight**
r	-0.357	-0.518	-0.607	-0.556
p	0.556	0.371	0.278	0.331
N	5	5	5	5

7.4.3. Daily Path Lengths and Ranges

7.4.3.1. *Indri indri*

The daily path length for *I. indri* determined in the present study varies seasonally from 250 to 947m (Figure 7.25: A to Y). On average the shortest daily path lengths are found in winter months (Figure 7.21).

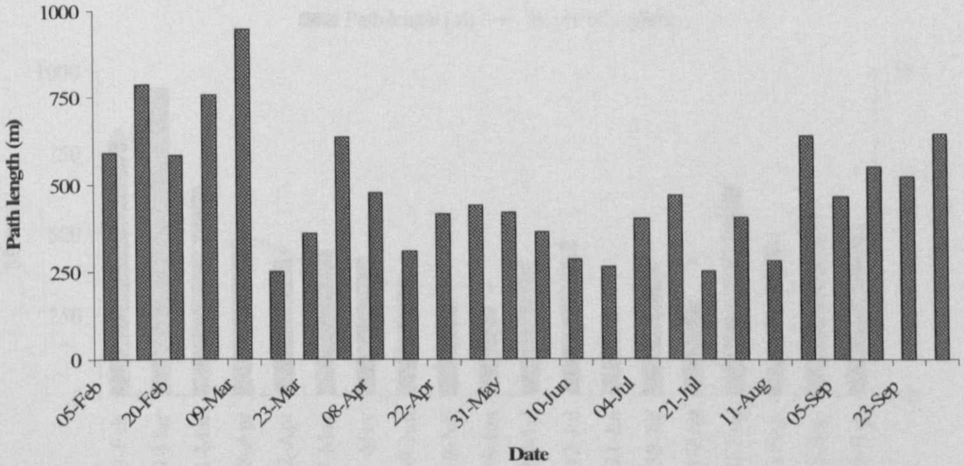


Figure 7.21. Daily path lengths (m) for each day following *I. indri* (2005).

Correlations were found between daily path length and a range of ecological and behavioural factors (Table 7.9). Path length is positively correlated at the 0.01 level with the period of daily activity (Figure 7.22), hours of daylight (Figure 7.23) and maximum temperature (Figure 7.24); increasing activity, daylight and maximum temperature lead to longer path lengths. There is a positive correlation at the 0.05 level between path length, and both daily minimum temperature and rainfall: an increase in rainfall and minimum temperature are associated with an increase in path length.

Table 7.9. Pearson correlation coefficients of daily path length for *I. indri*.

	Activity period	Hours of daylight	Maximum temperature	Minimum temperature	Rainfall
r	0.772**	0.829**	0.640**	0.485*	0.468*
p	0.000	0.000	0.003	0.035	0.043
N	19	19	19	19	19

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

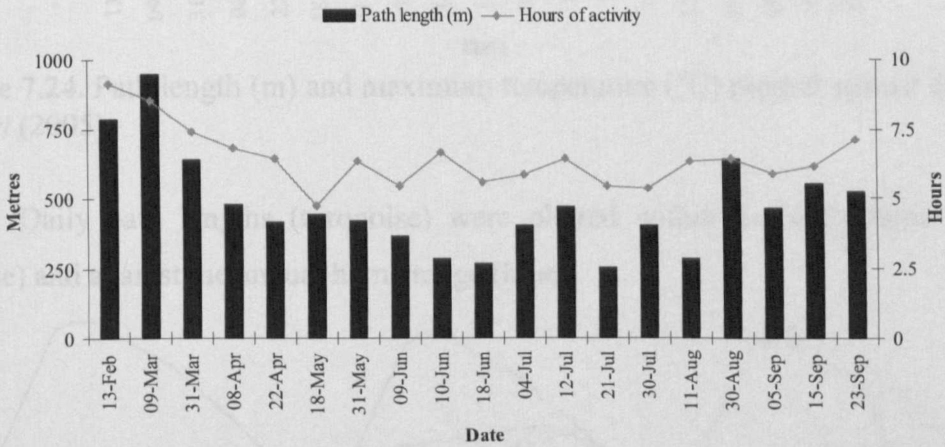


Figure 7.22. Path length (m) and hours of activity with date for *I. indri* (2005).

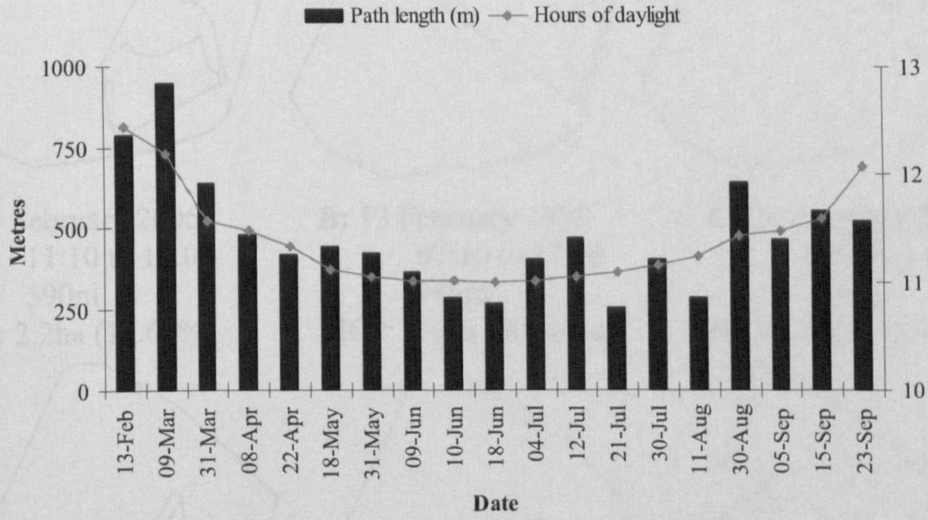


Figure 7.23. Path length (m) and hours of daylight with date for *I. indri* (2005).

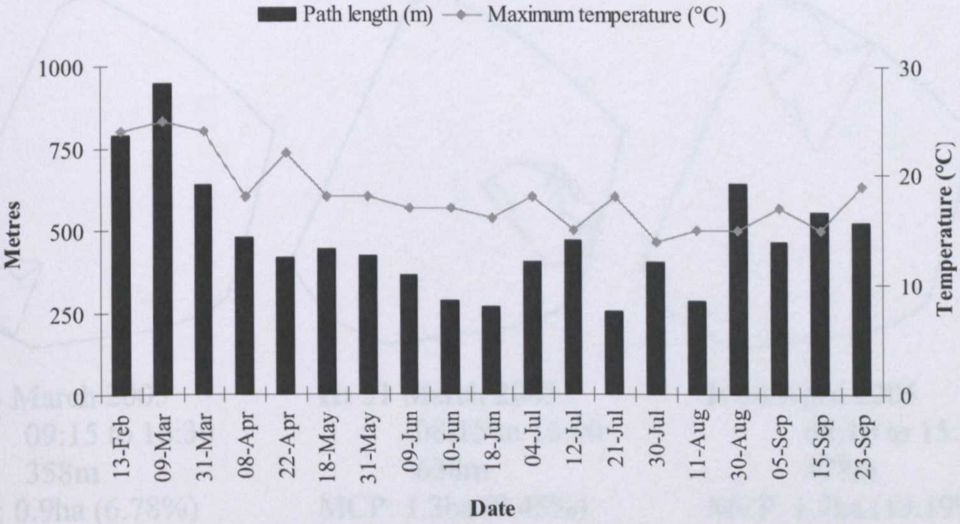
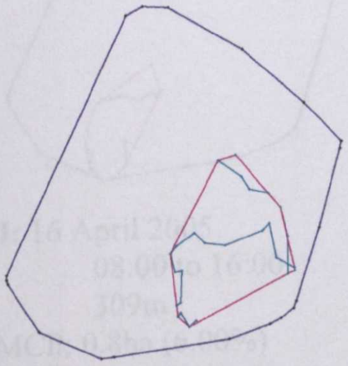
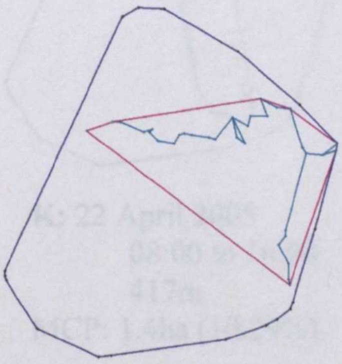


Figure 7.24. Path length (m) and maximum temperature (°C) plotted against date for *I. indri* (2005).

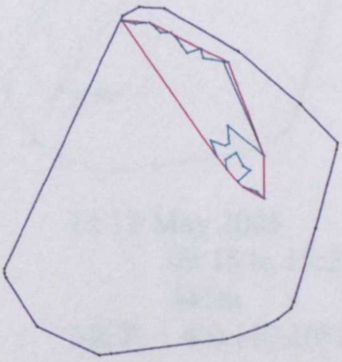
Daily path lengths (turquoise) were plotted within the daily home range (purple) and against the annual home range (blue).



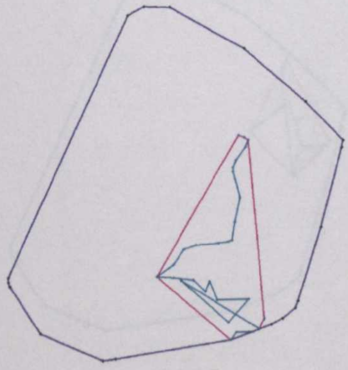
A: 05 February 2005
11:10 to 17:00
590m
MCP: 2.2ha (16.64%)



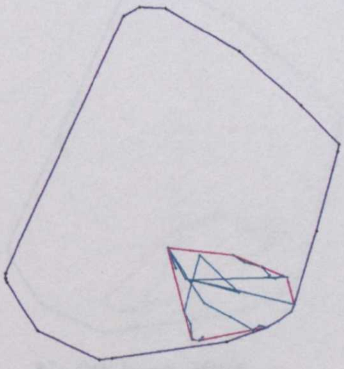
B: 13 February 2005
07:10 to 17:00
786m
MCP: 4.0ha (30.50%)



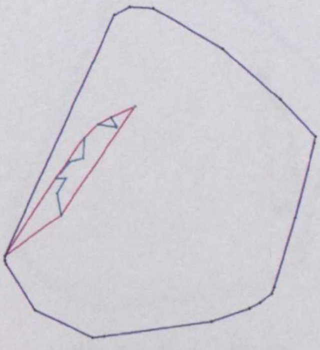
C: 20 February 2005
09:30 to 17:00
584m
MCP:1.6ha (11.77%)



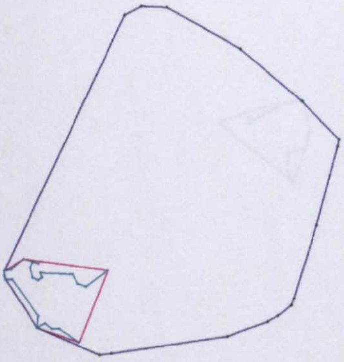
D: 02 March 2005
08:05 to 16:45
757m
MCP: 2.0ha (15.26%)



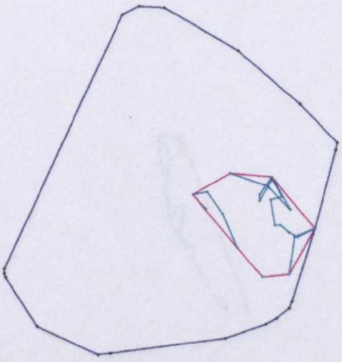
E: 09 March 2005
07:45 to 16:45
947m
MCP: 1.3ha (10.19%)



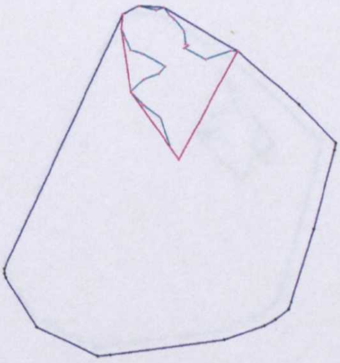
F: 22 March 2005
07:30 to 14:00
250m
MCP: 0.7ha (5.08%)



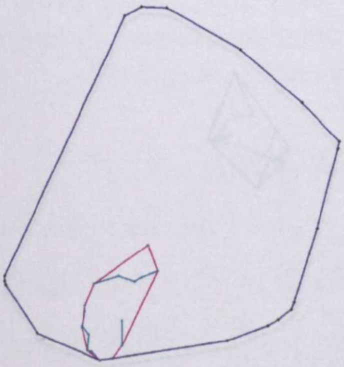
G: 23 March 2005
09:15 to 16:30
358m
MCP: 0.9ha (6.78%)



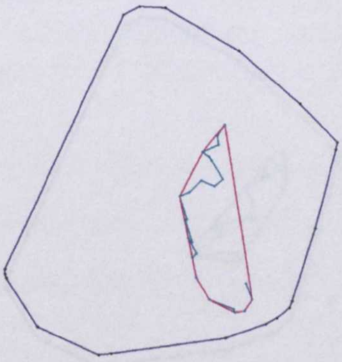
H: 31 March 2005
08:15 to 16:00
638m
MCP: 1.3ha (9.45%)



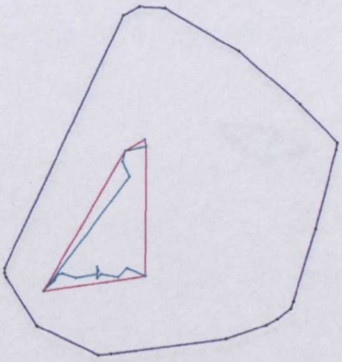
I: 08 April 2005
08:10 to 15:50
478m
MCP: 1.7ha (13.19%)



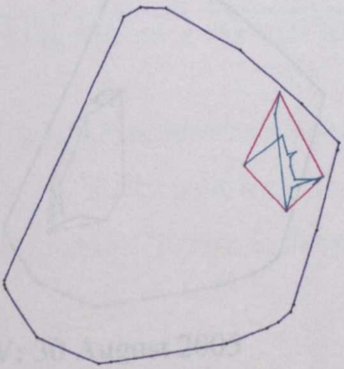
J: 16 April 2005
08:00 to 16:00
309m
MCP: 0.8ha (6.00%)



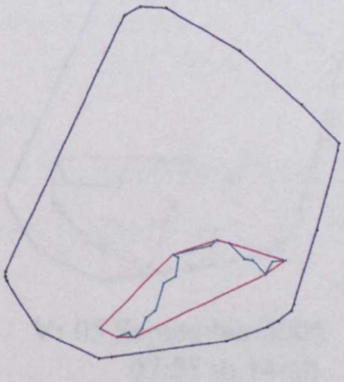
K: 22 April 2005
08:00 to 16:00
417m
MCP: 1.4ha (10.29%)



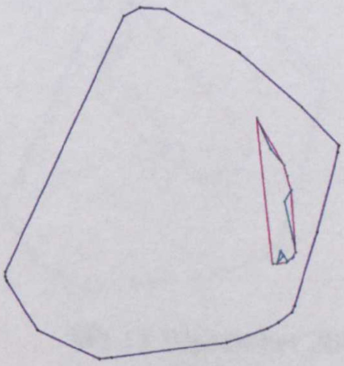
L: 18 May 2005
09:15 to 15:20
441m
MCP: 1.4ha (10.20%)



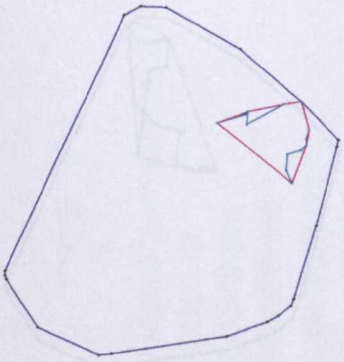
M: 31 May 2005
07:25 to 15:00
421m
MCP: 0.8ha (5.89%)



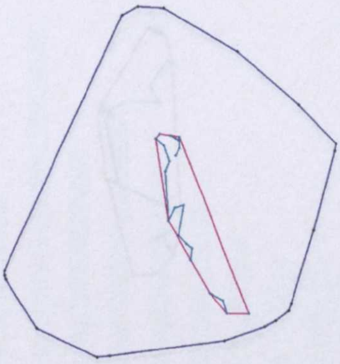
N: 09 June 2005
08:50 to 15:00
362m
MCP: 1.3ha (9.77%)



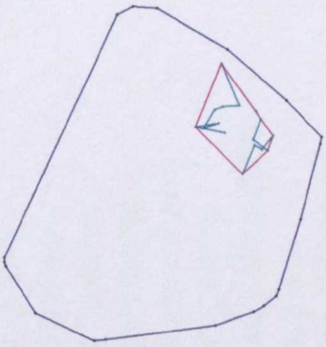
O: 10 June 2005
08:05 to 15:00
285m
MCP: 0.5ha (3.66%)



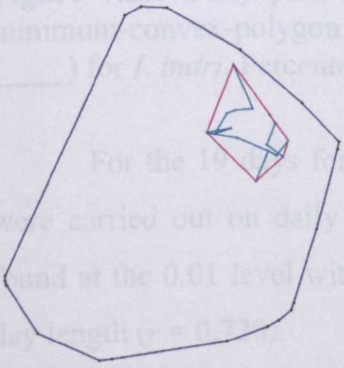
P: 17 June 2005
08:15 to 15:05
264m
MCP: 0.7ha (5.17%)



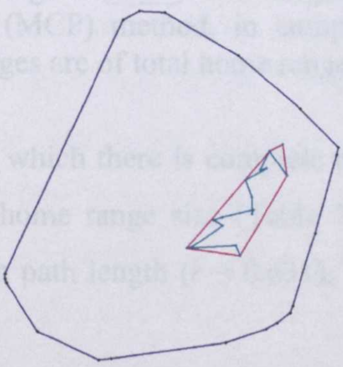
Q: 04 July 2005
07:50 to 14:35
401m
MCP: 1ha (7.82%)



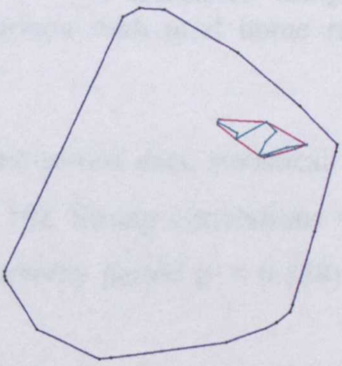
R: 12 July 2005
08:00 to 15:35
471m
MCP: 0.8ha (6.12%)



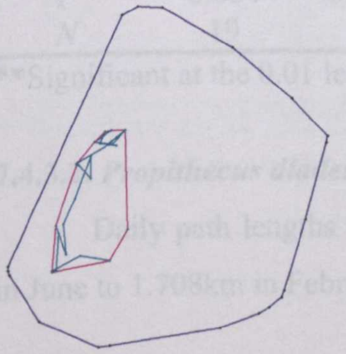
S: 21 July 2005
08:15 to 14:55
251m
MCP: 0.4ha (2.65%)



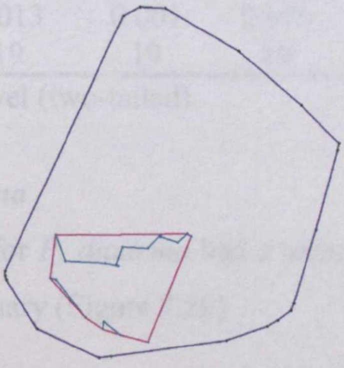
T: 30 July 2005
08:20 to 15:20
404m
MCP: 0.7ha (5.63%)



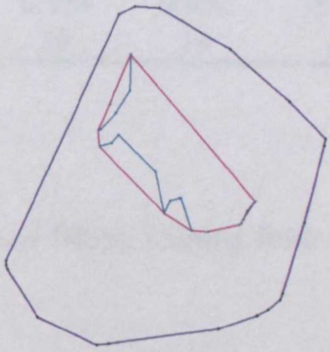
U: 11 August 2005
08:10 to 15:20
466m
MCP: 0.3ha (2.33%)



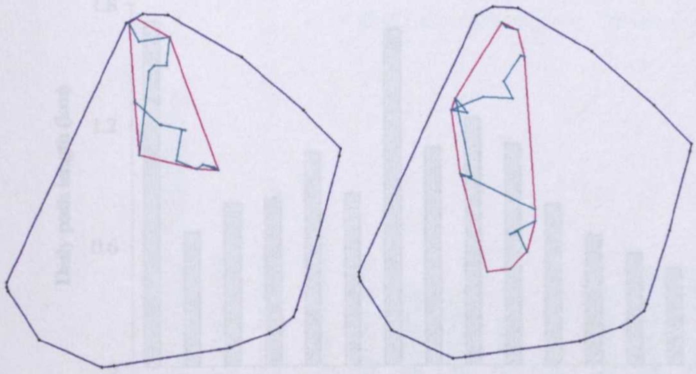
V: 30 August 2005
08:20 to 16:10
641m
MCP: 1.4ha (10.26%)



V: 05 September 2005
07:55 to 14:40
282m
MCP: 1.8ha (13.47%)



W: 15 September 2005
07:30 to 14:45
553m
MCP: 2.4ha (18.28%)



X: 23 September 2005
07:40 to 15:20
523m
MCP: 1.3ha (9.89%)

Y: 03 October 2005
08:15 to 16:20
644m
MCP: 2.4ha (18.37%)

Figure 7.25. Daily path lengths (____) and ranges (____), calculated using the minimum-convex-polygon (MCP) method, in comparison with total home range (____) for *I. indri*. Percentages are of total home range.

For the 19 days for which there is complete rest-to-rest data, statistical tests were carried out on daily home range size (Table 7.10). Strong correlations were found at the 0.01 level with path length ($r = 0.631$), activity period ($r = 0.558$) and day length ($r = 0.720$).

Table 7.10. Pearson correlation coefficient for daily ranges, determined by the minimum-convex polygon method, with ecological and behavioural parameters.

	Path length	**Activity period**	**Day length**	**Max temp**	**Min temp**	**Rainfall**	**Monthly range**
R	0.631**	0.558*	0.720**	0.425	0.273	-0.009	0.016
P	0.004	0.013	0.001	0.070	0.258	0.970	0.950
N	19	19	19	19	19	19	19

**Significant at the 0.01 level (two-tailed).

7.4.3.2. *Propithecus diadema*

Daily path lengths for *P. diadema* had a mean of 902m, ranging from 489m in June to 1.708km in February (Figure 7.26).

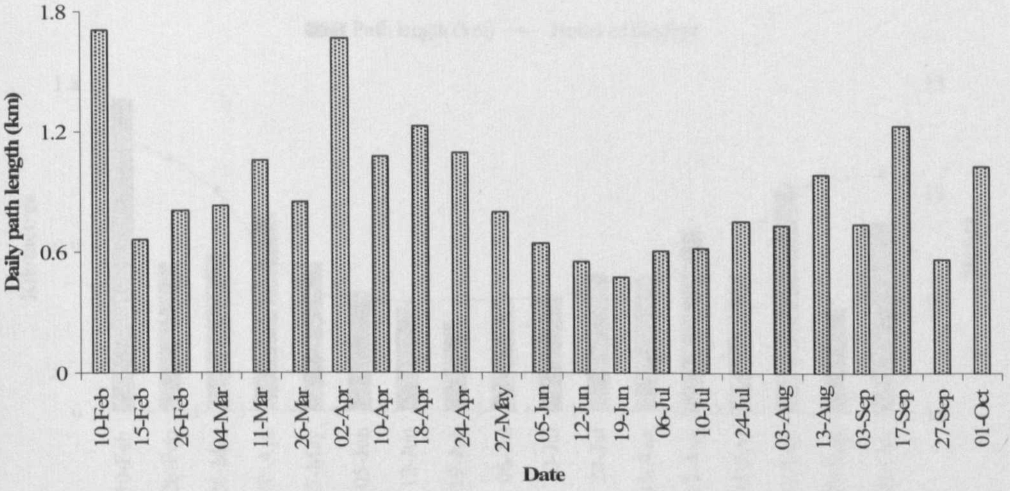


Figure 7.26. Daily path length (km) for each day following *P. diadema* (2005).

Correlations were observed between daily path length and various environmental and behavioural factors (Table 7.11). A positive correlation at the 0.05 level was fund between path length, period of daily activity (Figure 7.27) and maximum temperature: path lengths increased with increasing periods of activity and increasing daily maximum temperature. There is a positive correlation at the 0.01 level with the hours of daylight: path lengths increasing with increasing hours of daylight. There is a negative correlation at the 0.01 level between rainfall and path length (Figure 7.28): path length decreases with increasing rainfall.

Table 7.11. Pearson correlation coefficient for daily path length for *P. diadema*.

	Activity period	**Hours of daylight**	**Maximum temperature**	**Minimum temperature**	**Rainfall**
r	0.518*	0.635**	0.602*	0.314	-0.609**
p	0.033	0.006	0.011	0.219	0.010
N	17	17	17	17	17

**Significant at the 0.01 level (two-tailed). *Significant at the 0.05 level (two-tailed).

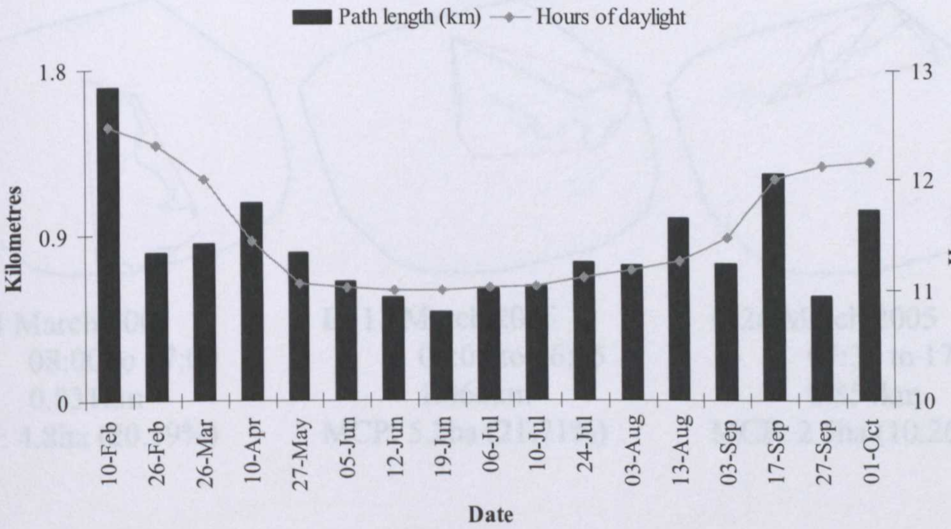


Figure 7.27. Path length (km) and hours of daylight plotted against date for *P. diadema* (2005).

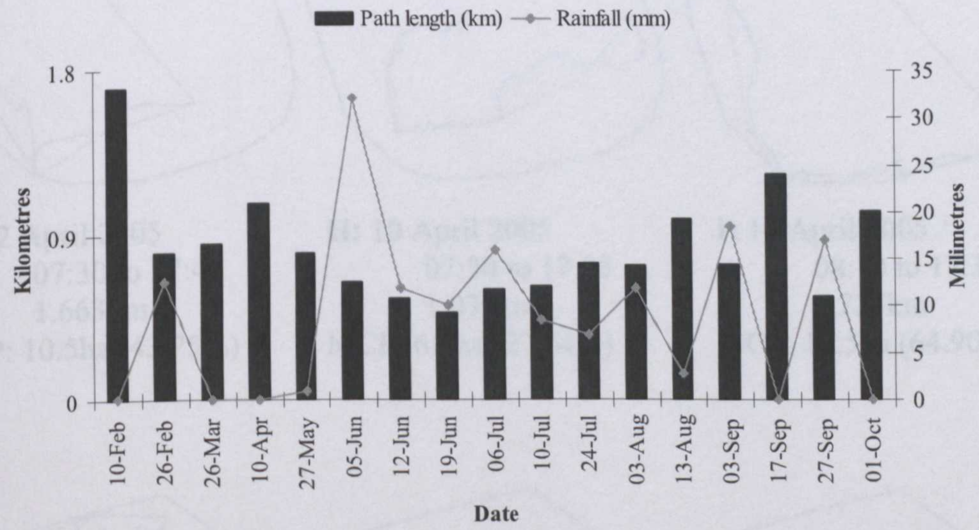
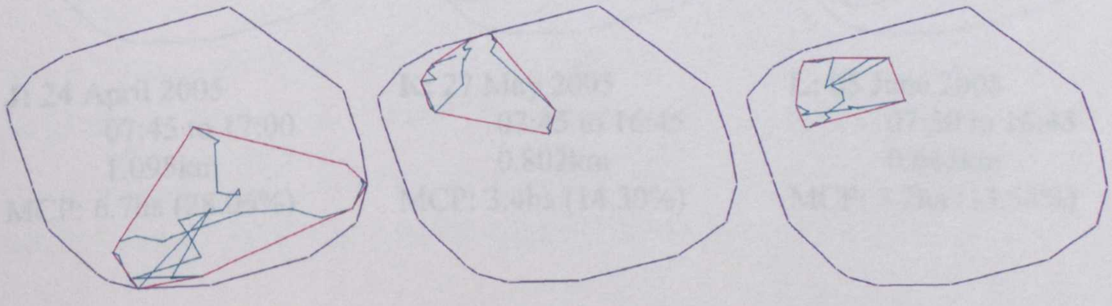


Figure 7.28. Path length (km) and rainfall (mm) plotted against date for *P. diadema* (2005).

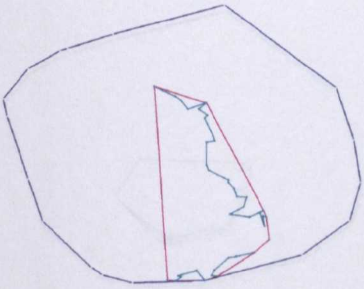
Daily path lengths and ranges were plotted on the total home range (Figure 7.29). Daily paths and ranges are smaller in the austral winter months.



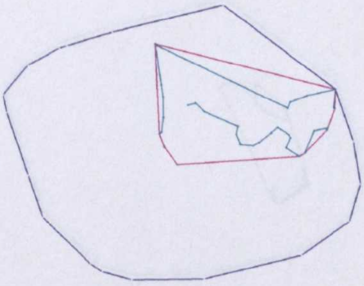
A: 10 February 2005
08:10 to 16:45
1.708km
MCP: 7.4ha (31.09%

B: 15 February 2005
07:15 to 14:10
0.664km
MCP: 2.6ha (11.04%)

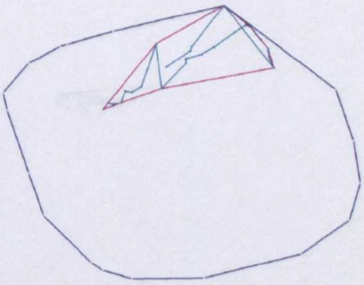
C: 26 February 2005
07:05 to 17:07
0.808km
MCP: 1.8ha (7.60%)



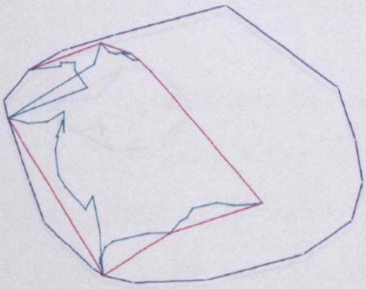
D: 04 March 2005
08:00 to 17:00
0.831km
MCP: 4.8ha (20.19%)



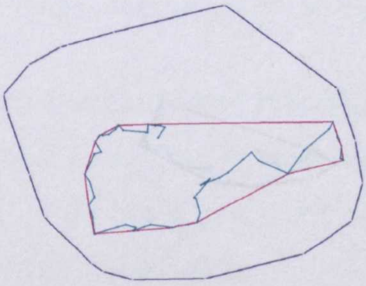
E: 11 March 2005
08:05 to 16:35
1.060km
MCP: 5.2ha (21.71%)



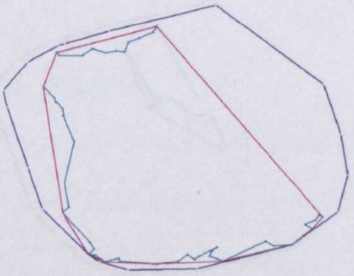
F:26 March 2005
07:35 to 17:00
0.854km
MCP: 2.5ha (10.26%)



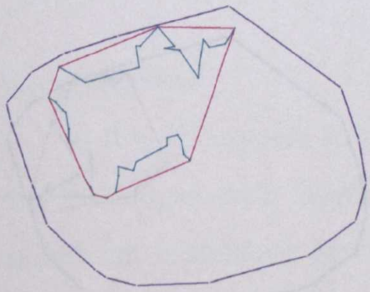
G: 02 April 2005
07:30 to 17:45
1.663km
MCP: 10.5ha (43.75%)



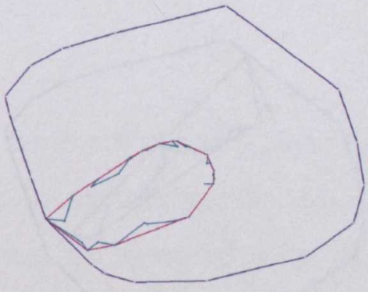
H: 10 April 2005
07:20 to 17:25
1.079km
MCP: 6.6ha (27.64%)



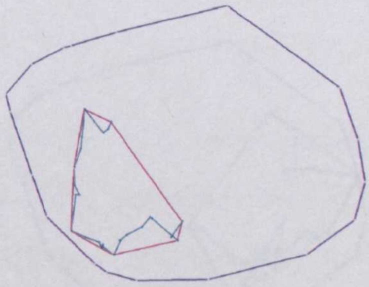
I: 17 April 2005
08:10 to 17:35
1.227km
MCP: 15.5ha (64.90%)



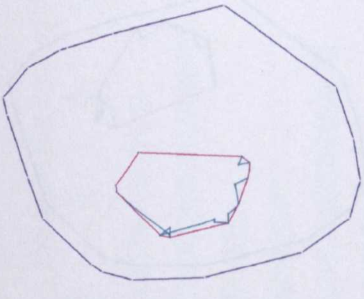
J: 24 April 2005
07:45 to 17:00
1.095km
MCP: 6.7ha (28.06%)



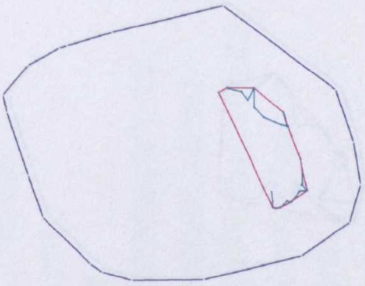
K: 27 May 2005
07:45 to 16:45
0.802km
MCP: 3.4ha (14.30%)



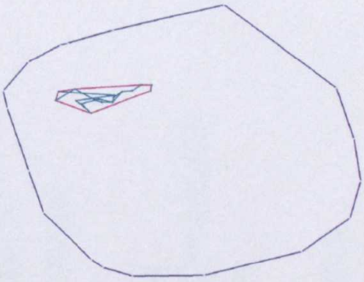
L: 05 June 2005
07:30 to 16:45
0.645km
MCP: 3.2ha (13.54%)



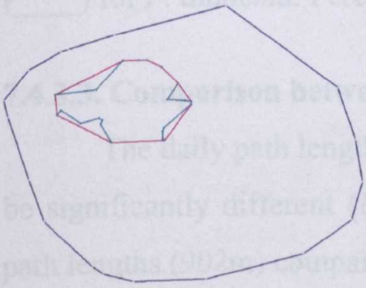
M: 12 June 2005
08:55 to 16:05
0.554km
MCP: 2.8ha (11.61%)



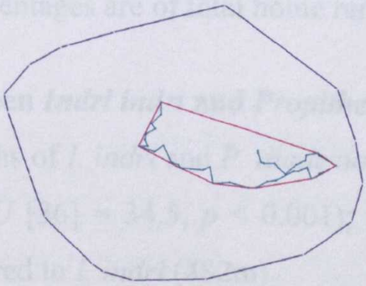
N: 19 June 2005
07:55 to 15:55
0.478km
MCP: 1.8ha (7.52%)



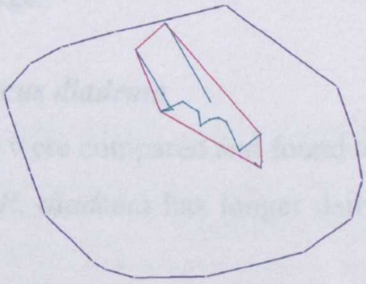
O: 06 July 2005
07:55 to 15:55
0.607km
MCP: 0.5ha (2.20%)



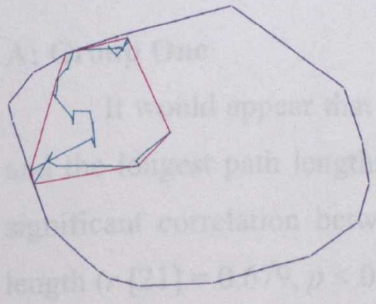
P: 10 July 2005
09:50 to 16:00
0.618km
MCP: 2.6ha (10.87%)



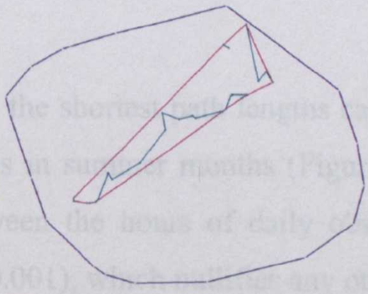
Q: 24 July 2005
08:25 to 16:50
0.752km
MCP: 3ha (12.36%)



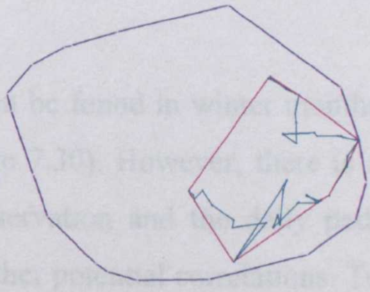
R: 03 August 2005
08:15 to 16:35
0.736km
MCP: 2.5ha (10.31%)



S: 13 August 2005
07:30 to 16:55
0.988km
MCP: 4.2ha (17.74%)



T: 03 September 2005
08:35 to 16:10
0.743km
MCP: 2.8ha (11.88%)



U: 17 September 2005
08:15 to 17:20
1.234km
MCP: 5.5ha (22.89%)

V: 27 September 2005
07:45 to 16:20
0.567km
MCP: 2.7ha (11.15%)

W: 01 October 2005
07:30 to 17:25
0.923km
MCP: 4.6ha (19.32%)

Figure 7.29. Daily path lengths (____) and ranges (____), calculated using the minimum-convex-polygon (MCP) method, in comparison with total home range (____) for *P. diadema*. Percentages are of total home range.

7.4.3.3. Comparison between *Indri indri* and *Propithecus diadema*

The daily path lengths of *I. indri* and *P. diadema* were compared and found to be significantly different (U [36] = 34.5, $p < 0.001$); *P. diadema* has longer daily path lengths (902m) compared to *I. indri* (482m).

7.4.3.4. *Hapalemur griseus griseus*

The daily path lengths of Group One (451m) and Two (433m) were compared and found not to be significantly different from each other (U [32] = 116.0, $p > -0.05$).

A: Group One

It would appear that the shortest path lengths can be found in winter months and the longest path lengths in summer months (Figure 7.30). However, there is a significant correlation between the hours of daily observation and the daily path length (r [21] = 0.679, $p < 0.001$), which nullifies any other potential correlations. To remove the factor of observation period days were selected when observations were from 08:00 to 16:00, and only the period between these two times was used to calculate path lengths. This produced no significant correlation (Table 7.12).

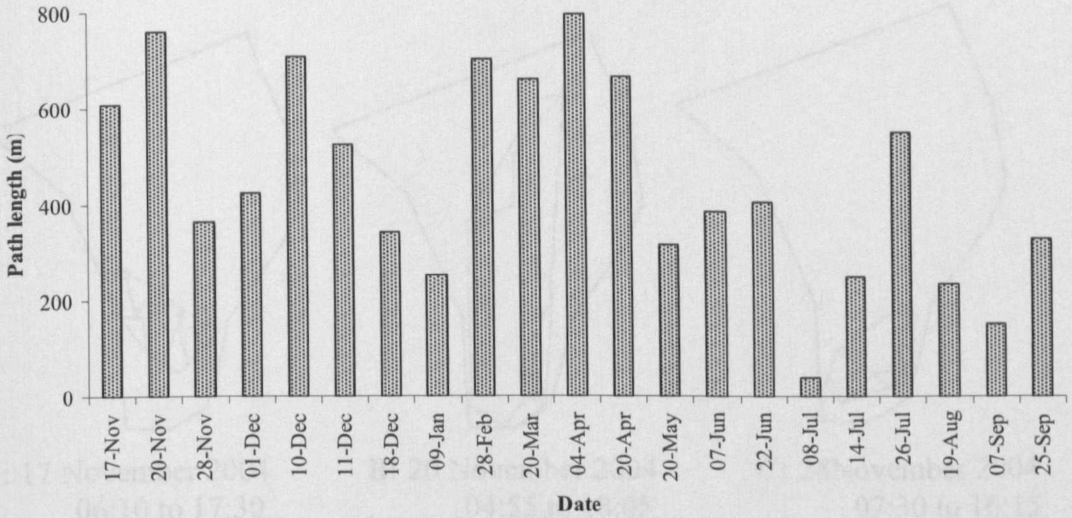
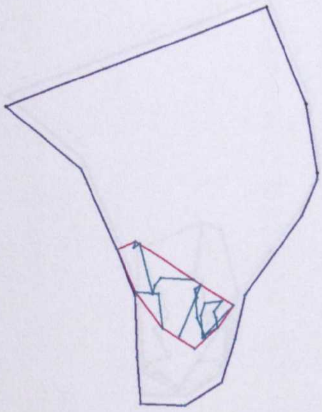


Figure 7.30. Daily path length (m) for each day following *H. g. griseus* Group One (2005).

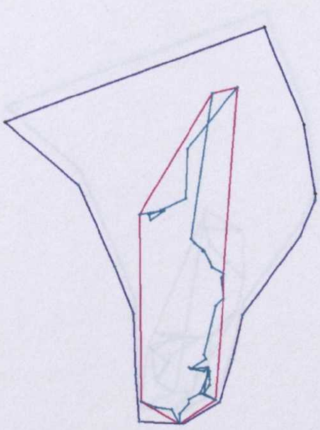
Table 7.12. Pearson correlation coefficient between path length and ecological factors for *H. g. griseus* Group One.

	Day length	Maximum temperature (°C)	Minimum temperature (°C)	Rainfall (mm)
r	-0.108	-0.099	0.306	0.249
p	0.767	0.785	0.390	0.488
N	10	10	10	10

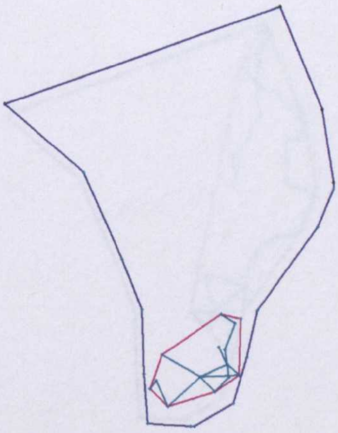
Daily path lengths and ranges of Group One *H. g. griseus* were plotted against the total home range (Figure 7.31). Between 0.98% (September) and 35.78% of their total home range was utilised daily.



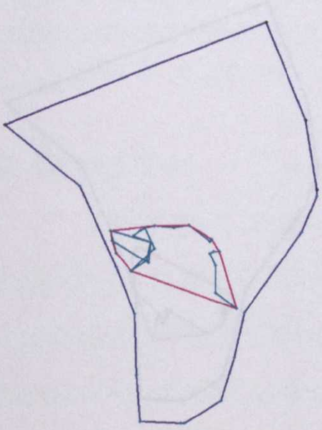
A: 17 November 2004
06:10 to 17:30
608m
MCP: 0.5ha (8.86%)



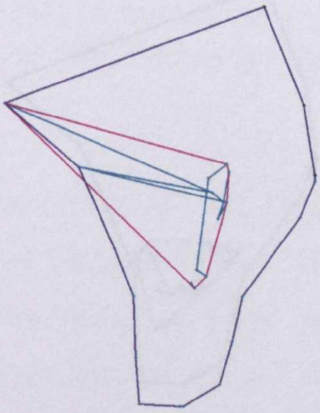
B: 20 November 2004
04:55 to 18:05
761m
MCP: 1.9ha (35.78%)



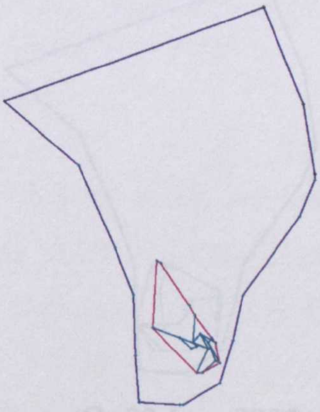
C: 28November 2004
07:30 to 16:15
363m
MCP: 0.4ha (7.32%)



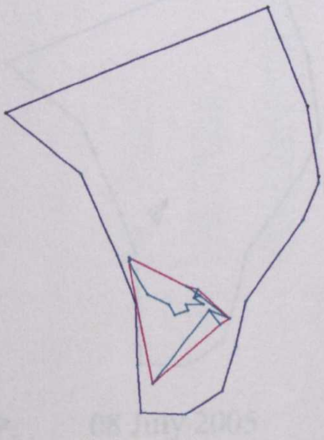
D: 01 December 2004
06:25 to 13:20
424m
MCP: 0.5ha (9.36%)



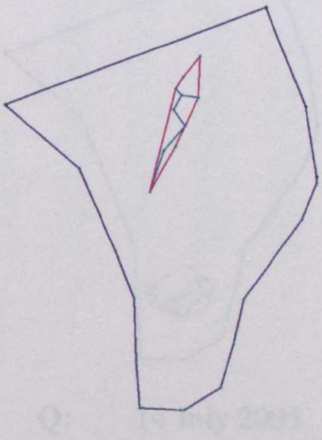
E: 10 December 2004
06:30 to 17:20
707m
MCP: 1.3ha (24.52 ha)



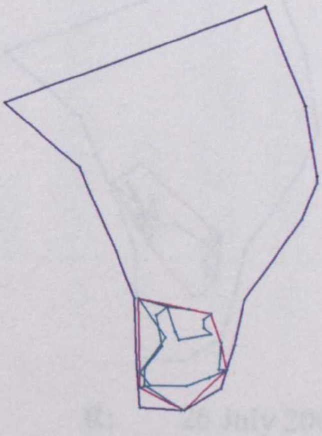
F: 11 December 2004
08:35 to 17:30
526m
MCP: 0.3ha (5.50%)



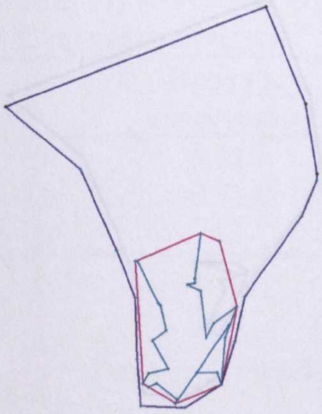
G: 18 December 2004
06:10 to 16:40
340m
MCP: 0.5ha (9.18%)



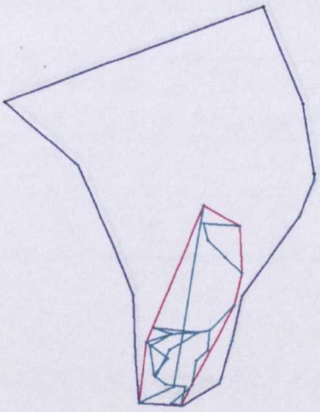
H: 09 January 2005
05:00 to 10:35
251m
MCP: 0.2ha (2.90%)



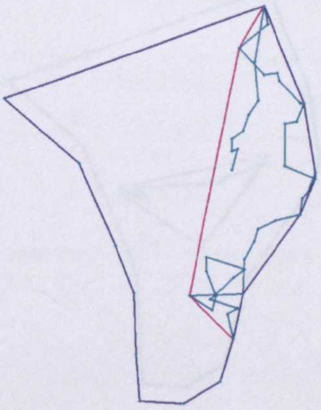
I: 28 February 2005
05:00 to 16:50
703m
MCP: 0.6ha (10.96%)



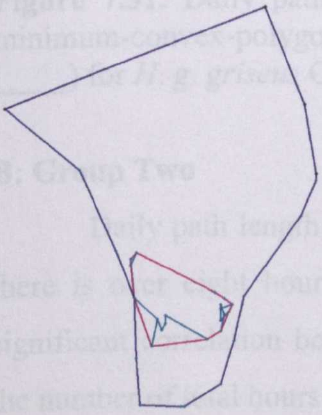
J: 20 March 2005
08:10 to 17:10
660m
MCP: 1.1ha (20.55%)



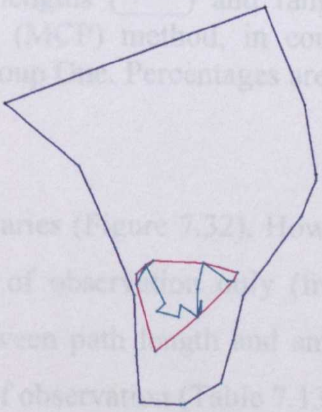
K: 04 April 2005
07:55 to 17:00
797m
MCP: 0.9ha (17.61%)



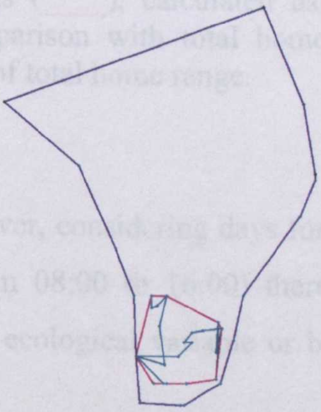
L: 20 April 2005
07:15 to 17:20
236m
MCP: 1.8ha (33.59%)



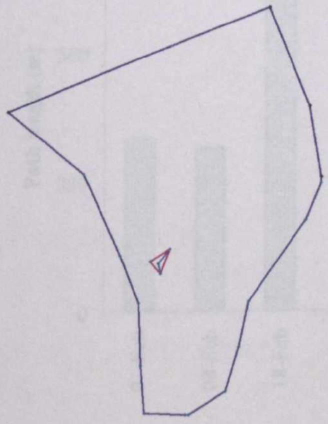
M: 20 May 2005
07:30 to 15:45
315m
MCP: 0.5ha (8.97%)



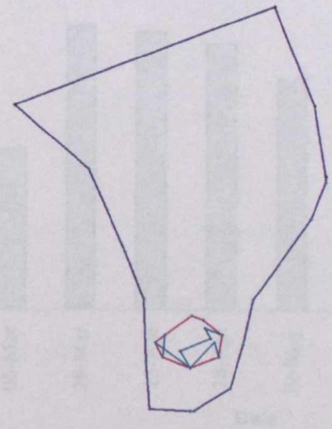
N: 07 June 2005
07:30 to 16:45
384m
MCP: 0.4ha (8.04%)



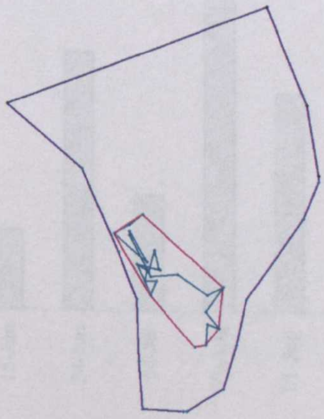
O: 22 June 2005
07:30 to 16:00
440m
MCP: 0.5ha (9.01%)



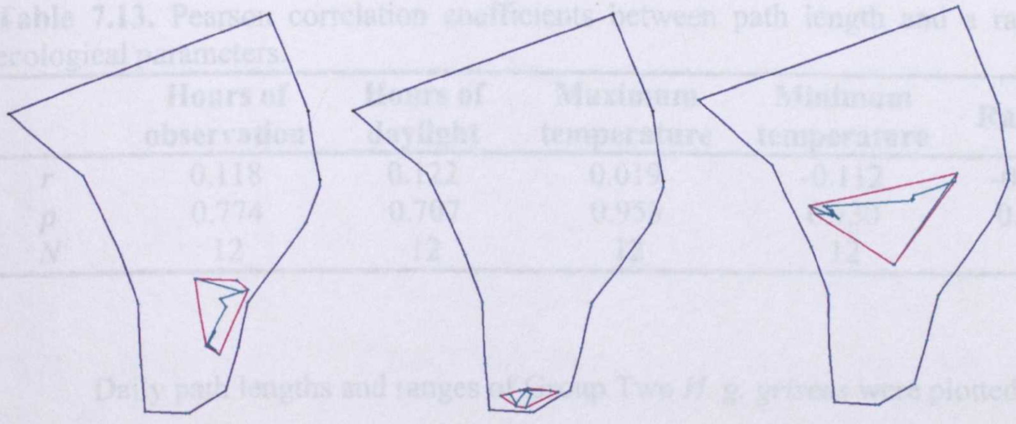
P: 08 July 2005
07:30 to 08:40
40m
MCP: 0.01ha (0.28%)



Q: 14 July 2005
07:35 to 16:00
250m
MCP: 0.2ha (3.44%)



R: 26 July 2005
08:25 to 17:05
550m
MCP: 0.6ha (10.40%)



S: 19 August 2005
08:10 to 17:15
236m
MCP: 0.2ha (3.83%)

T: 07 September 2005
08:40 to 16:00
153m
MCP: 0.05ha (0.98%)

U: 25 September 2005
07:20 to 16:00
331m
MCP: 0.5ha (9.47%)

Figure 7.31. Daily path lengths (——) and ranges (——), calculated using the minimum-convex-polygon (MCP) method, in comparison with total home range (——) for *H. g. griseus* Group One. Percentages are of total home range.

B: Group Two

Daily path length varies (Figure 7.32). However, considering days for which there is over eight hours of observation only (from 08:00 to 16:00) there is no significant correlation between path length and any ecological variable or between the number of total hours of observation (Table 7.13).

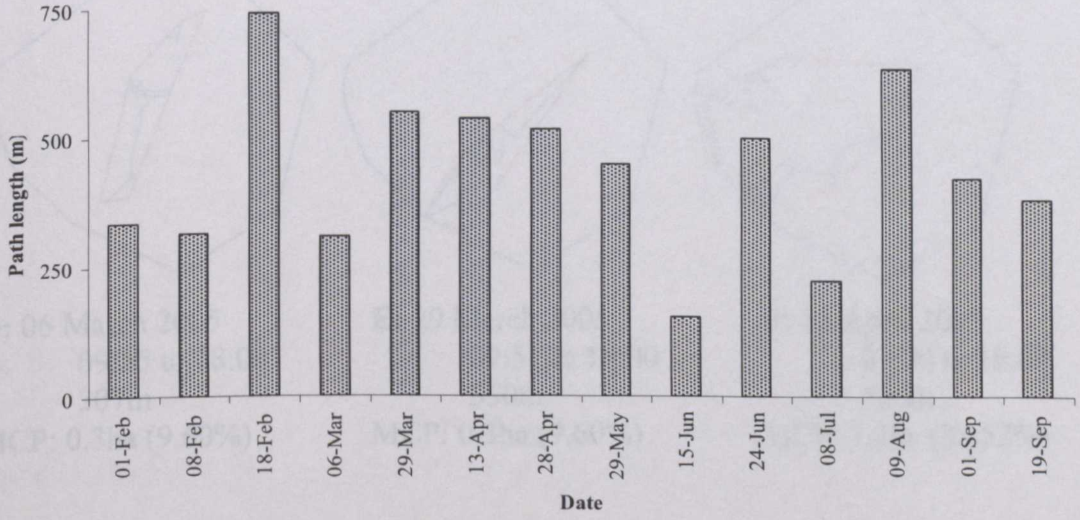
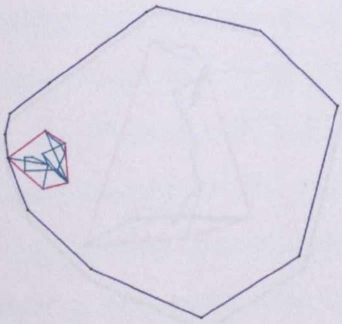


Figure 7.32. Daily path lengths (m) for each day following *H. g. griseus* Group Two.

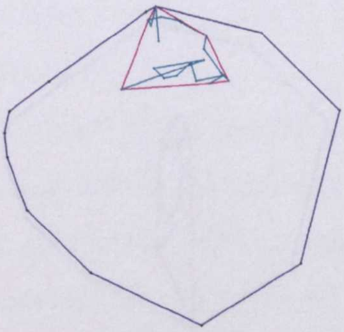
Table 7.13. Pearson correlation coefficients between path length and a range of ecological parameters.

	Hours of observation	**Hours of daylight**	**Maximum temperature**	**Minimum temperature**	**Rainfall**
r	0.118	0.122	0.019	-0.112	-0.215
p	0.774	0.707	0.953	0.730	0.503
N	12	12	12	12	12

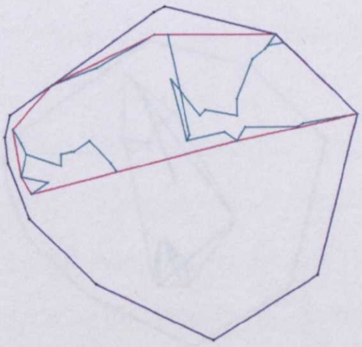
Daily path lengths and ranges of Group Two *H. g. griseus* were plotted on the total home range (Figure 7.33). Daily usage ranged from 3.03% to 40.84%, both in February.



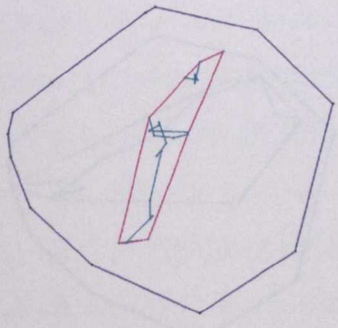
A: 01 February 2005
07:00 to 16:55
335m
MCP: 0.1ha (3.03%)



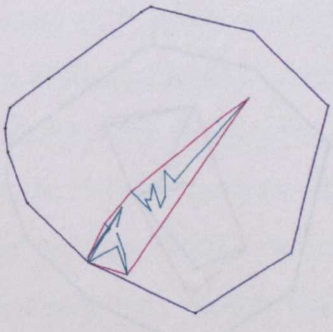
B: 08 February 2005
10:20 to 18:00
312m
MCP: 0.3ha (7.32%)



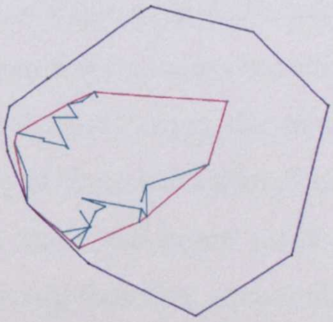
C: 18 February 2005
07:15 to 17:45
743m
MCP: 1.4ha (40.84%)



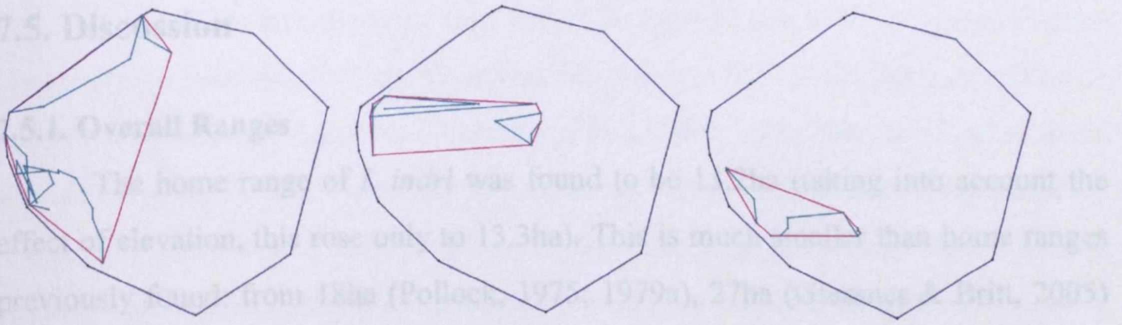
D: 06 March 2005
09:55 to 18:00
307m
MCP: 0.3ha (9.60%)



E: 29 March 2005
09:55 to 18:00
550m
MCP: 0.3ha (9.60%)



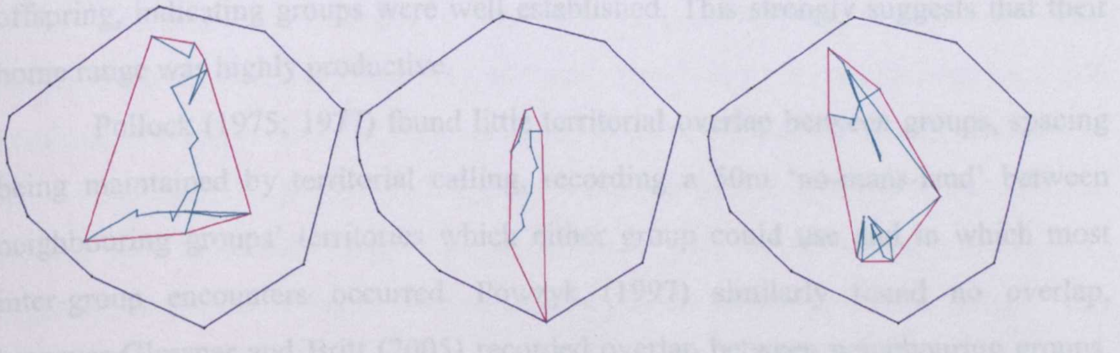
F: 13 April 2005
07:00 to 18:00
538m
MCP: 1.3ha (32.52%)



G: 28 April 2005
07:00 to 17:00
517m
MCP: 1.2ha (33.04%)

H: 29 May 2005
07:00 to 15:20
447m
MCP: 0.4ha (12.49%)

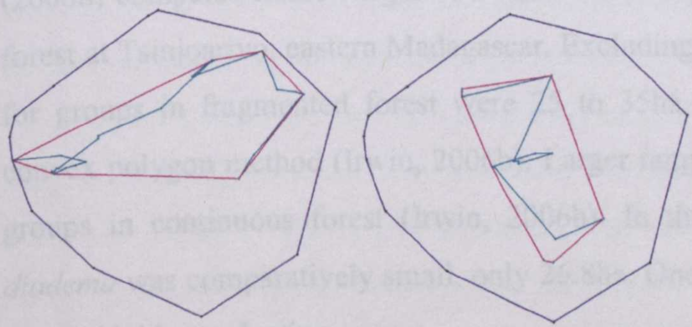
I: 15 June 2005
08:00 to 16:00
153m
MCP: 0.2ha (6.34%)



J: 24 June 2005
07:30 to 16:00
500m
MCP: 1.0ha (28.15%)

K: 08 July 2005
08:50 to 16:00
224m
MCP: 0.3ha (7.97%)

L: 09 August 2005
06:15 to 16:30
634m
MCP: 0.7ha (19.95%)



M: 01 September 2005
07:45 to 17:00
422m
MCP: 1.1ha (30.47%)

N: 19 September 2005
07:50 to 16:50
378m
MCP: 0.8ha (21.55%)

Figure 7.33. Daily path lengths (—) and ranges (—), calculated using the minimum-convex-polygon (MCP) method, in comparison with total home range (—) for *H. g. griseus* Group Two. Percentages are of total home range.

7.5. Discussion

7.5.1. Overall Ranges

The home range of *I. indri* was found to be 13.2ha (taking into account the effect of elevation, this rose only to 13.3ha). This is much smaller than home ranges previously found: from 18ha (Pollock, 1975; 1979a), 27ha (Glessner & Britt, 2005) to 40ha (Powzyk, 1997). Powzyk's home range result was of course from *I. indri* in the same reserve. The high density of *I. indri* (10adults/km^2) in the vicinity of the study group, also suggests that neighbouring groups have similarly small home ranges. The study group, as well as many neighbouring groups, had two dependent offspring, indicating groups were well established. This strongly suggests that their home range was highly productive.

Pollock (1975; 1977) found little territorial overlap between groups, spacing being maintained by territorial calling, recording a 50m 'no-mans-land' between neighbouring groups' territories which either group could use and in which most inter-group encounters occurred. Powzyk (1997) similarly found no overlap, however Glessner and Britt (2005) recorded overlap between neighbouring groups. In this study overlap between neighbouring groups is likely but cannot be proved.

Pollock (1979a) estimated home ranges of *P. diadema* were 20ha or more and Powzyk (1997) calculated ranges of 33 and 42ha in Mantadia National Park. Irwin (2006b) compared home ranges of *P. diadema* living in fragmented and continuous forest at Tsinjoarivo, eastern Madagascar. Excluding non-forested areas home ranges for groups in fragmented forest were 25 to 35ha, calculated using the minimum convex polygon method (Irwin, 2006b). Larger ranges of 50 to 60ha were found for groups in continuous forest (Irwin, 2006b). In this study the home range of *P. diadema* was comparatively small, only 26.8ha. One could therefore assume that the area is highly productive.

Both groups of *H. g. griseus* had similarly sized home ranges, of 5.4ha for Group One and 3.5ha for Group Two. These are relatively small, compared to 6 to 10ha at Analamazoatra (Wright 1986; Wright *et al.*, 1989) to 20ha (Overdorff *et al.*, 1997) recorded in the literature. The western extent of each groups' territory was, limited by the miners' road. Both groups were often found eating low growing *Clidemia hirta* (mazambody), a low growing herbaceous plant of which *H. g. griseus* ate the fruit, bordering the verges, but were never observed crossing the road.

Tan (1999) hypothesises that the difference between *H. g. griseus* home ranges at two locations in Ranomafana could be due to habitat disturbance and inter-specific competition; 15ha in Talatekely (Tan, 1999) and 20ha in Vatoharanana (Overdorff *et al.*, 1997). Talatekely has disturbed forest, with ample *Cathariostachys madagascariensis* (giant bamboo [Tan, 1999]). The presence of *Hapalemur aureus* (golden bamboo lemur) and *Prolemur simus* (greater bamboo lemur) could lead to increased competition, necessitating smaller home ranges. Vatoharanana is undisturbed, containing no *C. madagascariensis* and equally no *H. aureus* or *P. simus*. The importance of inter-specific competition may not be as high as the abundant availability of *C. madagascariensis*.

The small home ranges in this study suggest that the *H. g. griseus* home ranges are areas of high productivity, allowing groups to have small home ranges and resulting in a high density of *H. g. griseus*. This could be in due to the character of the forest in the *H. g. griseus* home ranges. Prior to the road, there was a small railway used to transport logged trees, running approximately adjacent to the road. Railway sleepers were found close to the road, in the territories of both groups. This selectively removed the larger trees, common in most other valleys. This has allowed secondary growth of *C. madagascariensis*, a main food of *H. g. griseus* in this study (Chapter 6). Both groups also relied heavily on the fruit of *C. hirta* found edging the road but rarely inside the forest. Potentially this high availability of food stuffs has allowed *H. g. griseus* to exist in smaller territories, indicating *H. g. griseus* are responding positively to the disturbed forest conditions.

Two groups studied by Tan (1999) at Ranomafana had overlapping home ranges. Similarly overlap was found in the present study. Maximum overlap corresponded to 27.5% of Group One's home range and 42.2% of Group Two's. Although inter-group conflict was observed, the two groups were most often found to tolerate close proximity of the other group. This again suggests that the forest is highly productive of the key dietary elements of *H. g. griseus*, *Cathariostachys madagascariensis*, and *C. hirta*, allowing the two groups to share almost half their home ranges with little conflict.

7.5.2. Daily Path Lengths and Ranges

Daily path lengths of *I. indri* ranged from 250 to 947m, comparable to daily path lengths found by Powzyk (1997 [330 to 1540m]) and Pollock (1975, 1979a [300 to 700m]). Thus although home ranges in the present study are much smaller than Powzyk's, *I. indri* travel a similar distance day to day. This suggests *I. indri* travel the minimum distance possible to obtain sufficient food, regardless of home range size.

Although Pollock (1977) thought daily ranges appeared dependent on food availability, no seasonality could be found in daily ranging behaviour. Seasonality was found in this study. The distance travelled daily is strongly positively correlated with hours of daylight, maximum temperature and period of daily activity, and to a lesser extent with minimum temperature and rainfall. Decreasing hours of daylight and activity, temperature and rainfall lead to decreased daily path lengths. *I. indri* travel further in the warmer, wetter austral summer and travel less in the colder austral winter. Activity period is correlated with hours of daylight and a clear connection can be seen between the activity period and onset of sunrise and sunset. If *I. indri* are less active during winter, they are likely to be travelling shorter distances. This would suggest that *I. indri* are conserving energy during the winter, when they need to maintain body temperature. This is consistent with a strategy of minimising energy expenditure in cold, low food availability, months as discussed in Chapter 5. Alternatively their food source might be more plentiful and sufficient available within smaller areas during winter: the data required to determine which of these hypotheses is correct remains to be gathered.

In contrast to the case in *I. indri,* daily path lengths in *P. diadema* (ranging from 478 to 1708m) are smaller than those in Powzyk (1997 [600 to 2575m]). However, in the present study *P. diadema* spent more of their time travelling (21%) than in Powzyk's (1997) study, where travel comprised only 6% of observations. The smaller daily distances could be explained in two dramatically contrasting ways. It is possible that the smaller home range in the present study results in a decreased availability of suitable food so that the diet of the *P. diadema* is lower in quality, and they have less energy for travel. Alternatively the home range could be highly productive of their favoured foods so that they have to travel less to obtain the same nutritional requirements. *P. diadema* in this study fed more (52%) compared to in Powzyk's (1997) study (42%), which suggests that food quality is lower in the region where the present study was carried out. However if this is the case, why do *P. diadema* not extend their range into areas apparently not utilised by any group of *P. diadema*?

Irwin (2006b) found seasonal variation in path length; daily path being lengths longer in January to March and shorter during May to July. This is in agreement with this study, where daily path length is positively correlated with activity period, hours of daylight and maximum (but not minimum) temperature, and negatively correlated with rainfall. This indicates that during warmer summer days *P. diadema* travel more than on cooler winter days. However on days of higher rainfall they travel less. Rainfall was recorded at approximately 17:30, so daily totals include rain from the night prior to observations. The same pattern was observed for activity and suggests that on wet days *P. diadema* use more energy to maintain body temperature and therefore have less energy to travel. This is consistent with minimising energy expenditure during cold periods as discussed in Chapter 5.

Group One travelled between 153 and 797m each day, while Group Two travelled between 153 and 783m. Correlations between daily path length and environmental factors were complicated as daily path lengths correlated with hours of observation; on no day was either group followed from rest to rest. In an attempt to remove the factor of hours of observation only the distance travelled between 08:00 to 16:00 was used. No correlations were found between distance travelled and environmental factors (day length, temperature and rainfall). This would suggest that the small-bodied *H. g. griseus* have minimum energy requirements compared to seasonal availability of foodstuffs and therefore do not need to travel further to find food in some seasons. Further personal observations would suggest that their favoured food, *Cathariostachys madagascariensis* (giant bamboo) is available throughout the year.

7.5.3. Monthly Ranging

Powzyk (1997) found that *I. indri* visited all the boundaries of their home range every 8 to 14 days of travel, and on five consecutive days in November *I. indri* only utilised the interior of their range. Pollock (1977) found that for every six day period, two groups at Analamazoatra used only just over 41% of their territory. In this study *I. indri* were found to use on average only 10% of the total range daily. On the two occasions when we have data from two subsequent days, 22 and 23 March, 9 and 10 June 2005, it would appear that *I. indri* shift areas within their home range daily. Monthly home range size in this study correlates with environmental influences, however it is difficult to confidently discern a pattern of monthly usage due to the low number of days sampled each month. There is a suggestion that discrete monthly ranges may exist: this would be contrary to the finding of Powzyk (1997). However, there is not enough data to draw firm conclusions on monthly ranging patterns from the present study.

P. diadema had significantly bigger monthly ranges than did *I. indri*. In April, when there were four days of observation (the highest from any month) they used 88% of their total range, suggesting that *P. diadema* use their entire range on a regular basis. This is in agreement with Powzyk (1997) who found they patrolled the boundaries of their home ranges every four to eight days. No correlations were found between monthly ranging in *P. diadema* and any external factor (temperature, rainfall, daylight). Warren and Crompton (1997b) found a similar distinction in ranging behaviour between A*vahi occidentalis* on the one hand, and *Lepilemur edwardsi* on the other, as obtain in this study between *P. diadema* and *I. indri*, and similar dietary, foraging strategy and energetic factors may well be at play in both cases.

Monthly home range usage of Group One ranged from 15% (July) to 48% (April) of annual home range. Group Two used from 21.4 (March) to 52.7% September) of their annual range monthly. The monthly range of Group One was positively correlated with minimum and maximum temperature, but no correlations were found with monthly ranges in Group Two.

7.6. Summary

Hypothesis 7.1 held that: following Sussman (1977) since *P. diadema* are more frugivorous they will have the largest home range. All other things being equal, the more folivorous *I. indri* and *H. g. griseus* will have smaller home ranges; but solely on a body size basis the expectation is that *I. indri* will have a larger home range than *H. g. griseus*.

This hypothesis is upheld; *P. diadema* had the largest home range (27ha), followed by *I. indri* (13ha), while *H. g .griseus* had the smallest home ranges (3.5 and 5.4ha).

Hypothesis 7.2 held that: following Warren and Crompton (1997b) *P. diadema* as a more selective feeder will use a larger proportion of its home range daily and monthly.

This hypothesis is upheld: on average *P. diadema* utilised 14% of their total home range daily and 53% monthly, while *I. indri* utilised 10% daily and 42% monthly.

Hypothesis 7.3 held that: *P. diadema* will have longer daily path lengths than *I. indri.*

This hypothesis is upheld: *P. diadema* had significantly longer daily path lengths; a mean of 902m, compared to 482m in *I. indri.*

Hypothesis 7.4 held that: daily path lengths in *I. indri* and *P. diadema* will be shorter in the austral winter.

This hypothesis is upheld: the daily path length in *I. indri* and *P. diadema* were found to positively correlate at the 0.01 level with hours of daylight; decreasing daylight in the austral winter leads to shorter path lengths.

Hypothesis 7.5 held that: since *H. g. griseus* are seasonally frugivorous they will be expected to have longer daily path lengths and monthly home ranges in the season when fruit is most commonly consumed.

This hypothesis is not upheld: although fruit was consumed from February to July, no seasonal effect of ranging or path length could be found for *H. g. griseus.*

Chapter 8 Observations on Heights

It was already noted that niche differentiation is often accomplished via differences in forest stratum, or height within the canopy (see e.g. Ganzhorn, 1989). Differences in stratum also affect support availability and continuity/discontinuity for locomotion, and hence energy costs and travel speed (Crompton, 1984). This chapter covers the vertical usage of the canopy by the three study species. It analyses heights of observation during different activities, height distinctions between individuals and at different seasons and times of the day and discusses findings in the context of the literature.

8.1 Background

8.1.1. Height and Niche Separation

For sympatric species, height differences are often an important means of niche separation. In Brazil, niche separation of sympatric *Saguinus fuscicollis weddelli* (Weddell's saddle-backed tamarin) and *Callithrix emiliae* (Emilia's marmoset) appeared in part to be controlled by height differences (Lopes & Ferrari, 1994). During the dry season, *S. f. weddelli* were found at a mean height of 5.95m, where as *C. emiliae* were found at a mean height of 10.7m.

According to Peres (1993) height differences also allow for niche separation in five sympatric diurnal primates elsewhere in Brazil: *Saguinus fuscicollis* (saddle-backed tamarin), *Saguinus mystax* (moustached tamarin), *Cebus apella* (tufted capuchin), *Pithecia albicans* (buffy saki) and *Lagothrix lagotricha* (woolly monkey). Peres (1993) found that height was correlated with body weight, smaller species being found lower in the canopy than larger species.

Singh *et al.* (2000) found feeding height differences in sympatric *Macaca silenus* (lion-tailed macaque) and *Presbytis johnii* (Nilgiri langur) in the Western Ghats, of southern India. *P. johnii* were found at higher levels in the canopy for all activity, compared to *M. silenus* (Singh *et al.*, 2000). The difference was even more pronounced when comparing heights of feeding on fruit, the only food item shared by the two species.

Ungar (1996) found that although feeding differences also played an important role, height differences contributed to niche separation in four sympatric primates in Sumatra, Indonesia. *Hylobates lar* (white-handed gibbon), *Macaca fascicularis* (long-tailed macaque), *Pongo abelii* (orang-utan) and *Presbytis thomasi* (Thomas' langur) were all found throughout the canopy, but feeding heights differed, despite dietary overlap.

Sympatric guenons (*Cercopithecus campbelli* [Campbell's guenon], *Cercopithecus petaurista* [lesser spot-nosed guenon] and *Cercopithecus diana* [Diana monkey]) in the Taï Forest, Ivory Coast differentiate niches by height, although differences in food items also exist (Buzzard, 2006). Each species was found at all levels, but *C. campbelli* was most often found below 5m, *C. petaurista* between 5 and 20m and *C. diana* at heights over 20m (for all activity).

8.1.2. Seasonal Height Changes

Primate species can exhibit seasonal height changes due to differing food resources or climatic conditions. *Cebus apella* display considerable differences in height between the dry and wet season in Brazil (Siemers, 2000). During the dry season *C. apella* was mostly found below 10m for all activity, spending some time at least terrestrially and in the wet season *C. apella* fed and was generally seen above 10m.

It is therefore to be expected that because of similar size and qualitatively similar diets: **Hypothesis 8.1: Niches of *I. indri* and *P. diadema* will be differentiated in part by height or stratum** and given the larger daily travel distances and larger home ranges of *P. diadema* (Chapter 7) and their generally higher quality and more diverse diet (Chapter 6): **Hypothesis 8.2: *P. diadema* will travel lower down in the canopy, where discontinuities are larger but fewer, to maximize travel speed** and given the dietary predominance of giant bamboo in H. g. griseus' diet (see Chapter 7): **Hypothesis 8.3: *H. g. griseus* will occupy a lower stratum than either of the indriids, where we have seen that most food is derived from trees (Chapter 7)** and with reference to seasonality, the demands of thermoregulation on metabolic costs would require that: **Hypothesis 8.4: All three species will be found lower in the canopy during the summer to avoid excessive heat.**

8.2 Methods

8.2.1. Field Methods

During observations, heights were recorded by two observers, Sabine Day and Mary Blanchard. During observations heights of individual lemurs were discussed, to ensure accuracy and agreement. Blanchard recorded heights alongside locomotor mode, whereas Day recorded height, activity and diet.

8.2.2. Statistical Methods

Heights of all three species were tested for normality by testing for skewness and kurtosis and by using the Kolmogorov-Smirnov (*D*) test for goodness of fit. Skewness measures the asymmetry of a distribution, and with a normal distribution skewness is zero (Kinnear & Gray, 2004). Positive skewness indicates a long right tail and negative skewness values a long left tail (Zar, 1999). If skewness is twice the standard error then there is a departure from symmetry. Values over 1 indicate a strongly skewed distribution and values between 0.5 and 1 indicate a moderately skewed distribution (Kinnear & Gray, 2004). Kurtosis measures the clustering of the points and in normal distributions the value is zero. Positive values show points are greater clustered and have a long tail, while negative values that there are shorter tails and less clustering (Kinnear & Gray, 2004).

A comparison of heights between species, within species between different individuals, and between observers has been carried out using the Mann-Whitney (*U*) test which uses the median, not the mean (Kinnear & Gray, 2004). This test is suitable for non-parametric samples, where variables are independent. In the Mann-Whitney test the significance criterion is met when $p \leq 0.05$.

To determine the significance of differing means temporally and seasonally, between locomotor modes and individuals within a species, the Kruskal-Wallis (*H*) test has been utilised. Kruskal-Wallis is a non-parametric equivalent of ANOVA (ANalysis Of VAriance [*F*] [Kinnear & Gray, 2004]). Although one-way ANOVA is a parametric test, it is robust to departures from normality and can be used with even considerable kurtosis and skewness (Zar, 1999). In instances where there are small group sample sizes, for example with locomotor modes, low-counting modes have been removed from analysis. Both Kruskal-Wallis and ANOVA are considered significant when $p \leq 0.05$. ANOVA is useful not only in itself, but associated post-hoc testing allows multiple comparisons of means. Duncan post-hoc testing was carried out in this study. Duncan's test is applicable when group sizes are unequal as it uses the harmonic mean. Duncan's test groups means in sub-groups, where all means in a sub-group are significantly similar, set at $p \geq 0.05$. Significance values close to 1 indicate the sub-group means are not significantly different from each other. The segregation of means into different subgroups therefore indicates that means within a subgroup are all significantly different from those in others.

Following a satisfactory determination of inter-observer accuracy (see below) Day's data has been used for activity and individual comparisons, while Blanchard's data has been used for comparison of heights during locomotion as well as examining spatial and temporal differences. The latter selection was made because of the larger number of data points.

When comparing individual *I. indri*, 'adult female: total' refers to all cases either after the infant's disappearance or prior to the disappearance when the adult female was not specifically carrying the infant on her back. 'Adult female: carrying infant' refers to all cases where the infant was specifically being carried by its mother. 'Infant' refers to all cases when the infant was active on its own and away from its mother, not being carried by her. 'Sub-adult female' and 'adult male: total' refers to all cases from the study, combined before and after the disappearance of the infant. To further investigate the impact of the infant, observation cases of the 'adult female' and 'adult male' were split into: those while the infant was present; and those when it was not. The group was sub-divided in this way to allow investigation of the presence of the infant on height.

8.3. Results

8.3.1. A Check for Normality of Data

8.3.1.1. *Indri indri*

Heights of observation of *I. indri* have a skewed distribution (Figure 8.1). There is a strong positive skewness (skewness = 1.764, *SE* = 0.027) showing a long right tail. Positive kurtosis (kurtosis = 3.069, *SE* = 0.055) shows that heights have a longer tail than in a normal distribution.

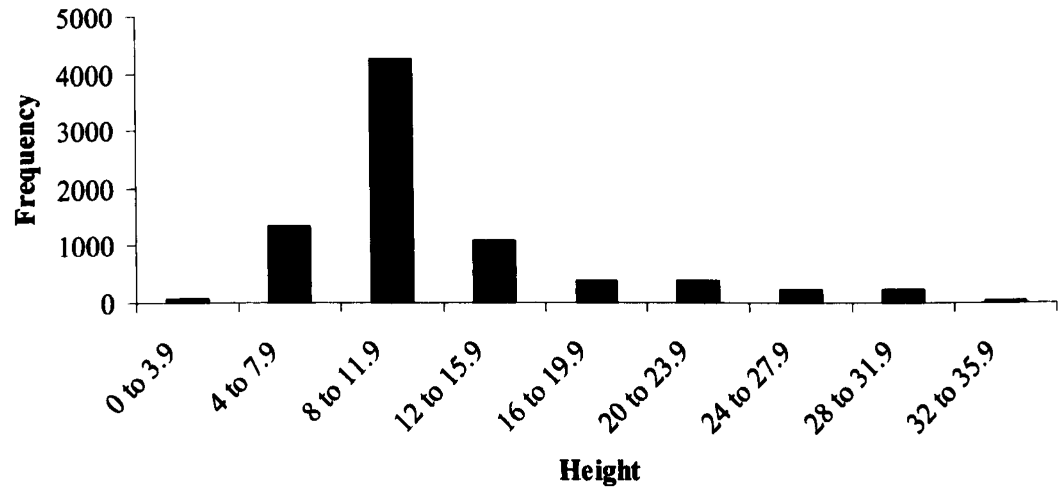


Figure 8.1. Frequency distribution of Blanchard's observations of heights utilised by *I. indri.*

8.3.1.2. *Propithecus diadema*

There is a skewed distribution of heights used by *P. diadema* (Figure 8.2). Skewness is over twice the standard error and is over 1 indicating a highly skewed data set. There is a strong positive skewness (skewness = 1.073, *SE* = 0.023) indicating a long right tail. A positive kurtosis (kurtosis = 1.466, *SE* = 0.047) indicates the heights have a longer tail than in a normal population. The

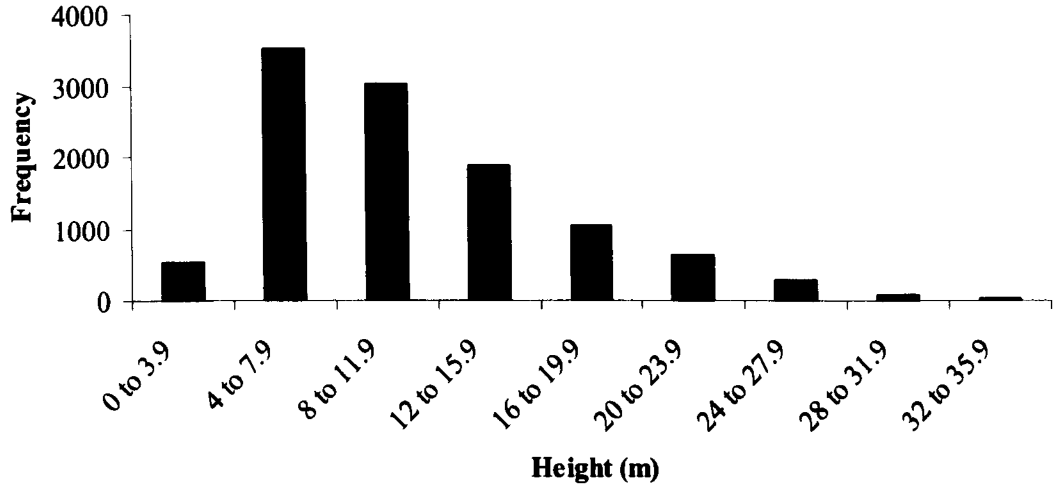


Figure 8.2. Frequency distribution of Blanchard's observations of heights utilised by *P. diadema*.

8.3.1.3. *Hapalemur griseus griseus*

Heights utilised by *H. g. griseus* have a skewed distribution (Figure 8.3). The positive skewness (skewness = 0.585, *SE* = 0.020) indicates a long right tail and the value is over twice its standard error, showing the distribution is not symmetrical. The kurtosis (kurtosis = -0.195, SE = 0.039) is negative, indicating a smaller tail than if the population was normal. Although the distribution of heights departs from normality, the distribution is only moderately skewed and has low kurtosis.

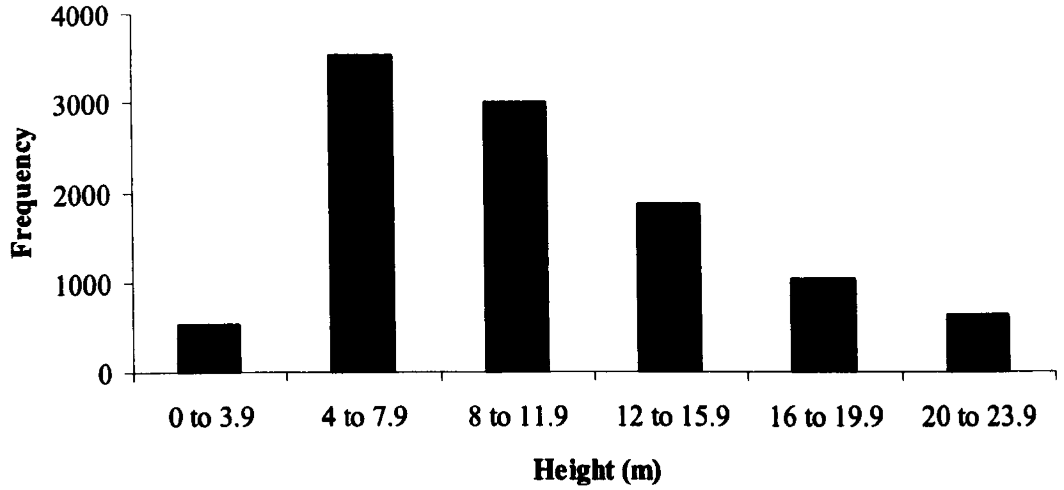


Figure 8.3. Frequency distribution of Blanchard's observations of heights utilised by *H. g. griseus*.

8.3.2. Determination of Accuracy between Day and Blanchard

Heights recorded by Day and Blanchard were compared using Mann-Whitney *U* tests, to detect any sizeable variation. Results are given by species and for *H. g. griseus*, also by group.

8.3.2.1. *Indri indri*

Median heights for Day's and Blanchard's (Table 8.1) observations of *I. indri* show a 1m difference, which is not significant ($U = 7.5, p > 0.05$ns).

Table 8.1. Heights (m) of *I. indri* from Blanchard and Day.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Blanchard	7956	12.62	6.74	0	51	11
Day	2267	12.45	6.8	0	40	10

8.3.2.2. *Propithecus diadema*

The median height of *P. diadema* in the observations of Blanchard and Day show no difference (Table 8.2 [$U = 1003.5, p > 0.05$ns]).

Table 8.2. Heights (m) of *P. diadema* from Blanchard and Day.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Blanchard	10984	10.58	5.76	0	51	9
Day	2496	10.30	6.04	0	35	9

8.3.2.3. *Hapalemur griseus griseus*

A: Group One

Median heights from Day and Blanchard for *H. g. griseus* Group One are within 0.5m of each other (Table 8.3), which is not significantly different ($U = 9109.5, p > 0.05$ns).

Table 8.3. Heights (m) of *H. g. griseus* Group One from Blanchard and Day.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Blanchard	8023	5.72	3.25	0	21	5.5
Day	1941	5.88	3.49	0	20	6

B: Group Two

Day's and Blanchard's median heights for *H. g. griseus* Group Two differ only by 1m (Table 8.4), which is not a significant difference ($U = 2326, p > 0.05$ns).

Table 8.4. Heights (m) of *H. g. griseus* Group Two from Blanchard and Day.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Blanchard	7632	5.85	3.84	0	20	5
Day	1008	6.39	3.91	0	20	6

8.3.3. Comparison between *Hapalemur griseus griseus* Groups One and Two

A comparison of median heights from Blanchard for *H. g. griseus* shows that the two groups show no significant differences in height of observation ($U = 163647.5, p > 0.05$ns). Day's median heights for the two groups of *H. g. griseus* also show no significant difference ($U = 2208.5, p > 0.05$ns). This permits data from both groups to be analysed together.

8.3.4. Comparison between *Indri indri, Propithecus diadema* and *Hapalemur griseus griseus.*

A comparison of heights of observation of *P. diadema* and *I. indri* (Table 8.5) indicates that *I. indri* are found 2m higher in the canopy, at a median of 11m, compared to *P. diadema* (9m), a statistically significant difference ($U = 34089652, p < 0.001$).

Table 8.5. Heights (m) from Blanchard for *P. diadema, I. indri* and *H. g. griseus.*

	N	*M* (m)	*SD*	Min	Max	Median (m)
P. diadema	10917	10.55	5.75	0	51	9
I. indri	7348	12.62	6.88	0	51	11
H. g. griseus	15568	5.78	3.54	0	21	5

The mean (and median) heights of all three species were significantly different from each other ($H\,[2] = 8603.977, p < 0.001$; $F\,[22, 33830] = 5328.677, p < 0.001$). The Duncan post-hoc test (Table 8.6) shows that *H. g. griseus* were found lowest in the canopy and *I. indri* the highest.

Table 8.6. Duncan post-hoc test for mean heights (m) for each study species.

	N		**Subsets**	
		1	**2**	**3**
H. g. griseus	15568	5.78		
P. diadema	10917		10.57	
I. indri	7348			12.63
Subset significances		1.000	1.000	1.000

8.3.5. Seasonal Height Changes

Blanchard's data was used to examine the relationship between date and height utilisation. The non-parametric Kruskal-Wallis test was used to test for differences between medians, followed by a one-way ANOVA with Duncan's post-hoc test to determine groupings of means.

8.3.5.1. *Indri indri*

Comparing mean daily heights over time for *I. indri* (Figure 8.4) shows there were also differences over the period of the present study at Mantadia. There is a tendency for higher means towards the end of the study, and lower means at the beginning.

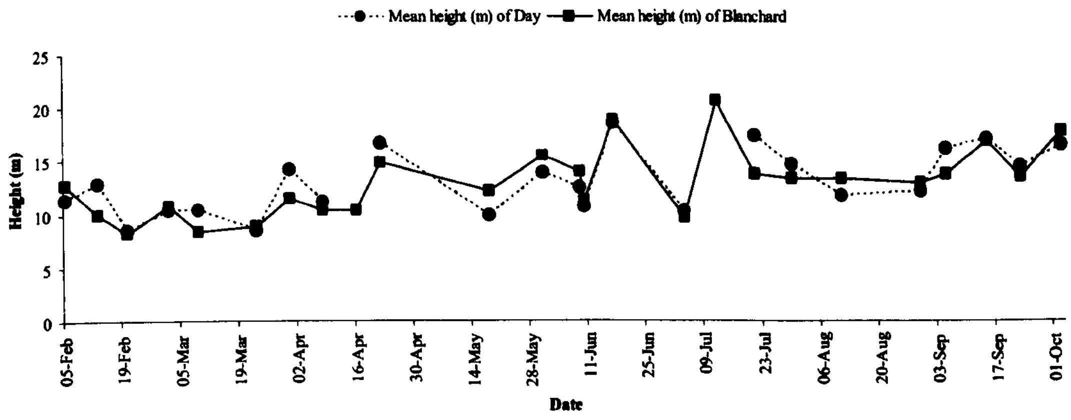


Figure 8.4. Daily mean height (m) of *I. indri* for Day and Blanchard, during 2005. Missing values indicate observer absence.

Statistical testing confirms that there are indeed significant differences between daily mean, and median, heights in *I. indri* (*H* [22] = 1608.327, $p < 0.001$; *F* [22, 7445] = 94.481, $p < 0.001$). To determine the nature of this association a Duncan post-hoc test was performed (Table 8.7). Daily mean heights are not grouped consecutively by date. This suggests that differences in daily mean heights are not directly controlled by seasonality. There is however a trend for lower mean heights at the beginning of the study and higher means towards the end.

Table 8.7. Duncan post-hoc test of mean height (m) of observation days of *I. indri* 2005, with median (m) values.

	N	Median	Subsets												
		(m)	1	2	3	4	5	6	7	8	9	10	11	12	13
20-Feb	376	11.5	8.15												
09-Mar	304	7	8.38												
23-Mar	344	8	8.88	8.88											
04-Jul	292	9		9.68	9.68										
13-Feb	394	11			10.00										
16-Apr	396	8			10.37	10.37									
08-Apr	382	9			10.42	10.42									
02-Mar	448	9			10.77	10.77									
10-Jun	520	10				11.32	11.32								
31-Mar	470	11				11.47	11.47								
18-May	78	12.5					12.19	12.19							
05-Feb	288	11.5						12.69	12.69						
30-Jul	244	12							13.27	13.27					
23-Sep	236	11							13.41	13.41					
05-Sep	358	11.5							13.70	13.70	13.70				
21-Jul	188	13.3							13.71	13.71	13.71				
09-Jun	324	14								13.92	13.92				
22-Apr	422	14									14.77	14.77			
31-May	198	15										15.42			
15-Sep	244	16											16.79		
03-Oct	480	18											17.73		
17-Jun	232	16.8												18.81	
12-Jul	250	20													20.63
Subset significances			0.184	0.126	0.059	0.058	0.114	0.335	0.079	0.269	0.058	0.209	0.070	1.000	1.000

To examine this relationship further, monthly mean heights were used and significant differences were found between monthly mean heights (*F* [7, 7460] = 127.613, $p < 0.001$). Grouping heights by month gives a clearer picture in the post-hoc test (Table 8.8): the lowest monthly means are found from February to April.

Table 8.8. Duncan post-hoc test for monthly mean heights (m) of *I. indri* during 2005, including median (m) values.

	N	Median (m)	Subsets				
			1	2	3	4	5
February	1058	9	10.08				
March	1566	8	10.10				
April	1200	10		11.93			
June	1076	14.6			13.72		
July	974	12			14.17	14.17	
May	276	12				14.51	
September	838	13				14.52	
October	480	18					17.73
Subset significances			0.939	1.000	0.195	0.339	1.000

8.3.5.2. *Propithecus diadema*

Mean heights of *P. diadema* by contrast appear largely constant over time (Figure 8.5).

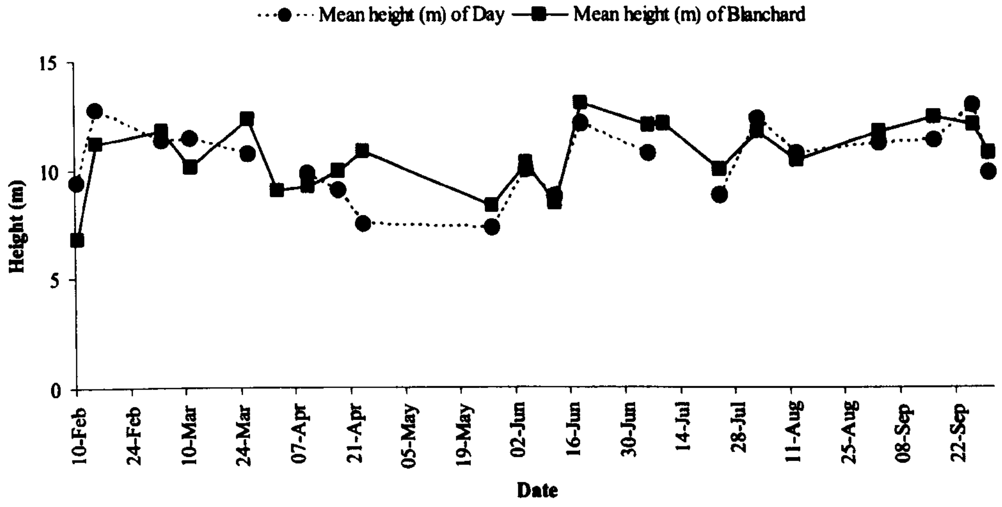


Figure 8.5. Daily mean height (m) of *P. diadema*, as recorded by Day and Blanchard during 2005. Missing values indicate observer absence.

Daily means (and medians) are significantly different from one another (H [19] = 714.659, $p < 0.001$; F [19, 10509] = 31.953, $p < 0.001$), however the Duncan post-doc test (Table 8.9) does not group daily means chronologically.

Table 8.9. Duncan-post hoc test of mean height (m) for different observation-days of *P. diadema* during 2005, with median (m) values.

	N	Median	Subsets								
		(m)	1	2	3	4	5	6	7	8	9
27-May	454	7	8.27								
12-Jun	340	8	8.39								
02-Apr	812	8	8.98	8.98							
10-Apr	1080	6		9.20	9.20						
18-Apr	632	8			9.88	9.88					
24-Jul	580	9			9.96	9.96	9.96				
11-Mar	326	8				10.07	10.07				
13-Aug	688	9.5				10.25	10.25				
05-Jun	560	10				10.26	10.26				
01-Oct	773	10				10.70	10.70	10.7			
24-Apr	712	10					10.78	10.8			
15-Feb	334	10						11.2	11.19		
03-Aug	318	10.2							11.72	11.72	
03-Sep	418	11							11.74	11.74	
06-Jul	444	10							11.97	11.97	
27-Sep	118	13								12.05	
10-Jul	378	11								12.15	
26-Mar	366	12								12.34	12.34
17-Sep	594	12								12.40	12.40
19-Jun	602	12									13.04
Subset significances			0.08	0.57	0.06	0.06	0.06	0.23	0.06	0.13	0.09

Monthly mean (and median) heights also differ significantly from one another (H [8] = 400.478, $p < 0.001$; F [8, 10520] = 36.270, $p < 0.001$). The Duncan post-hoc test does not however group months in order (Table 8.10), strongly suggesting there is no overall seasonal pattern of height change for *P. diadema.*

Table 8.10. Duncan post-hoc test for monthly mean heights (m) of *P. diadema* during 2005, with median (m) values.

	N	Median (m)	Subsets 1	2	3	4
May	454	7	8.27			
April	3236	8		9.62		
October	773	10			10.70	
August	1006	10			10.71	
June	1502	10			10.95	
July	1402	10			11.19	
February	334	10			11.19	
March	692	9			11.27	
September	1130	12				12.12
Subset significances			1.000	1.000	0.082	1.000

8.3.5.3. *Hapalemur griseus griseus*

Mean (and median) daily heights of *H. g. griseus* show variation (Figure 8.6) and daily mean, and median, heights are significantly different (H [30] = 1021.867, $p < 0.001$; F [30, 15629] = 8.646, $p < 0.001$), however once again the Duncan post-hoc test (Table 8.11) does not group dates consecutively.

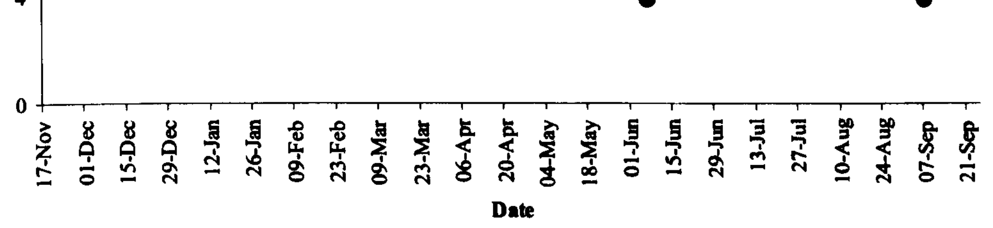


Figure 8.6. Daily mean height (m) of *H. g. griseus*, for Blanchard and Day data, from November 2004 to September 2005. Missing values indicate observer absence.

Table 8.11. Duncan post-hoc test for daily mean height (m) for *H. g. griseus* Group One, from December 2004 to September 2005, with median (m) values.

	N	**Med (m)**	**Subsets 1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
18Dec	320	4	4.19											
27Nov	284	4	4.34											
04Apr	552	4	4.42	4.42										
08Feb	446	4	4.54	4.54	4.54									
11Dec	436	5	4.59	4.59	4.59	4.59								
28Feb	366	4	4.60	4.60	4.60	4.60								
29Mar	678	4.75	4.65	4.65	4.65	4.65								
19Feb	710	4.2	4.80	4.80	4.80	4.80	4.80							
28Apr	1048	4	5.06	5.06	5.06	5.06	5.06	5.06						
07Sep	444	5.2	5.18	5.18	5.18	5.18	5.18	5.18	5.18					
01Feb	306	5	5.33	5.33	5.33	5.33	5.33	5.33	5.33	5.33				
19Aug	476	5	5.35	5.35	5.35	5.35	5.35	5.35	5.35	5.35				
20Mar	638	5	5.44	5.44	5.44	5.44	5.44	5.44	5.44	5.44	5.44			
01Sep	442	5		5.79	5.79	5.79	5.79	5.79	5.79	5.79	5.79	5.79		
22Jun	512	6		5.82	5.82	5.82	5.82	5.82	5.82	5.82	5.82	5.82		
29May	320	6			5.90	5.90	5.90	5.90	5.90	5.90	5.90	5.90		
24Jun	614	5				6.00	6.00	6.00	6.00	6.00	6.00	6.00		
14Jul	520	6				6.01	6.01	6.01	6.01	6.01	6.01	6.01		
07Jun	726	6				6.02	6.02	6.02	6.02	6.02	6.02	6.02		
26Jul	618	6.7					6.10	6.10	6.10	6.10	6.10	6.10		
01Dec	230	6					6.19	6.19	6.19	6.19	6.19	6.19		
06Mar	384	5.2					6.23	6.23	6.23	6.23	6.23	6.23		
20Apr	682	6						6.34	6.34	6.34	6.34	6.34		
09Aug	382	6.5							6.54	6.54	6.54	6.54		
19Sep	404	6								6.75	6.75	6.75		
20May	556	7									6.81	6.81		
15Jun	490	8										7.00		
08Jul	324	7										7.11		
13Apr	1132	7										7.18		
25Sep	494	6											8.87	
09Jan	126	10.6												10.5
Subset significance			0.09	0.05	0.06	0.05	0.05	0.08	0.06	0.05	0.06	0.06	1.00	1.00

Tests were carried out on monthly means (and medians) and significant differences were found (H [10] = 537.622, $p < 0.001$; F [10, 15649] = 12.219, $p < 0.001$). The Duncan post-hoc test (Figure 8.13) does not however group months in consecutive order, indicating that there is no seasonal change in height.

Table 8.12. Duncan post-hoc test of mean monthly height (m) for *H. g. griseus*, from November 2004 to September 2005, with median (m) values.

	N	Median (m)	Subsets 1	2	3	4
November	284	4	4.34			
February	1828	4.2	4.78			
December	986	5	4.83			
March	1700	5	5.30	5.30		
August	858	6		5.88	5.88	
April	3414	5		5.92	5.92	
June	2342	6		6.18	6.18	
July	1462	6.45		6.29	6.29	
May	876	6.85			6.48	
September	1784	5.85			6.71	
January	126	10.6				10.49
Subset significances			0.075	0.074	0.146	1.000

8.3.6. Diurnal Height Changes

Diurnal changes in height were investigated using data from Blanchard. Kruskal-Wallis was used, together with one-way ANOVA and subsequent Duncan post-hoc testing. Data was used regardless of date, individual and activity. Times were grouped hourly: 05:00 to 05:59; 06:00 to 06:59 etc.

8.3.6.1. *Indri indri*

Mean hourly heights of *I. indri* appear to show diurnal variation (Figure 8.7); heights are higher in the middle of the day, but lower mid-morning and late afternoon.

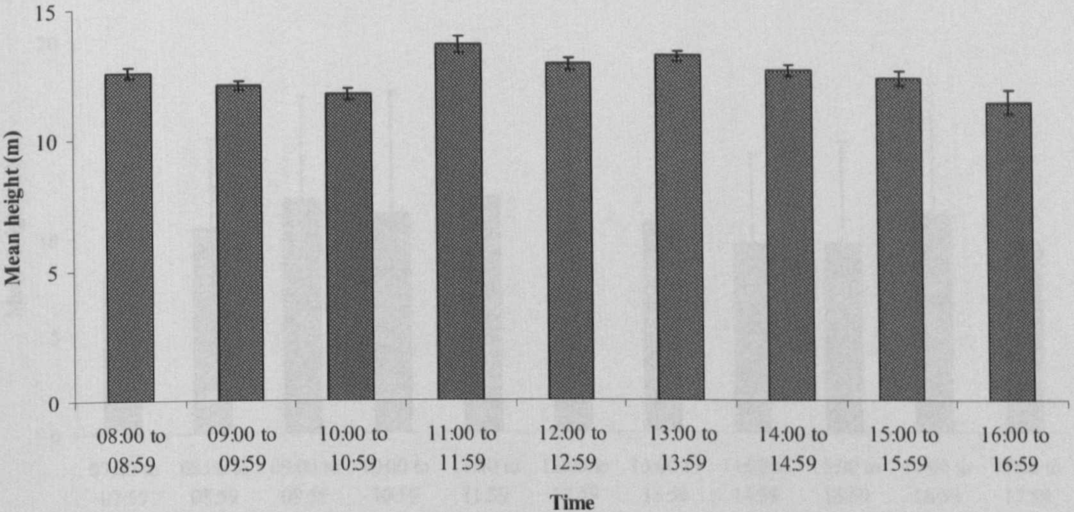


Figure 8.7. Diurnal variation in mean height (m) of *I. indri*. Errors bars represent the standard deviation from the mean, set at the 95% level.

The hourly means (and medians), further, do differ significantly ($H [8] = 68.218, p < 0.001$; $F [8, 7447] = 6.851, p < 0.001$). The Duncan post-hoc test (Table 8.13) has overlapping groups, suggesting no clear pattern of diurnal vertical space usage. However, lowest hourly means are found mid-morning (09:00 to 10:59) and mid-afternoon (15:00 to 16:59) and highest means are found in the middle of the day (11:00 to 13:59).

Table 8.13. Duncan post-hoc test for diurnal variation in mean height (m) of *I. indri*, with median (m) values.

	N	Median (m)	Subsets				
			1	2	3	4	5
16:00 to 16:59	132	9.25	11.42				
10:00 to 10:59	1120	10	11.79	11.79			
09:00 to 09:59	1048	12	12.09	12.09	12.09		
15:00 to 15:59	634	9.75		12.34	12.34	12.34	
08:00 to 08:59	738	12		12.55	12.57	12.57	
14:00 to 14:59	1024	10.5		12.68	12.68	12.68	
12:00 to 12:59	924	11			12.92	12.92	12.92
13:00 to 13:59	1162	11				13.23	13.23
11:00 to 11:59	674	12					13.67
Subset significances			0.129	0.056	0.078	0.058	0.087

8.3.6.2. *Propithecus diadema*

Comparing diurnal hourly mean heights of *P. diadema* (Figure 8.8) suggests that *P. diadema* are found low in the canopy early morning and mid-afternoon, reaching high means mid- to late morning and late afternoon.

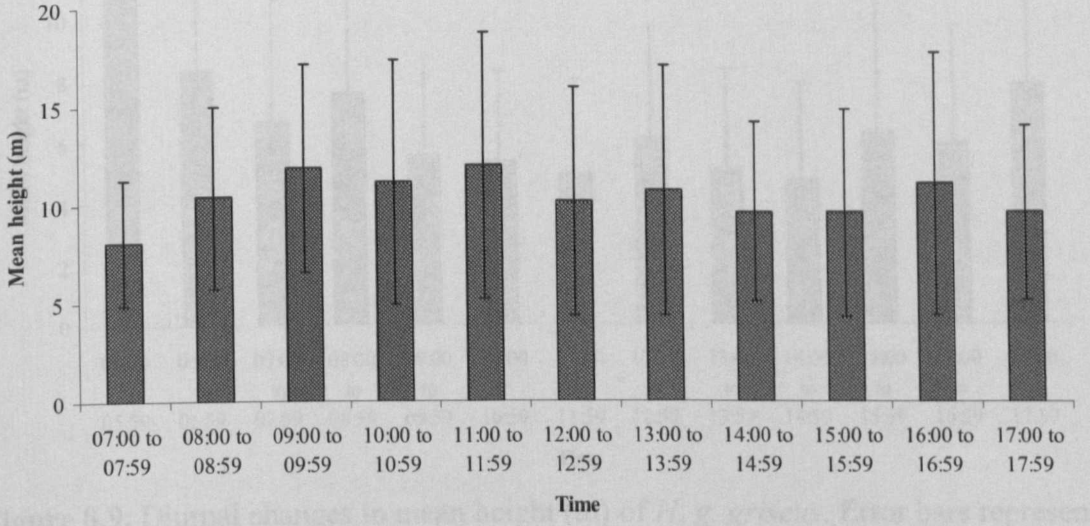


Figure 8.8. Diurnal variation in mean height (m) for *P. diadema*. Error bars represent the standard deviation from the mean, set at the 95% level.

Hourly mean, and median, heights are significantly different from one another (H [10] = 258.359, $p < 0.001$; F [10, 10970] = 29.498, $p < 0.001$). The Duncan post-hoc test indicates (Table 8.14) high means in the morning (09:00 to 11:59), with low means early morning (07:00 to 07:59) and afternoon (14:00 to 15:59).

Table 8.14. Duncan post-doc test for diurnal variation in mean height (m) of *P. diadema*, with median (m) values.

	N	Median (m)	Subsets 1	2	3	4	5
07:00 to 07:59	274	8.5	8.03				
15:00 to 15:59	1388	8		9.58			
17:00 to 17:59	168	8		9.58			
14:00 to 14:59	1416	9		9.64			
12:00 to 12:59	1237	10		10.18	10.18		
08:00 to 08:59	832	9.55			10.36		
13:00 to 13:59	1436	9			10.72	10.72	
16:00 to 16:59	550	9.5				11.06	
10:00 to 10:59	1414	10				11.15	
09:00 to 09:59	1128	11					11.86
11:00 to 11:59	1138	11					11.99
Subset significances			1.000	0.094	0.115	0.216	0.699

8.3.6.3. *Hapalemur griseus griseus*

There appears to be a pattern of higher mean heights in the early morning and lower mean heights in the late morning to early afternoon (Figure 8.9).

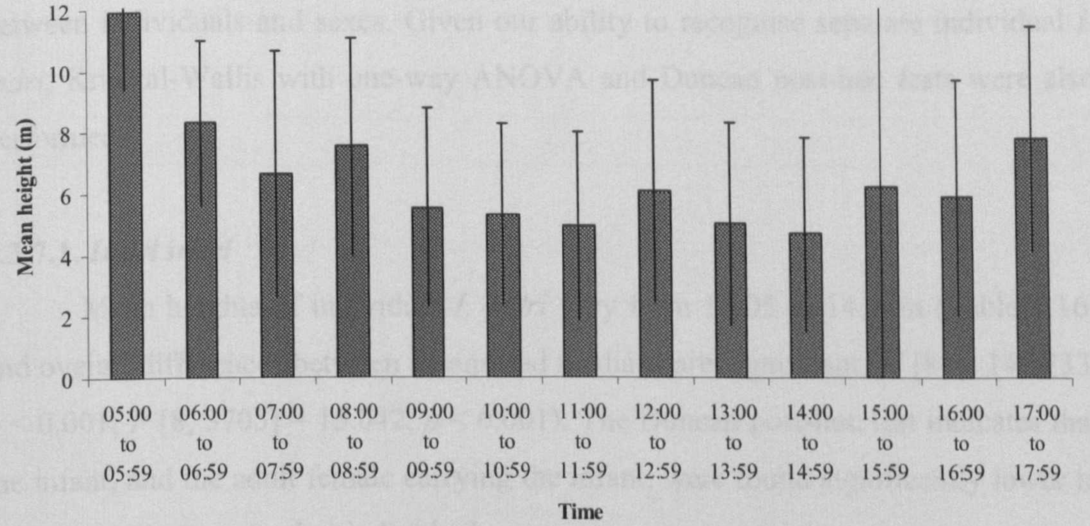


Figure 8.9. Diurnal changes in mean height (m) of *H. g. griseus*. Error bars represent the standard deviation from the mean, set at 95%.

Hourly means, and medians, differ significantly from one another (*H* [12] = 1162.816, $p < 0.001$; *F* [12, 15647] = 18.223, $p < 0.001$). The post-hoc test (Table 8.15) indicates a statistically significant trend for higher mean heights earlier in the day (05:00 to 08:59), and lower mean heights at mid-day (11:00 to 14:00).

Table 8.15. Duncan post-hoc test for diurnal variation in mean height (m) of *H. g. griseus*, with median (m) values.

	N	Median (m)	Subsets 1	2	3	4	5	6
14:00 to 14:59	2614	4.2	4.70					
11:00 to 11:59	1096	5	4.94	4.94				
13:00 to 13:59	1896	4.6	5.03	5.03				
10:00 to 10:59	650	5	5.32	5.32	5.32			
09:00 to 09:59	1126	5.5	5.56	5.56	5.56			
16:00 to 16:59	1524	5	5.89	5.89	5.89			
12:00 to 12:59	1384	6	6.10	6.10	6.10			
15:00 to 15:59	2072	5.5		6.22	6.22			
07:00 to 07:59	1122	6.8			6.65	6.65		
08:00 to 08:59	1530	7				7.55	7.55	
17:00 to 17:59	494	7.4				7.77	7.77	
06:00 to 06:59	80	8					8.32	
05:00 to 05:59	72	13						11.89
Subset significances			0.060	0.089	0.071	0.099	0.262	1.000

8.3.7. Individual Height Comparisons

The Mann-Whitney test was used on Day's height data to allow comparison between individuals and sexes. Given our ability to recognise separate individual *I. indri*, Kruskal-Wallis with one-way ANOVA and Duncan post-hoc tests were also performed.

8.3.7.1. *Indri indri*

Mean heights of individual *I. indri* vary from 10.05 to 14.27m (Table 8.16) and overall differences between means and medians are significant (*H* [8] = 149.233, $p < 0.001$; *F* [8, 3705] = 15.042, $p < 0.001$). The Duncan post-hoc test indicates that the infant, and the adult female carrying the infant, were found significantly lower in the canopy than were other individuals.

Table 8.16. Heights (m) of individual *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Adult female: total	707	12.97	7.15	1	40	10
Adult female: infant present	315	11.67	5.55	4	30	10
Adult female: infant not present	392	14.01	8.07	1	40	12
Adult female: carrying infant	257	10.05	3.87	2	20	9
Adult male: total	740	12.72	6.52	0	35	10
Adult male: infant present	443	12.20	6.90	1	35	10
Adult male: infant not present	297	13.49	5.84	0	30	12
Sub-adult female	319	14.27	6.66	2	30	15
Infant	244	10.31	6.92	3	35	8
Total	3714	12.60	6.74	0	40	10

Table 8.17. Duncan post-hoc test for mean heights (m) of individual *I. indri*.

	N	Subsets				
		1	**2**	**3**	**4**	**5**
Adult female: carrying infant	257	10.05				
Infant	244	10.31				
Adult female: infant present	315		11.67			
Adult male: infant present	443		12.20	12.20		
Adult male: total	740			12.72	12.72	
Adult female: total	707			12.97	12.97	
Adult male: infant not present	297				13.48	13.48
Adult female: infant not present	392					14.01
Sub-adult female	319					14.27
Subset significances		0.606	0.287	0.146	0.146	0.136

Comparing height data from Blanchard also indicates a significant difference in height while the infant *I. indri* was present, and when it was not (Table 8.18). The group was 2.5m lower in the canopy when the infant was present, than when it was not, a statistically significant difference ($U = 4266436, p < 0.001$).

Table 8.18. Heights (m) of *I. indri* while the infant was present, and when the infant was not.

	N	*M* (m)	*SD*	Min	Max	Median (m)
No infant	5517	13.26	7.16	0	51	11.5
Infant	1951	10.72	5.49	0	36	9
Total	7468	12.59	6.85	0	51	11

8.3.7.2. *Propithecus diadema*

The 2m median difference between the overall heights at which male and female *P. diadema* were found within the canopy was not a significant difference ($U = 582082, p > 0.05$ns).

Table 8.19. Heights (m) of male and female *P. diadema*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Male	1860	10.37	6.29	0	35	8
Female	633	10.07	5.26	1	30	10
Total	2493	10.29	6.04	0	35	9

The adult female carrying the infant was found an average of 1.34m below the mean for all other individuals during the period she was carrying the infant (Table 8.20). This is a significant difference ($U = 44468, p < 0.01$).

Table 8.20. Heights (m) of the adult female carrying her infant, compared to all other individuals, during the period that the infant was present in the group.

	N	*M* (m)	*SD*	Min	Max	Median (m)
All other individuals	332	11.55	6.34	0	30	10
Female carrying infant	305	10.15	5.53	1	30	10
Total	637	10.88	6.00	0	30	10

8.3.7.3. *Hapalemur griseus griseus*

There was no difference between heights of male and female *H. g. griseus* (Table 8.21 [$U = 256319, p > 0.05$ns]).

Table 8.21. Heights (m) for male and female *H. g. griseus*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Male	414	5.78	3.03	0	13	6
Female	1304	6.15	3.71	0	20	6
Total	1718	6.06	3.56	0	20	6

8.3.8. Heights and Locomotor Mode

The Kruskal-Wallis test was used to test for differences in median height between each locomotor mode. A one-way ANOVA with Duncan post-hoc testing was utilised to examine differences between means. Blanchard's data was used for this purpose. Low numbers of data points for some modes of locomotion make statistical testing difficult. Brief descriptions of locomotor modes are given here (Table 8.22), more detailed descriptions can be found in Chapter 9.

Table 8.22. Brief description of locomotor modes used in this study.

Name	Definition for purposes of this study
Leap	Jump across any discontinuity using an extension of the hind limbs
Vertical climb	Gain or loss of height on a single support, with a vertical body posture
Quadrupedal walk	Walking along a support, with at least three limbs in contact at any time
Cantilever	Maintaining contact with the support while reaching across a gap to grasp another support
Hop	Jumps along a support with both hind and fore limbs maintaining contact
Bipedal walk	Walk on hind limbs with vertical body posture, can be assisted with forearms held above
Two-handed suspension	Hanging and moving using forelimbs beneath a support
Four-handed suspension	Hanging and moving using fore and hind limbs beneath a support
Run	Fast quadrupedal locomotion with only two limbs in contact with a support
Drop	Suspension by forelimbs before releasing and falling to a support beneath onto hind limbs
Foliage cross	Reaching across a gap to grasp foliage with one limb before moving across remainder of limbs
Kangaroo hop	A series of jumps along a support, with only hind limbs in contact with the support

8.3.8.1. *Indri indri*

It is apparent there are differences in heights between modes of locomotion (Figure 8.10 and Table 8.23). Leaping was observed lowest in the canopy, and quadrupedal walking highest.

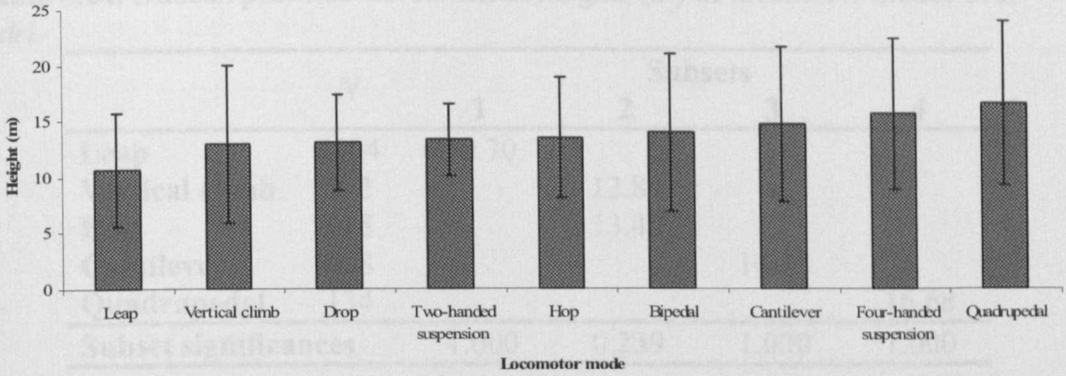


Figure 8.10. Mean height (m) for locomotor modes of *I. indri*, independent of individual, combining heights for initial and terminal supports. Error bars represent the standard deviation from the mean at the 95% level.

Table 8.23. Heights (m) for each locomotor mode recorded for *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Leap	6404	10.70	5.05	0	40	10
Vertical climb	792	12.89	7.02	0	36	11
Drop	2	13.00	4.24	10	16	13
2-hand suspension	22	13.34	3.19	9	20	14
Hop	118	13.45	5.40	5	31	12
Bipedal walking	4	13.90	7.05	7.6	20	14
Cantilever	468	14.77	6.92	3.5	40	13.5
4-hand suspension	12	15.75	6.78	9	29.5	14.5
Quadrupedal	134	16.68	7.42	6	34	15
Total	7956	11.31	5.62	0	40	10

The medians of each locomotor mode are significantly different from one another (H [8] = 442.112, $p < 0.001$). Due to low sample sizes the locomotor categories drop, two-handed suspension, bipedal walking and four-handed suspension were removed from ANOVA and Duncan post-hoc analysis (F = [4, 7911] = 3589.752, $p < 0.001$). The Duncan post-hoc test (Table 8.24) indicates significant differences in the mean heights at which *I. indri* perform each remaining locomotor mode; leaping being performed lowest in the canopy and quadrupedal walking highest.

Table 8.24. Duncan post-hoc test for mean heights (m) of locomotor modes of *I. indri*.

	N	Subsets			
		1	**2**	**3**	**4**
Leap	6404	10.70			
Vertical climb	792		12.89		
Hop	118		13.45		
Cantilever	468			14.77	
Quadrupedal	134				16.68
Subset significances		1.000	0.239	1.000	1.000

8.3.8.2. *Propithecus diadema*

There are differences in average heights of observation of each of the main modes of locomotion (Figure 8.11 and Table 8.30). Leaping occurs lowest and dropping the highest.

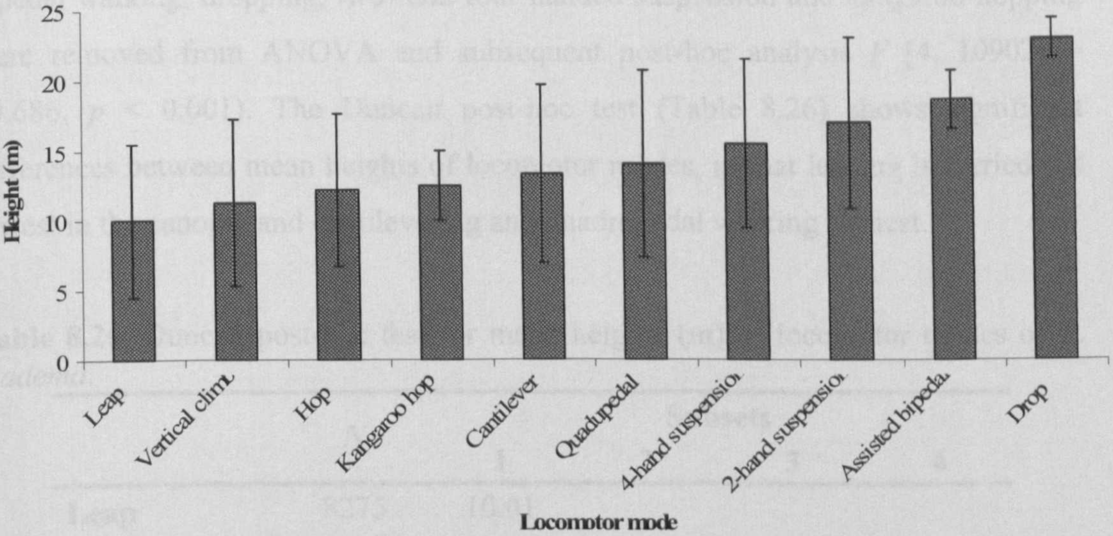


Figure 8.11. Mean height (m) for locomotor modes of *P. diadema*, combining heights for initial and terminal supports. Errors bars represent the standard deviation from the mean set at the 95% level.

Table 8.25. Heights (m) for each locomotor mode recorded for *P. diadema*, independent of date or individual.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Leap	8275	10.01	5.48	0	51	9
Vertical climb	1456	11.29	5.96	0	42	10
Hop	126	12.17	5.45	1	25	12
Kangaroo hop	6	12.50	2.49	10	15.5	12
Cantilever	806	13.32	6.36	1	42	12
Quadrupedal	244	14.05	6.62	4	41	12
4-hand suspension	26	15.50	6.01	6	25	15.5
2-hand suspension	36	17.00	6.10	4	27	16
Assisted bipedal	6	18.67	2.07	16	20	20
Drop	2	23.00	1.41	22	24	23
Total	10983	10.58	5.76	0	51	9

Median heights of each locomotor mode are significantly different (H [9] = 441.473, $p < 0.001$). Due to low numbers of data points, the locomotor categories bipedal walking, dropping, two- and four-handed suspension and kangaroo-hopping were removed from ANOVA and subsequent post-hoc analysis F [4, 10902] = 99.686, $p < 0.001$). The Duncan post-hoc test (Table 8.26) shows significant differences between mean heights of locomotor modes, in that leaping is carried out lowest in the canopy, and cantilevering and quadrupedal walking highest.

Table 8.26. Duncan post-hoc test for mean heights (m) of locomotor modes of *P. diadema*.

	N	Subsets			
		1	2	3	4
Leap	8275	10.01			
Vertical climb	1456		11.29		
Hop	126			12.17	
Cantilever	806				13.32
Quadrupedal	244				14.05
Subset significances		1.000	1.000	1.000	0.086

8.3.8.3. Comparison between *Indri indri* and *Propithecus diadema*

I. indri and *P. diadema* shared all modes of locomotion except assisted bipedal walking and kangaroo hopping, observed for *P. diadema* but not *I. indri*. Comparing the two species (Figure 8.12) shows that *I. indri* move higher for almost all locomotor categories. Only for two-handed suspension and dropping are *P. diadema* observed higher.

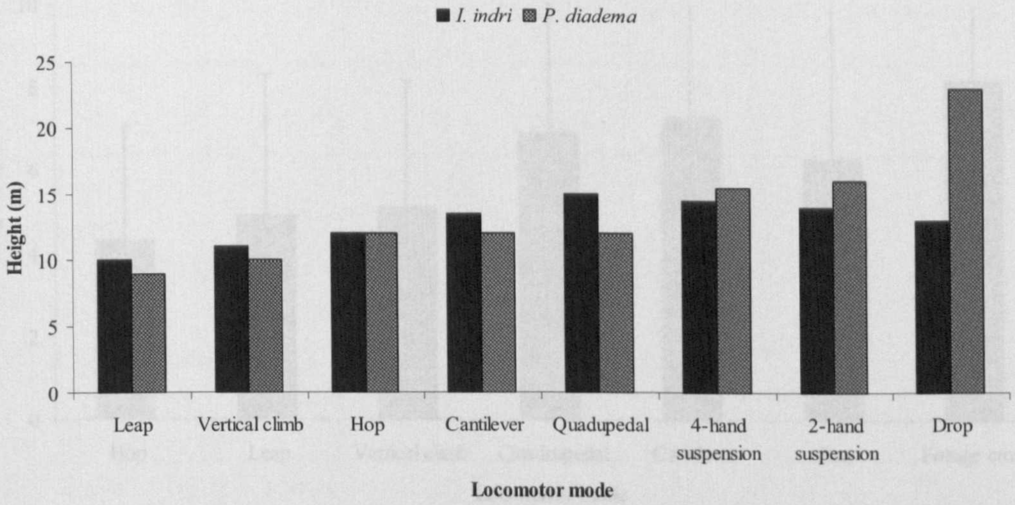


Figure 8.12. Comparison of median height (m) for each locomotor mode, independent of data and individual of *I. indri* and *P. diadema*.

I. indri leap 1m, higher in the canopy than *P. diadema* (Table 8.27). *P. diadema* vertical-climb 1m, lower than *I. indri*. The median height of cantilevering is also higher in *I. indri* than *P. diadema*. *I. indri* use quadrupedal walking 3m, higher than do *P. diadema*. However, *P. diadema* use two-handed suspension 2m higher than *I. indri*. All these interspecific differences are statistically significant.

Table 8.27. Mann-Witney *U* statistics for height differences of locomotor modes between *I. indri* and *P. diadema*.

	U	***P***
Leap	23212555.5	0.000**
Vertical climb	508764	0.000**
Hopping	6569	0.116
Cantilevering	170752	0.005**
Quadrupedal walking	170752	0.005**
4-hand suspension	143	0.682
2-hand suspension	231.5	0.008**
Dropping	0.000	0.121

**Significant at the 0.01 level (two-tailed).

8.3.8.4. *Hapalemur griseus griseus*

There is considerable difference in the mean heights of different modes of locomotion for *H. g. griseus* (Figure 8.13 and Table 8.28). Hopping, leaping and vertical climbing occur low in the canopy. Quadrupedal walking, running and cantilevers occur at higher levels, while foliage crossing is conducted at the highest heights.

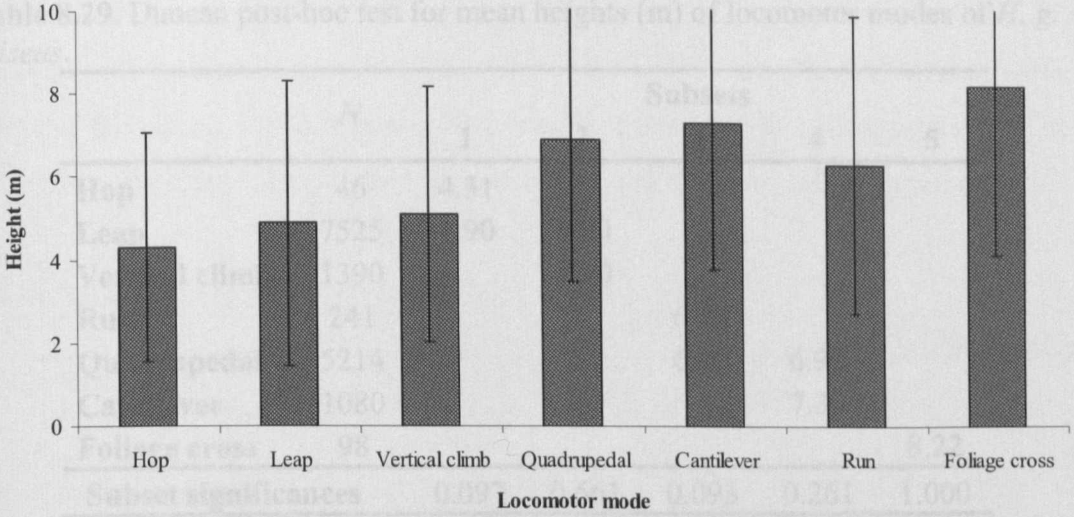


Figure 8.13. Mean height (m) of the locomotor modes in *H. g. griseus*. Error bars represent the standard deviation from the mean set at 95%.

Table 8.28. Heights (m) for locomotor modes of *H. g. griseus*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Hop	46	4.31	2.75	0	11.6	4.15
Vertical climb	1390	5.10	3.09	0	15	4.75
Leap	7525	4.90	3.43	0	21	4
Run	241	6.30	3.60	0.5	15	6
Quadrupedal	5214	6.90	3.41	0	20	7
Cantilever	1080	7.30	3.50	0.25	20	7
Foliage cross	98	8.22	4.09	0.75	18	8
Total	15594	5.79	3.55	0	21	5.1

There are significant differences in mean and median heights of each mode of locomotion for *H. g. griseus* ($H [6] = 1422.771, p < 0.001$; $F [6, 15587] = 234.030, p < 0.001$). The Duncan post-hoc test (Table 8.29) groups the categories hopping and leaping, which have low mean heights, while foliage crossing falls in a group on its own at the greatest mean height.

Table 8.29. Duncan post-hoc test for mean heights (m) of locomotor modes of *H. g. griseus*.

	N	Subsets				
		1	2	3	4	5
Hop	46	4.31				
Leap	7525	4.90	4.90			
Vertical climb	1390		5.10			
Run	241			6.30		
Quadrupedal	5214			6.90	6.90	
Cantilever	1080				7.30	
Foliage cross	98					8.22
Subset significances		0.097	0.561	0.093	0.261	1.000

8.3.9. Heights and Activity

Day's height data were used in Mann-Whitney tests to study the effect of activity on height.

8.3.9.1. *Indri indri*

There is no significant difference (Table 8.31) between the heights (Table 8.30) at which all individuals of *I. indri* rested and travelled; nor between the heights at which they rested and fed. However travelling is conducted at a significantly different median height compared to feeding.

Table 8.30. Activity height (m), independent of individual and date for *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Rest	830	12.36	6.60	2	40	10
Travel	917	12.20	6.53	1	40	10
Feed	518	13.04	6.99	0	35	10
Total	2265	12.45	6.67	0	40	10

Table 8.31. Mann-Whitney statistics for heights of activity for *I. indri*.

	U	*p*
Rest and travel	375815	0.651
Rest and feed	201959	0.060
Travel and feed	219952.5	0.019*

*Significant at the 0.05 level (two-tailed).

A: Individual Differences while Resting

Mean resting heights of individual *I. indri* range from 9.95 to 14.41m (Table 8.32). There are significant differences in the mean and median resting heights for individual *I. indri* (*H* [7] = 57.314, $p < 0.001$; *F* [8, 1343] = 6.839, $p < 0.001$). The Duncan post-hoc test (Table 8.33) shows that the infant, and the adult female while carrying the infant, rested lowest in the canopy. Following the disappearance of the infant, however, the sub-adult female and adult female rested highest in the canopy.

Table 8.32. Height (m) during resting for individual *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Adult female: total	257	13.24	7.33	2	40	10
Adult female: carrying infant	94	9.95	4.04	4	20	9
Adult female: infant present	117	11.84	5.39	5	30	10
Adult female: infant not present	140	14.41	8.47	2	40	12
Adult male: total	265	12.14	6.18	2	35	10
Adult male: infant present	168	11.46	6.21	2	35	10
Adult male: infant not present	97	13.33	5.96	2	30	15
Sub-adult female	126	14.20	6.27	2	30	15
Infant	88	10.39	7.13	3	35	8
Total	1352	12.49	6.68	2	40	10

Table 8.33. Duncan post-hoc test for mean heights (m) individual heights of *I. indri* during resting.

	N	Subsets				
		1	**2**	**3**	**4**	**5**
Adult female: carrying infant	94	9.95				
Infant	88	10.39	10.39			
Adult male: infant present	168	11.46	11.46	11.46		
Adult female: infant present	117		11.84	11.84	11.84	
Adult male	265			12.14	12.14	
Adult female	257				13.24	13.24
Adult male: no infant present	97				13.33	13.33
Sub-adult female	126					14.20
Adult female: no infant present	140					14.41
Subset significances		0.080	0.093	0.433	0.096	0.194

B: Individual Differences while Travelling

Mean heights of travelling vary between individuals, from 9.96 to 13.42m (Table 8.34) and these overall inter-individual mean and median differences are significant (H [8] = 52.223, $p < 0.001$; F [8, 1502] = 5.387, $p < 0.001$). The Duncan post-hoc test (Table 8.35) indicates that the adult female carrying the infant and the infant travelled lowest in the canopy, but when the infant disappeared the sub-adult female and adult female travelled the highest.

Table 8.34. Height (m) during travel for individual *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Adult female: total	285	12.38	6.80	2	40	10
Adult female: infant present	127	10.85	4.69	4	25	10
Adult female: infant not present	158	13.60	7.91	2	40	11.5
Adult female: carrying infant	105	9.96	3.82	4	20	9
Adult male: total	309	12.57	6.34	1	30	10
Adult male: infant present	188	12.02	6.61	1	30	10
Adult male: infant not present	121	13.42	5.82	4	30	12
Sub-adult female	121	13.87	6.78	2	30	13
Infant	97	10.85	7.52	3	35	8
Total	1511	12.31	6.54	1	40	10

Table 8.35. Duncan post-hoc test for mean heights (m) of individual *I. indri* during travelling.

	N	Subsets			
		1	**2**	**3**	**4**
Adult female: carrying infant	105	9.96			
Infant	97	10.85	10.85		
Adult female: infant present	127	10.85	10.85		
Adult male: infant present	188		12.02	12.02	
Adult female: total	285		12.38	12.38	12.38
Adult male: total	309			12.57	12.57
Adult male: infant not present	121			13.42	13.42
Adult female: infant not present	158			13.60	13.60
Sub-adult female	121				13.87
Subset significances		0.275	0.066	0.064	0.081

C: Individual Differences while Feeding

Mean heights of feeding for individual *I. indri* range from 9.03 to 14.10m (Table 8.36); differences between means and medians are significant (H [8] = 848.000, $p < 0.001$; F [8,840] = 4.992, $p < 0.001$). The Duncan post-hoc test (Table

8.37) indicates clearly that the infant, and the female while carrying the infant, fed lower in the canopy than all other group members.

Table 8.36. Height (m) during feeding for individual *I. indri*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Adult female: total	165	13.58	7.43	1	30	11
Adult female: infant present	71	12.87	6.92	4	30	10
Adult female: infant not present	94	14.10	7.79	1	30	11
Adult female: carrying infant	57	10.46	3.70	2	20	10
Adult male: total	166	13.91	7.24	0	35	10
Adult male: infant present	87	14.03	8.39	2	35	12
Adult male: infant not present	79	13.77	5.77	0	25	13
Sub-adult female	72	15.08	7.13	2	30	15
Infant	58	9.03	5.03	3	25	8.5
Total	849	13.31	7.13	0	35	11

Table 8.37. Duncan post-hoc test for mean heights (m) of individual *I. indri* while feeding.

	N	Subsets	
		1	**2**
Infant	58	9.03	
Adult female: carrying infant	57	10.46	
Adult female: infant present	71		12.87
Adult female: total	165		13.58
Adult male: infant not present	79		13.77
Adult male: total	166		13.91
Adult male: infant present	87		14.03
Adult female: infant not present	94		14.11
Sub-adult female	72		15.08
Subset significances		0.194	0.082

8.3.9.2. *Propithecus diadema*

A: Sex Differences in Resting, Travel and Feeding Heights

All known males and females were grouped together for analysis, regardless of individual. Male *P. diadema* rest and feed higher in the canopy than females (Figure 8.14 and Table 8.38), but females travel slightly higher in the canopy. These differences are not however significant: rest ($U = 61346$, $p > 0.05$ns); travel ($U = 96214.5$, $p > 0.05$ns) and feed ($U = 38879$, $p > 0.05$ns).

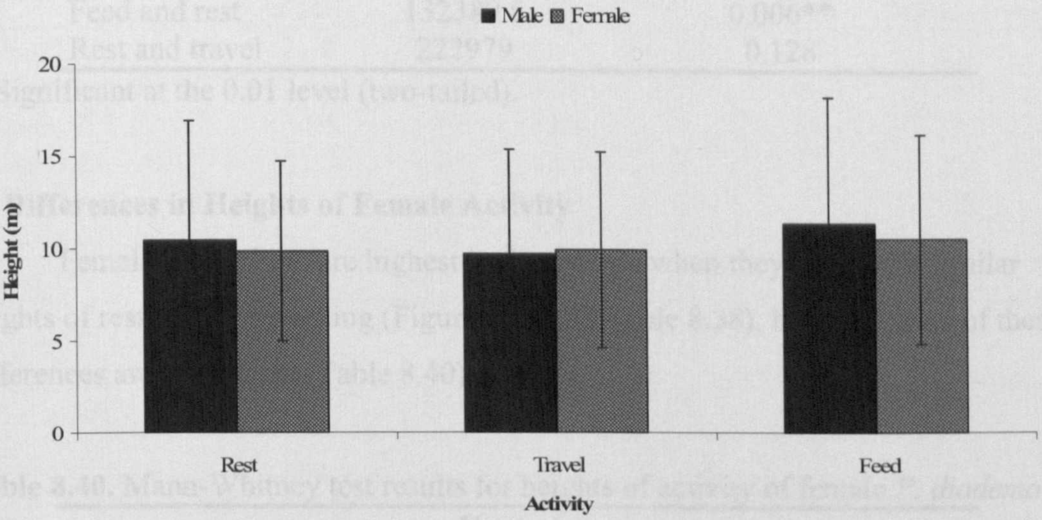


Figure 8.14. Sex differences in mean height (m) of resting, travelling and feeding for male and female *P. diadema*. Errors bars represent the standard deviation at the 95% level.

Table 8.38. Heights (m) of resting, travelling and feeding for male and female *P. diadema*.

Sex and activity	*N*	*M* (m)	*SD*	Min	Max	Median (m)
Male: resting	608	10.41	6.45	0	35	9
Male: travelling	770	9.68	5.715	0	35	8
Male: feeding	482	11.41	6.81	0	35	10
Female: resting	202	9.86	4.83	1	28	9
Female: travelling	263	9.94	5.31	1	30	9
Female: feeding	168	10.53	5.65	1	30	10
Total	2493	10.29	6.04	0	35	9

B: Differences in Heights of Male Activity

Male *P. diadema* are highest in the canopy during feeding and lowest during travelling, resting at an intermediate level (Figure 8.14 and Table 8.38). Males travel 2m (Table 8.39) below their median height of feeding (a significant difference) and feed approximately one metre above the height at which they rest (again, a significant difference) Although male *P. diadema* rest higher than they travel, this difference is not significant.

Table 8.39. Mann-Whitney test results for heights of activity of male *P. diadema*.

	U	*p*
Travel and feed	132389.5	0.006**
Feed and rest	132389.5	0.006**
Rest and travel	222979	0.128

**Significant at the 0.01 level (two-tailed).

C: Differences in Heights of Female Activity

Female *P. diadema* are highest in the canopy when they feed, with similar heights of resting and travelling (Figure 8.14 and Table 8.38), however none of these differences are significant (Table 8.40).

Table 8.40. Mann-Whitney test results for heights of activity of female *P. diadema*.

	U	*p*
Feed and rest	15894	0.292
Feed and travel	20515	0.209
Rest and travel	26350	0.882

8.3.9.3. Comparison between Heights of Activity for *Indri indri* and *Propithecus diadema*

I. indri are found higher in the canopy compared to *P. diadema* in all activity groups; rest, travel and feed (Figure 8.15 and Table 8.41). There are significant differences (Table 8.42) in the heights at which they rest, travel and feed; *I. indri* being higher.

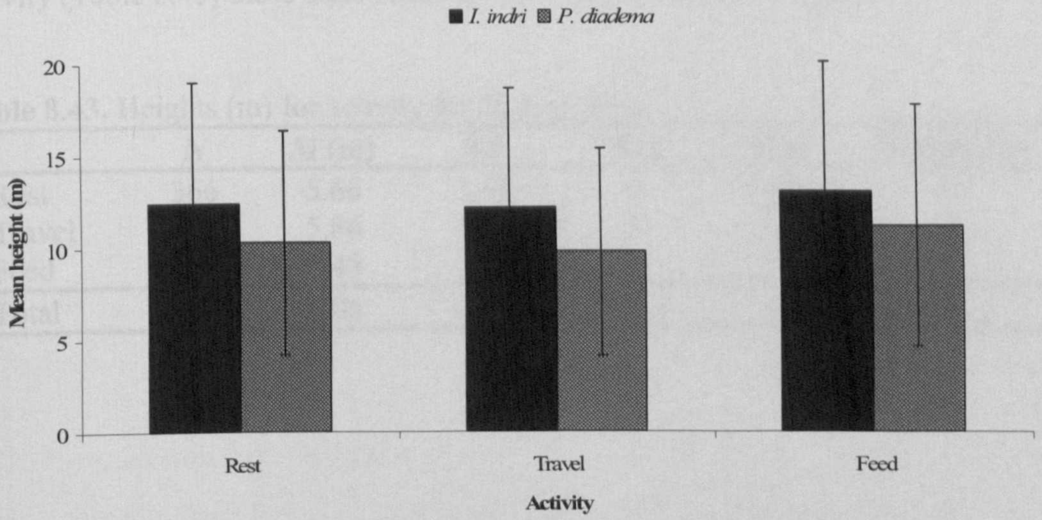


Figure 8.15. Comparison of mean height (m) of activity between *I. indri* and *P. diadema*, for all individuals and dates. Error bars represent the standard deviation from the mean at the 95% level.

Table 8.41. Comparison of heights (m) of activity between *I. indri* and *P. diadema*, for all individuals and dates.

	M (m)	*N*	*SD*	Min	Max	Median (m)
I. indri: rest	12.36	830	6.61	2	40	10
I. indri: travel	12.20	917	6.53	1	40	10
I. indri: feed	13.04	518	7.00	0	35	10
P. diadema: rest	10.27	810	6.09	0	35	9
P. diadema: travel	9.75	1034	5.61	0	35	9
P. diadema: feed	11.19	652	6.53	0	35	10
Total	11.32	4761	6.44	0	40	10

Table 8.42. Mann-Whitney tests for the difference in activity heights between *I. indri* and *P. diadema*.

	U	*p*
Rest	269297.5	0.000**
Travel	363784	0.000**
Feed	143358	0.000**

** Significant at the 0.01 level (two-tailed).

8.3.9.4. *Hapalemur griseus griseus*

There were also differences found in this study in the median heights of activity for *H. g. griseus* (Table 8.43) although there are no significant differences between heights of resting and travelling (Table 8.44). Feeding occurs higher than travelling or resting: significant differences are observed between heights of feeding and resting (by 1m) and feeding and travelling (by 1m). Although there are differences in median heights at which male and female *H. g. griseus* perform each activity (Table 8.45) these differences are not significant (Table 8.46).5

Table 8.43. Heights (m) for activity for *H. g. griseus*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Rest	366	5.66	3.69	0	20	6
Travel	682	5.86	3.34	0	20	6
Feed	670	6.49	3.67	0	17	7
Total	1718	6.06	3.56	0	20	6

Table 8.44. Mann-Whitney test for heights of activity in *H. g. griseus*.

	U	*p*
Feed and rest	106094.5	0.000**
Feed and travel	203599.5	0.001**
Rest and travel	119440	0.249

**Significant at the 0.01 level (two-tailed).

Table 8.45. Heights (m) for activity of male and female *H. g. griseus*.

	N	*M* (m)	*SD*	Min	Max	Median (m)
Male: rest	87	4.93	2.85	0	12	5
Male: travel	175	5.60	2.85	0	12	6
Male: feed	152	6.48	3.19	0	13	7
Female: rest	279	5.89	3.89	0	20	6
Female: travel	507	5.94	3.49	0	20	6
Female: feed	518	6.49	3.80	0	17	7
Total	1718	6.061	3.56	0	20	6

Table 8.46. Mann-Whitney tests for heights of activity between male and female *H. g. griseus*.

	U	*p*
Rest	10527	0.061
Travel	42299.5	0.357
Feed	38926	0.832

8.4. Discussion

8.4.1. Overall Heights

Mean heights of observation of *I. indri* (12.6m) are lower than those from a study at Analamazoatra, which found *I. indri* at a mean height of 14m (Pollock, 1977). Powzyk (1997) recorded *P. diadema* as utilising all levels within the forest from 0 to 30m, with a mean of approximately 10m, comparable to the mean height of 10.6m found in this study. At Analamazoatra Wright *et al.* (1987) recorded *H. g. griseus* at all heights, including on the ground. In this study the mean height of *H. g. griseus* was found to be 5.8m.

8.4.2. Comparison between Species

Significant differences were found in the mean heights of *I. indri* (12.6m) and *P. diadema* (10.6m). Although Powzyk (1997) recorded that *I. indri* were observed higher in the canopy than *P. diadema*, this difference did not achieve statistical significance. Although *I. indri* and *P. diadema* both use the entire vertical structure of the forest, having the same minimum (0m) and maximum (51m) heights, the two-metre difference in mean height of observation signals a substantial degree of niche separation between the two indriids. Ganzhorn (1989) found that where height acts as a niche separator between two sympatric species, dietary content was similar. It might therefore be assumed that *I. indri* and *P. diadema* do not choose different foods based on their chemical content. Height differences have been found to act as a niche separator between *Galago moholi* (southern lesser bushbaby), found at a mean 2.97m and *Otolemur crassicaudatus* (6.46m [thick-tailed greater bushbaby]) in South Africa (Crompton, 1980). Further, *Lepilemur edwardsi* (Milne Edwards's sportive lemur) was found at a mean height 1m lower than *Avahi occidentalis* (western woolly lemur [Warren & Crompton, 1997b]), a statistically significant difference linked to niche separation.

Further *H. g. griseus* are also found lower than both the larger indriids. As noted in the introduction, niche separation in sympatric diurnal primates is often achieved through vertical height separation (see e.g. Peres, 1993; Lopes & Ferrari, 1994; Ungar, 1996; Singh *et al.*, 2000; Buzzard, 2006). Peres (1993) found height to be correlated with body weight; smaller species being found lower in the canopy, larger species higher. This relationship is found here too: the smaller *H. g. griseus* (~800g) is found lowest in the canopy and the largest species *I. indri* (~7kg) highest. Although home ranges did not overlap, *H. g. griseus* observed on an ad-hoc basis within the ranges of *I. indri* and *P. diadema* were also at a lower height. The primary food source for study groups of *H. g. griseus*, *Cathariostachys madagascariensis* (giant bamboo) has a maximum height of approximately 6m and *Cephalostachyum* cf. *perrieri* (vine bamboo) was observed to primarily grow at low levels; although *H. g. griseus* are capable of going higher in the canopy, there is little reason for them to do so. The vertical height separation between *I. indri* and *P. diadema* is more difficult to explain. It is possible that risk from aerial predation may play a part. Larger adult *I. indri* may well be at lower risk of raptor predation than the smaller *P. diadema* and may therefore be liable to remain higher.

8.4.3. Seasonal Changes

There are significant differences in mean heights of *I. indri* through the study period. Mean monthly heights were lower at the start of the study (February [10.1m] to April [11.93m]), compared to the end (October [17.7m]). This has a number of potential causes. Seasonality is known to affect the vertical spatial usage of primates (Siemers, 2000) and the group could occupy lower levels in warmer months to avoid direct solar radiation but higher levels in colder months to benefit from direct solar radiation. Alternatively the presence of the infant (February to May) could have resulted in lower heights being adopted by the entire group, potentially as a result of an increased predation risk from aerial predators. Seasonal variation has been observed for *I. indri* in Anjanaharibe-Sud, where *I. indri* were found lower in the canopy in November and December as a response to the presence of biting horseflies (Thalman *et al.*, 1993).

Although monthly means differed (from 8.3 to 12.1m) no distinct pattern of seasonality in monthly mean heights was found for *P. diadema*. Neither could a direct seasonal effect on monthly mean heights of *H. g. griseus* be found. Monthly means had a wide range (4.3 to 10.5m) but low and high means were found in consecutive months (December and January).

8.4.4. Diurnal Changes

Diurnal height changes are observed in *I. indri*. There is a peak in heights around midday (11:00 to 13:59). *P. diadema* are similar, although they reach a peak in heights earlier (09:00 to 11:59). Both species appear to take nightly rest lowest in the canopy, moving higher throughout the morning before decreasing their heights towards the time of rest in the afternoon. Heights of nightly rest spots can be inferred from early morning heights and suggest that *I. indri* rest higher (12.6m) than do *P. diadema* (8.0m). This difference is greater than the 2m mean height difference between the two species, and nightly rest locations are 2m lower than the overall mean height for *P. diadema*; but for *I. indri* the mean height of nightly rest is comparable to their overall mean height. The lower nightly rest height for *P. diadema* is not one would naturally expect from known predation patterns. Neither species will be at risk of predation from nocturnal raptors as no owl is large enough to take either of them, so there is no benefit to being lower in the canopy at night. However *Cryptoprocta ferox* (fossa) are known to predate *P. edwardsi* at Ranomafana during the night (Wright 1995; Wright, 1998) and might be expected to predate *P. diadema* in a similar manner. Powzyk (1997) considered the disappearance of an infant *I. indri* during the night was due to *C. ferox* predation. *C.*

ferox are a terrestrial predator, but with climbing ability, and it would appear that the lower an animal the rested the greater the risk from *C. ferox*. It is possible that the apparent absence of *C. ferox* in the study area has removed the risk, but why they should therefore rest lower is unknown.

The pattern for *H. g. griseus* is reversed. In the early morning (05:00 to 08:00) they are high in the canopy, reaching a low mean height at mid-day (11:00 to 14:00). They may move and rest high in the canopy early in the day in order to aid with warming up after the night. The mid-day low approximates the period of their long mid-day rest. This suggests that they may rest low in the canopy during the day, as a tactic for avoiding aerial predators. Indeed in their daily rests the group would be found 'clumped' together in a dense tangle of vegetation. However at night the groups are found at high levels. From this it could be inferred that *H. g. griseus* perceives diurnal raptors as a threat, but that they are not concerned about nocturnal raptors. The potential effect of terrestrial predators is harder to quantify. If a predator detected prey by sight or by its movements, then during the day *H. g. griseus* would be protected by 'hiding' in vegetative tangles. At night their higher resting-level might suggest that there is a greater risk of predation from below.

8.4.5. Individual Differences

The main differences when examining mean heights of individual *I. indri* relate to the impact the infant had on heights. The infant, and the adult female while she was carrying the infant, were observed at the lowest mean height (10m). The adult male, and the female (when not carrying the infant) but while the infant was present, were also observed relatively low down, the female substantially lower than the male (11.7 versus 12.2m respectively). Subsequent to the infant's disappearance the adult female and male were observed significantly higher in the canopy (14.0 and 13.5m respectively) and at the same height as the sub-adult female (14.3m). The most obvious explanation of these findings is a threat of predation on the infant from diurnal raptors. No differences were found between mean heights of male and female *I. indri*.

No significant differences were found in the mean heights of male and female *P. diadema*. However, the adult female, during the period she was carrying the infant, and at times within this period when she was carrying it, was observed significantly lower than the rest of the group (10.2 compared to 11.6m). Similarly to the case in *I. indri* it is probable that this reflects the risk of diurnal-raptor predation on the infant. It is of course possible that the risk of injury incurred from an uncoordinated infant falling, would lead to a decrease in the height of a female with an infant. There is little difference in falling from 10 or 12m; the infant will still be injured. Further *Lemur catta* (ring-tailed lemurs) mothers are known to abandon infants that fall regardless of whether the infant has survived (Day, S. pers. comm.). An infant that falls may be regarded as weak and therefore not worth further energetic expenditure by to the mother.

The most striking difference between *I. indri* and *P. diadema* in 'parenting' is that while the infant was present in the *I. indri* group, all individuals moved lower, whereas in *P. diadema* only the adult female carrying the infant was lower. This can possibly be explained by social structure and life history. Adult *I. indri* form monogamous pairs and there is a low interbirth-interval (3 years) suggesting that a high degree of parental investment is likely. However *P. diadema* have a multi-male, multi-female sociality and can bear infants annually so there is less need for investment by the group.

Unlike the findings of Grassi (2002), where females were found lower in the canopy than males, no significant differences were found in heights of male and female *H. g. griseus*. This could be due to observer bias in the sample size: there were 1304 female records compared to 414 male records.

8.4.6. Locomotor Heights

There is a clear stratification of mean heights of observation of each of the four main locomotor modes of *I. indri*: leap at a mean of 10.7m, vertical climb and hop at 12.9 and 13.5m respectively, cantilever at 14.8m and quadrupedal walking at 16.7m. The same separation is observed for *P. diadema*; leaping at a mean 10.0m; vertical climbing at 11.3m, hopping at 12.2m and cantilevers and quadrupedal walking at 13.3 and 14.1m respectively. These differences can be linked with differing support preferences for each mode of locomotion and support availability, as discussed in Chapter 2. Briefly, leaping is preferably carried out on branch-free vertical supports, mostly found at mid-levels, while quadrupedal walking requires horizontal supports mostly found in the upper canopy.

Significant differences are observed in locomotor mode heights between *I. indri* and *P. diadema*. *I. indri* were observed significantly higher than *P. diadema* during leaping (by 0.7m), cantilevering (by 1.4m), vertical climbing (by 1.6m), and in quadrupedal walking (by 2.6m). *P. diadema* were observed significantly higher than *I. indri* only for two-handed suspension (by 3.7m). No significant differences were observed for hopping, four-handed suspension and dropping. The lack of significance in the latter three modes is likely to be due to a combination of low numbers of data points and small mean height differences.

To a substantial degree the significant differences in locomotor height can be viewed as a reflection of the overall difference in mean height between the two species; *I. indri* are observed at on average two metres higher than *P. diadema*. However the variations in the mean height differences between locomotor modes are interesting. Although significant, there is more similarity between the heights at which both species leap compared to heights at which they perform all other locomotor activities. This would indicate there is a smaller range of appropriate heights within the canopy for leaping compared to all other locomotor modes. The smaller difference in mean heights of leaping is even more notable since it is the predominant locomotor mode for both species. More substantial height differences in locomotor mode, including leaping, were found between *Avahi laniger* and *Lepilemur occidentalis* (Warren, 1994; Warren & Crompton, 1997b), suggesting that forest structure differs in the two sites.

H. g. griseus use different locomotor modes at different heights. Leaping (at a mean 4.9m) and vertical climbing (at 5.1m) were observed to occur lowest; running (at a mean 6.3m), quadrupedal walking (at 6.9m) and cantilevers (at 7.3m) at mid-height and foliage crossing (at a mean 8.2m) highest. These differences can be linked with support preference and availability, discussed in Chapter 2. Leaping and vertical climbing require vertical branch-free supports, most common low down, whereas foliage crossing is best suited to movement on the smallest (<0.5cm) supports, commonly found in the tops of trees.

8.4.7. Heights and Activity

Powzyk (1997) found that *I. indri* rested at a mean of 11.82m, travelled at 9.51m and fed at 12.70m. At Betampona however, the main feeding height was between 5 and 20m, only 0.7% of feeding bouts occurring above 25m (Britt *et al.*, 2002). A significant difference was found in the present study in the heights at which *I. indri* travelled and fed; travelling low down (mean 12.2m) but feeding high (mean

13.0m). The main mode of locomotion while travelling is leaping, at 81% of all bouts, and this can occur most readily low down, between branch-free tree-trunks. However feeding concentrates on resources found in the tree-tops: leaves, fruit and flowers.

The individual pattern for travelling and feeding in *I. indri* is the same as for individuals analysed as a whole. However there is a dramatic effect when comparing feeding. The infant and adult female while carrying the infant, are again found lowest. This difference between activities is the only statistically significant one, regardless of whether or not the infant was present. This suggests a lower flexibility in the choice of heights by group members while feeding. It also indicates that the adult female was potentially sacrificing food sources while carrying the infant in order to ensure its safety from predation (or falling).

Powzyk (1997) found that *P. diadema* rested at a mean 10.67m, travelled at 10.09m and fed at 10.92m. *P. diadema* living in continuous forest in Tsinjoarivo fed preferentially at a mean of 13m, rested and performed social activities between 9 and 10m, and travelled at 8 to 9m, although no statistical testing were performed (Irwin, 2006b). In the present study no significant differences were found in the heights at which male and female *P. diadema* were observed in the canopy for any activity, but male (but not female) *P. diadema* were found higher while feeding (mean 11.4m) than when travelling (mean 9.7m) and resting (mean 10.4m). This pattern agrees with that reported by Powzyk (1997) and Irwin (2006b).

I. indri were observed significantly higher than *P. diadema* for all activities: resting (by 2.1m), travelling (by 2.45m) and feeding (by 1.85m), stressing that height appears to be acting as a niche separator between the two species. Niche separation is especially important during feeding, where there is dietary overlap (Ungar, 1996). However the two species were closer in height during feeding than during any other activity, which would militate against a dietary difference related to height as they are eating the 'same' food. Ganzhorn (1989) found that where lemurs used the same microhabitat the chemical composition of their food differed, while species choosing food containing the same plant chemicals differed in their microhabitat. This relative similarity in feeding height would therefore indicate that the two species do differ in the chemical content of their diet.

H. g. griseus at Ranomafana fed most often at between 7 and 10m in the canopy, and were rarely observed in the upper canopy (Grassi, 2002). Females tended to feed lower, adult males above them and sub-adult males highest. Females were found most often between 0 and 5m, all sexes between 6 and 10m, adult males between 11 and 15m and sub-adult males over 16m (Grassi, 2002).

In the present study, significant differences were found between mean heights of different activities in *H. g. griseus*. Feeding (mean 6.5m) is observed significantly higher than travel (5.9m) and rest (5.7m). That rest occurs lower in the canopy could again suggest a requirement for protection against raptor predation. Again, that travel occurs relatively low down stresses the role of leaping in lateral movement, despite the greater role of quadrupedalism in this species than in the two indriids.

8.5. Summary

Hypothesis 8.1 held that: niches of *I. indri* and *P. diadema* will be differentiated in part by height or stratum

This is upheld: *I. indri* were found significantly higher (12.62m) compared to *P. diadema* (10.55m).

Hypothesis 8.2 held that: *P. diadema* will travel lower down in the canopy, where discontinuities are larger but fewer, to maximize travel speed.

This is upheld; *P. diadema* travelled at a mean height of 9.75m, while *I. indri* travelled at a mean height of 12.20m.

Hypothesis 8.3 held that: *H. g. griseus* will occupy a lower stratum than either of the indriids.

This is upheld: *H. g. griseus* were found at a mean height of 7.78m, lower than that of both *I. indri* (12.62m) and *P. diadema* (10.55m).

Hypothesis 8.4 held that: All three species will be found lower in the canopy during the summer to avoid excessive heat.

This is not upheld: No seasonal trend was found in height utilisation for any species. Differences in heights of *I. indri* over time are most likely due to the presence (or absence) of the infant and not due to seasonal effects.

Chapter 9 Locomotion

Locomotion interacts with many ecological and life variables: it enables animals to access food, and to avoid becoming food for other animals; it enables animals to locate mates. Its interactions with variables such as body size exert ecological and behavioural influences not only between species, but between sexes and age-categories (see e.g. Oxnard et al., 1990; Crompton & Sellers, 2007). This chapter analyzes the differences in locomotion between the three species, but since all three fall into Napier and Walker's (1967) 'vertical clinging and leaping' locomotor category, the category is reviewed at the beginning of the chapter, followed by a brief discussion of a major focus of this chapter, the mechanics of prosimian leaping as they relate to substrate use, which provides most of the Hypotheses 9.1-5, to be tested. Definitions of locomotor modes used within this study are provided before proceeding to results and discussion of the observations made in this study.

9.1. Vertical Clinging and Leaping

Vertical clinging and leaping was first described by Napier and Walker (1967) as a mode of locomotion used by arboreal animals adapted to leaping, with a vertical clinging posture at rest, and where hind limbs provided most propulsion. They attributed this mode to prosimians including *Tarsius* spp. (tarsiers), *I. indri*, the indri, *Propithecus* spp. (sifaka and simpona), *Avahi* spp. (woolly lemurs), *Lepilemur* spp. (sportive lemurs), *Prolemur simus* (greater bamboo lemur), *Galago* spp. (bushbabies) and *Euoticus* spp. (needle-clawed bushbabies). Napier and Walker (1967) suggested that as vertical clinging and leaping is found amongst extinct Eocene primates, it might have been the earliest locomotor specialisation of the primates, pre-adaptive for other modes such as quadrupedalism, brachiation and bipedalism, found in most other primates. They proposed a series of anatomical traits of vertical clingers and leapers: typically small to medium sized primates; hindlimbs capable of extended ranges of flexion and extension and elongated relative to forelimbs, which are short, giving a high brachial index. Oxnard *et al.* (1989) demonstrated that the category conflates rather distinct locomotor adaptations and leaping styles, and advocated a quantitative rather than qualitative approach to locomotor studies. Crompton *et al.*

(1993) further distinguished mechanically specialized and unspecialized prosimian leapers, with respect to takeoff trajectory and choice of takeoff and landing supports.

Leaping locomotion is acyclic and hence expensive: it may be may be seven times more expensive than level running (Demes *et al.* 1995; 1999). Theoretically, energy requirements might be decreased if kinetic energy was stored as elastic energy between subsequent leaps, as might be possible in richochetal leaping of indriids, or returned from external energy stored in compliant branches (Warren & Crompton, 1998). Neither possibility has yet been tested experimentally or under field conditions. The latter is probably less likely to occur: energy stored in a compliant branch during foot contact cannot be returned unless recoil occurs before the animal loses contact with the substrate, a situation that has only been demonstrated so far for branch-swinging in orang-utans (Thorpe *et al.*, 2007).

As Demes and Günther (1989) point out, leaping presents different problems to small and large leapers: small leapers have a large cross-section of muscle (and hence, muscle force) relative to body mass, but short limbs with which to accelerate their centre of mass at takeoff and (by resistance to limb flexion) decelerate it on landing and hence avoid high peak landing forces, although landing forces are lower than those at takeoff (Demes *et al.* 1999). They tend to accelerate with high forces over short time periods. The inverse applies to large bodied leapers, but their problems are complicated by the dietary correlates of large body mass: folivory is more common at large body size and yet folivores, especially arboreal folivores (McNab, 1978) tend to have relatively little muscle compared to body mass. For a large leaper the problems of limited muscle and force generation capacity, on the one hand, and limited bone cross-section (and hence strength) on the other suggest that since support compliance implies loss of energy to the support (increasing takeoff costs but reducing peak force on landing) **Hypothesis 9.1: the (large bodied) indriids will use small, compliant, supports for landing leaps to absorb energy and will use larger, less compliant, supports for take-off to minimise energy loss,** although when Demes *et al.* (1995) examined leaping in wild *I. indri* and *Propithecus edwardsi* (Milne-Edward's simpona) they suggested a preference for small diameter supports for both takeoff and landing.

Demes *et al.* (1995) also found that smaller bodied *H. g. griseus* had relatively higher takeoff and landing forces than the larger *Propithecus verreauxi* (Verreaux's sifaka), indicating that takeoff and landing forces decrease with increased body mass (Demes *et al.*, 1999). Similarly, younger animals generate higher relative forces, which could be a factor of their smaller body or lack of neuromuscular experience (Demes *et al.*, 1999). Thus, **Hypothesis 9.2: the relatively higher take-off and landing forces predicted to be incurred by *H. g. griseus* should result in the use of smaller landing, but larger take off supports compared to *I. indri* and *P. diadema* during leaping.**

Demes *et al.* (1999) claim that specialist leapers generate less force than generalist species; probably due to longer hind limbs, and found that their specialists (*I. indri* and *Propithecus* spp.) preferred small vertical substrates, while generalists (*Lemur catta* [ring-tailed lemur]) chose horizontal supports, thus **Hypothesis 9.3: *I. indri* and *P. diadema* will use vertical supports more than the (presumed) less specialized *H. g. griseus*** and **Hypothesis 9.4: that as the supposedly more specialized leaper (Oxnard *et al.*, 1990) *I. indri* will use vertical take-off, and perhaps landing, supports more than *P. diadema*, to permit ballistically optimal, more efficient leaps, where an orthograde body posture both locates the centre of gravity located along or near a ballistic trajectory from the hindlimb, and also directs force along the more stable long axis of the support.**

There has been an assumption that all leaping primates will adopt high-trajectory ballistic paths which minimise both energy costs and loads applied to the body; however experimental and field studies have shown that this is not necessarily the case and ecological factors such as support availability and flight time may be a primate's main consideration (Crompton *et al.*, 1993; Crompton & Sellers, 2007). Further, in a previous study of smaller-bodied leapers neither *Otolemur crassicaudatus* (thick tailed greater bushbaby) nor *Tarsius bancanus* (western tarsier) selected larger diameter takeoff supports with increasing jump length (Crompton *et al.*, 1993). Leaps over 1.6m in *Galago moholi* (southern lesser bushbaby) were however made from larger initial supports than shorter jumps, and *T. bancanus* did use larger terminal supports in longer jumps. Crompton *et al.*, (1993) hypothesised that this was due to the requirements of a stable landing support for this small-bodied species which lands feet first; thus **Hypothesis 9.5: for all three species longer leaps will end on larger, more stable supports to provide a safer landing**. For bushbabies and tarsiers longer jumps in general resulted in a height gain, but in shorter jumps a loss of height (Crompton *et al.*, 1993). Crompton *et al.* (1993) suggested that leaping may be an energetically more efficient way of changing height than climbing. An apparent tendency for flatter trajectories in unspecialized leapers (Crompton *et al.* 1993) may relate also to body design: animals which are strongly hindlimb dominated, and can flex their hindlimbs deeply, can more easily locate their centre of mass directly in line with the energetically optimum 45^O takeoff directory (Crompton *et al.*, 1993). The link between vertical clinging and leaping is a related phenomenon: orthograde body posture makes it easier to accelerate the body centre of mass into a high, energetically optimal trajectory and may direct more of the takeoff force along the stiffer axis of the takeoff support (Crompton & Sellers, 2007).

9.2. Methods

9.2.1. Field Observations

Locomotor observations (Table 9.1) followed the approach of Warren and Crompton (1997a). For the purpose of this study records were collected *ad libitum* on all individuals in a group, independent of age or sex. It was not always possible to identify the individual involved in a recorded locomotor bout; however, individual identification was recorded where possible. Of all species, *I. indri* was the easiest for which to identify individuals and the majority of locomotor bouts were recorded for known individuals. Individuals of *P. diadema* and *H. g. griseus* were harder to distinguish. Unless exceptionally obvious (e.g. a collared animal or female carrying young) identification of individuals of these species was difficult and was not attempted for the purposes of observations of locomotion. (NB: in the text below "previously collared male" refers to an individual *P. diadema* which was found to be collared at the start of the study. It is thought that this individual was collared by Powzyk [1997]. However, if so, as the study area of Powzyk was further north than that in the present study, this male must have migrated into this group.)

Locomotor modes were based on categories taken from Warren and Crompton (1997a), but refined so as to be more accurate descriptors of the present study species. Additional locomotor modes were added as required. Full definitions of each mode can be found below.

Table 9.1. Schedule of locomotor observations

1	Date
2	Species and individual identification where applicable
3	Time
4	Locomotor mode (see section 9.2.2)
5	Initial support diameter (Table 9.2)
6	Initial support orientation (Table 9.3)
7	Terminal support diameter (Table 9.2)
8	Terminal support orientation (Table 9.3)
9	Initial height (m)
10	Terminal height (m)
11	Horizontal distance travelled (m)
12	Activity
13	Continuous from previous? (yes/no)
14	Notes

Support diameter (Table 9.2) and orientation (Table 9.3) classes were taken from Warren and Crompton (1997a), definitions again being altered slightly to suit the present study. Modes of locomotion beginning or ending on the ground were classed as being from or to ">15.1cm", horizontal supports as appropriate.

Table 9.2. Categories of support diameter.

Support diameter categories
0 to <0.5cm
0.6 to 5cm
5.1 to 10 cm
10.1 to 15 cm
>15.1cm (includes ground)

Table 9.3. Definitions of support orientation

Name	Definition for purposes of this study
Horizontal	-10° to 10° (includes ground)
Oblique	11° to 45° and -11° to -45°
Angle	46° to 80° and -46° to -80°
Vertical	81° to 90° and -81° to -90°
Fork	Two or more supports
Foliage	Multiple very small (<0.5cm) supports

9.2.2 Definitions and Descriptions of Locomotor Modes

Locomotor modes are discussed here only when relevant to one of the three study species. Category names used were based on Warren and Crompton (1997a), and defined according to Preuschoft *et al.* (1989) and particularly the standardized locomotor categories defined by Hunt *et al.* (1996). Where appropriate the codes assigned to each mode by Hunt *et al.* (1996) are given in brackets.

9.2.2.1. Vertical Climbing

Preuschoft *et al.* (1989) define Vertical Climbing as locomotion on a vertical or steeply inclined substrate, or using a series of hand and foot holds at various levels. Inherent in climbing is a gain or loss of height (Preuschoft *et al.*, 1989). While Preuschoft *et al.* (1989) subsume suspension in this category, for the purposes of this study suspension was held separate. Hunt *et al.* (1996) separate vertical climbing (L8) into 12 categories, which include three observed in this study: 'flexed-elbow vertical climb' (L8a) is described as ascending on substrates angled at greater than, or equal to, 45° to the horizontal. The body is orthograde and almost parallel to the support, forelimbs elevating the body and propulsion provided by hind-limbs; 'Pulse climb' or 'vertical bounding' (L8e) is defined by Hunt *et al.* (1996) as ascent of supports angled at equal or greater than 45°, where the forelimbs grasp the support as hindlimbs are gathered underneath and push back to propel the body upwards (Hunt *et al.*, 1996). This behaviour was categorized as hopping during the present study. 'Rump first descent' (L8g) is vertical quadrupedal descent of a support angled at equal or greater than 45° (Hunt *et al.*, 1996).

9.2.2.2 Leaping

Leaping is described by Preuschoft *et al.* (1989) as covering distances in free flight, and by Connour *et al.* (2000) as hindlimb-propelled jumping. Hunt *et al.* (1996) combine these factors, adding that hindlimbs and back are flexed and forcefully extended, often aided by the forelimbs. Take-off and landing can be on vertical or horizontal supports, including the ground, and acceleration at take-off and controlled deceleration on landing is implied; during free flight, rotation is possible, where hindlimbs swing from the back to the front of the body to break the impact of landing (Preuschoft *et al.*, 1989).

Connour *et al.* (2000) characterises leapers by an ability to bipedally hop, cling vertically, and maintain a vertical body posture during leaps. The latter is however true only for the most specialized prosimian leapers (Oxnard *et al.* 1989). Oxnard *et al.* (1989) distinguished three groups of leapers, each with a different method of leaping; specialist leapers with an elongated femur (indriids, *Hapalemur* spp. [bamboo lemurs] and *Lepilemur* spp.), generalists which occasionally leap (galagine-cheirogaleine group [except *Galago moholi* and *Galago alleni* {Allen's squirrel bushbaby}], with *Varecia* spp. [ruffed-lemurs], *Eulemur* spp. [true lemurs] and the Cheirogaleinae [dwarf and mouse lemurs]), and specialist leapers with an elongated foot (*Galago*-tarsier group, i.e. tarsiers plus *G. moholi* and *G. alleni*). Only the two groups of specialized leapers usually land hindlimb first.

The study species all utilised 'vertical clinging leaping' (L12c [Hunt *et al.*, 1996]); where the leap begins with a torso-orthograde clinging posture on a relatively vertical support, pushoff being predominantly hind limb powered.

9.2.2.3. Quadrupedal Walking

Preuschoft *et al.* (1989) describe the mode 'Quadrupedal Walk' as locomotion on a more or less level substrate using alternating left or right fore- and hindlimbs for support; the sequence of footfall being variable. Hunt *et al.* (1996) note that usually all four limbs contact the support in a particular sequence, distinguishing symmetrical (L1a) and asymmetrical (L1b) gaits: in this study gait was found to be symmetrical (L1a), with a diagonal sequence. Hunt *et al.*, 1996 note that in Quadrupedal Walk the torso is held roughly parallel to the support

9.2.2.4. Quadrupedal Running

Quadrupedal running is a faster version of quadrupedal walking, where there is a period of free flight (L5 [Hunt *et al.*, 1996]).

9.2.2.5. Bipedal Walking

Hunt *et al.* (1996) describe this as walking where support and propulsion is provided by the hindlimbs, with insignificant contributions from other parts of the body (L3a). In the case of *I. indri* and *P. diadema*, arms were also used for balance, holding onto supports above or to the side (cf. the 'hand-assisted bipedality' of orang-utans [Thorpe *et al.*, 2007]).

9.2.2.6. Two-handed Suspension or Brachiation: Torso-Orthograde Suspensory Locomotion

Hunt *et al.* (1996) describe these as hand over hand orthograde suspensory locomotion where forelimbs bear more than half of the body weight (L9a). The trunk rotates almost 180° (Hunt *et al.*, 1996), the humerus is often strongly abducted and the elbow, strongly extended.

9.2.2.7. Four-Handed/Footed Suspension or Inverted Quadrupedal Run: Torso Pronograde Suspensory Locomotion

In this mode, according to Hunt *et al.*, 1996 all four hands/feet are used with limbs in tension (L10a). The torso is pronograde, or roughly parallel to the support (Hunt *et al.*, 1996).

9.2.2.8. Cantilevering or Bridging

"A gap-closing movement where hands reach out to grasp a support on one side of a gap and cautiously pull the body across the open space with the feet retaining their grips until a secure position is established on the other side" (L11a [Hunt *et al.*, 1996]).

9.2.2.9. Foliage Crossing

Quadrupedal locomotion where an animal reaches across a gap to grasp foliage (less than 0.5cm in diameter) with one hand, slowly moving the other limbs across one at a time (Warren, 1994; Warren & Crompton, 1997a).

9.2.2.10. Dropping

A 'drop' is achieved by falling after releasing the support with no substantial muscle propulsion (Hunt *et al.*, 1996). *I. indri* and *P. diadema* performed 'bimanual suspensory drops' (L13d), where suspension prior to the drop was by both forelimbs.

9.2.2.11. Kangaroo Hop

A series of jumps along a continuous support, where only the hind limbs are in contact with the support (Warren, 1994; Warren & Crompton, 1997a).

9.2.11 Statistical Analyses

Pearson's Chi-Squared (χ^2) is often used to determine the presence of a statistical association between nonparametric, ordered, nominal variables. A positive Pearson Chi-Squared result only indicates that there is an association between two variables. It does not indicate the strength or direction of that association. Pearson's Chi-Squared spans from *p* equal to 0 to *p* equal to 1, where 0 demonstrates the two variables are associated and 1 that they are not (Kinnear & Gray, 2004). Pearson's Chi-Squared test involves forming a table (cross-tabulation) of two variables each with two or more categories (Kinnear & Gray, 2004). Due to a requirement for the data to be naturally ordered, in analyses in this chapter the 'fork' and 'foliage' categories have been excluded from this analysis. Difficulties with Pearson's Chi-Squared arise with low expected values. It is suggested that results are not valid when, in the case of tables greater than two by two, the expected cell frequencies are less than 1, or where more than 20% of cells have expected frequencies less than 5 (Kinnear & Gray, 2004). Comparing the standardized residuals from cross-tabulations offers the best indication of association, with values over 2 (or -2), indicating a difference from the expected.

To examine the strength of the association further another statistical parameter, Cramér's V, was calculated. This is especially suitable in tables with more than two variables in each category, because it still achieves a maximum value (1.000) of unity (Kinnear & Gray, 2004). Cramér's V gives a value of 0 to 1, where 0 shows there is a weak association between the variables and 1 a strong association (Kinnear & Gray, 2004).

Further, as an exploratory tool to examine the influence of multiple factors on individual variables, log-linear analysis has been essayed, following the approach of Thorpe and Crompton (2005) and Thorpe *et al.* (2007) which may be referred to for the rationale and detailed method, only covered briefly below. Log-linear modelling is particularly suitable for the 'messy' and often not-naturally-ordered categorical data which result from fieldwork, since data does not need to originate from a normal population (Crook, 1997). Similar to Chi-Squared actual cell counts are compared to expected values and no (or as few as possible) cells should by empty (Thorpe & Crompton, 2005): the 'zero-zero' rule. This often requires variables with more than two categories to be collapsed, or conflated, a somewhat arbitrary process which requires biological judgement. This process requires multiple testing with different groupings (e.g. height grouped by 5m, 10m, and 20m intervals) in order to find the most effective explanations. The process seeks to find significant (greater than 0.05) variable combinations. Standardized χ^2 values are obtained for each significant combination of variables, allowing them to be ranked.

To test for similarities between *H. g. griseus* Groups One and Two, to see if the data from both groups could safely be analysed together, Pearson Chi-Squared values were obtained for group against each factor tested. No association was found between group and support usage and there was only a weak association between group and locomotor mode ($p < 0.014$ and $V = 0.045$). There is no significant relationship between group and horizontal distance travelled (U [7784] = 7376536, $p < 0.05$). The above findings permit Groups One and Two to be analysed together.

Since horizontal distance alone ignores the most energetically expensive element of locomotion, motion against the gravity vector, horizontal and absolute vertical height change for each locomotor bout were used to calculate a mechanically effective bout length based on Pythagoras:

$$c = \sqrt{(a^2 + b^2)}$$

Equation 9.1. Pythagoras' theorem, where ***c*** is the mechanically effective bout length, ***a*** the vertical height change (in meters) and ***b*** the horizontal distance travelled (in metres) for any given locomotor bout.

This was used only to determine metres per kilometre travelled in each locomotor mode. 'Raw' vertical and horizontal heights were used for all analysis.

9.3. Results

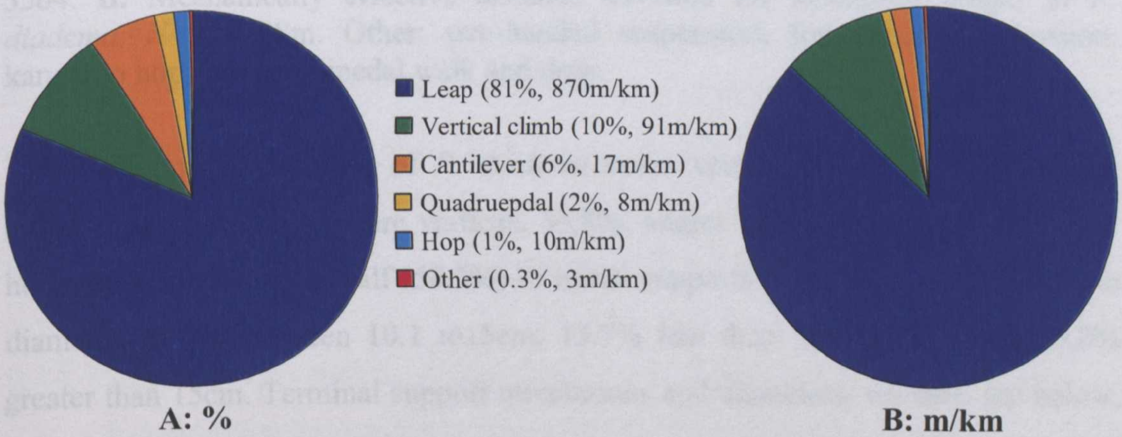
The first task is to provide descriptive statistics for comparison of the locomotor repertoire of the three subject species. Can the two large bodied indriids validly be described as vertical [clingers and] leapers; and how specialised, or generalist is *H. g. griseus* in its locomotion? Raw horizontal travel distance will be investigated to observe which modes of locomotion contribute most to travel distances. This is followed by an examination of vertical spatial usage: which locomotor modes are utilised to achieve height change, and which are used most often for negative (downward movement) or positive (upwards movement) change? The relationship between support use and height is then investigated; asking if there is a within-species relationship between support use and height within the canopy.

Categorical (Log-linear) Modelling and other techniques are then used to explore relationships between species, locomotion, stratum and support use. The results section then explores the key topic of within-species relationships between support use and locomotion, including the relationship of leap length and support characteristics, before an examination of the relationship between locomotor mode and activity.

9.3.1. Locomotor Descriptions

9.3.1.1. *Indri indri*

The predominant mode of locomotion for *I. indri*, in terms of frequency, is leaping, which comprises 81% of all recorded bouts (Figure 9.1 A). The remaining 19% is comprised of seven locomotor modes, of which the most frequent were vertical climbing (10%) and cantilevering (6%). Leaping becomes even more important when considering the mechanically effective distance travelled in each locomotor mode (Figure 9.1 B).



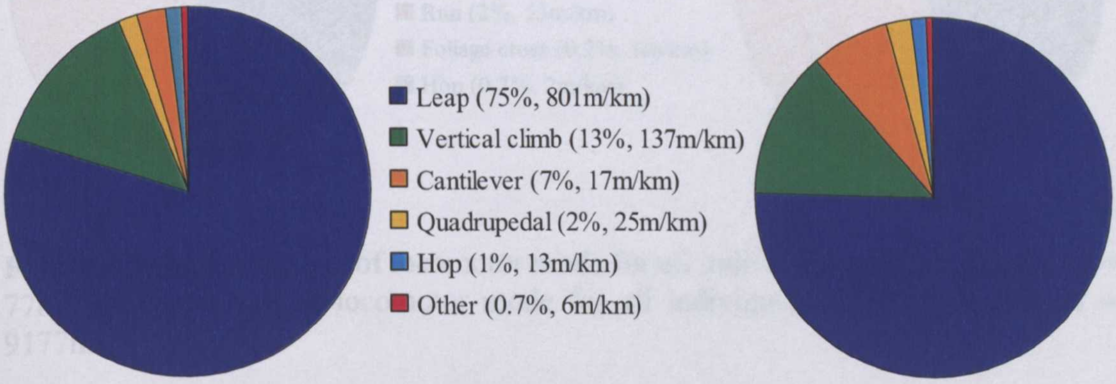
A: % **B: m/km**

Figure 9.1. **A:** Percentage of locomotor mode for all individuals of *I. indri*. $N = 3812$ bouts. **B:** Mechanically effective distance travelled for locomotor modes in *I. indri*. $N = 9310$m. Other: two- and four-handed suspension and assisted bipedal walking.

The use of initial support orientations are verticals 40.6%, angles 23.5%, obliques, 23% and horizontals 12.9%. Over half (50.5%) of initial supports lie between 5.1 to 10cm in diameter, 30% between 10.1 to 15cm, 12.1% greater than 15cm, and only 7.4% less than 5cm diameter. Terminal support orientations and diameters, we shall see below, tend to follow the initial support.

9.3.1.2. *Propithecus diadema*

The main locomotor mode of *P. diadema* is leaping, which occurs in 75% of locomotor bouts (Figure 9.2 A). The remaining 25% is split between nine locomotor modes, with vertical climbing (13%) and cantilevering (7%) being the most important. The importance of leaping decreases when comparing the mechanically effective distance travelled per kilometre (Figure 9.2 B). This is opposite to the case in *I. indri*.



A: %

B: m/km

Figure 9.2. A: Percentage of locomotor mode for all individuals of *P. diadema*. $N = 5504$. **B:** Mechanically effective distance travelled for locomotor modes in *P. diadema*. $N = 9788$m. Other: two-handed suspension, four-handed suspension, kangaroo hop, assisted bipedal walk and drop.

Support orientations of *P. diadema* stress verticals more than in *I. indri*: initial support orientations are verticals 53.8%, angles 18.4%, obliques 17.3 % and horizontals 10.5%. Over half (58.2%) of initial supports lie between 5.1 to 10cm in diameter, 19.2% between 10.1 to15cm, 13.7% less than 5cm diameter and 9.0% greater than 15cm. Terminal support orientations and diameters, we shall see below, tend to follow the initial support.

9.3.1.3. *Hapalemur griseus griseus*

In this study *H. g. griseus*, like the two indriids, use leaping most frequently (48%). However the next commonest mode is quadrupedal walking (33%), rather than vertical climb (Figure 9.3 A). The situation is similar when comparing the percentage of the total distance travelled (Figure 9.3 B). Here the importance of leaping is slightly reduced, while that of quadrupedal walking increases.

Comparing the frequency and m/km counts for locomotor mode (Figure 9.3), suggests that from an energetic perspective the importance of cantilevering is overestimated and that of running slightly underestimated.

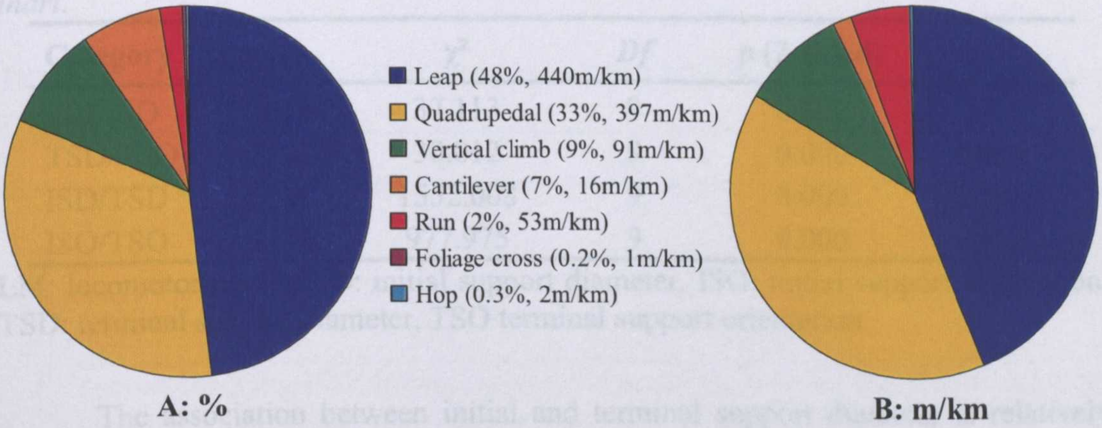


Figure 9.3. A: Percentage of locomotor mode for all individuals of *H. g. griseus*. $N = 7784$. **B:** Percentage of locomotor mode for all individuals of *H. g. griseus*. $N = 9177$m.

Leaping is a less dominant component of *H. g. griseus*' locomotion, and support orientations (calculated for all modes) stress horizontals far more than in the indriids: initial support orientations are horizontals 34.0%, obliques 24.7%, angles 12.0% and verticals 29.3%. Over half (60.4%) of initial supports in all locomotor modes lie between 0.6 to 5cm in diameter, 30.4% between 5.1 to 10cm, 3.2% between 10.1 to 15cm and 2.6% greater than 15 cm. Terminal support orientations and diameters, we shall see below, tend to follow the initial support.

9.3.2. Within-Species Relationships between Locomotion and Support Usage

It should first be noted that sample sizes for terminal supports are lower than those for initial supports, as not all locomotor modes had a terminal support. Modes of locomotion such as vertical climbing and quadrupedal walking which occurred on one continuous support, are only considered to have an initial support in this analysis.

9.3.2.1. *Indri indri*

Pearson Chi-Squared (χ^2) values (Table 9.4) indicate significant associations between supports, although these associations are not strong. The strongest associations are found between initial and terminal diameter, and initial and terminal orientation.

Table 9.4. Pearson Chi-Squared (χ^2) and Cramér's *V* values for support use in *I. indri*.

Category	*N*	χ^2	*Df*	*p* (2-sided)	*V*
ISD/ISO	3916	37.113	9	0.000	0.055
TSD/TSO	3407	30.012	9	0.000	0.055
ISD/TSD	3407	1552.008	9	0.000	0.391
ISO/TSO	3374	977.975	9	0.000	0.317

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

The association between initial and terminal support diameter is relatively strong. There is a relatively strong association between initial and terminal support orientation. Standardized residuals from cross-tabulations (Appendix F1 and F2) indicate a preference for 'like to like' supports.

9.3.2.2. *Propithecus diadema*

There are associations between support diameter and orientation (Table 9.5) but they are not very strong. The strongest associations are found between initial and terminal diameter, and initial and terminal orientation.

Table 9.5. Pearson Chi-Squared (χ^2) and Cramér's *V* values for support use in *P. diadema*.

Category	*N*	χ^2	*df*	*p* (2-sided)	*V*
ISD/ISO	5423	91.62	9	0.000	0.075
TSD/TSO	4510	44.77	9	0.000	0.058
ISD/TSD	4510	1618.54	9	0.000	0.346
ISO/TSO	4510	1262.09	9	0.000	0.305

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

There is also a relatively strong association between initial and terminal support diameter. There is a relatively strong association between initial and terminal support orientation. Standardized residuals from cross-tabulations (Appendix F3 and F4) indicate both of these associations are 'like to like'.

9.3.2.3. *Hapalemur griseus griseus*

There are associations between support diameter and orientation (Table 9.6) although these associations are not especially strong. The strongest association is between initial and terminal support diameter.

Table 9.6. Pearson Chi-Squared (χ^2) and Cramér's *V* values for support use in *H. g. griseus*.

	N	χ^2	*df*	*p* (2-sided)	*V*
ISD/ISO	7743	199.200	12	0.000	0.093
TSD/TSO	4289	157.911	12	0.000	0.111
ISD/TSD	4091	2024.361	9	0.000	0.406
ISO/TSO	4289	1330.377	9	0.000	0.322

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

There is a strong association between initial and terminal support diameter. There is a relatively strong association between initial and terminal support orientation. Standardized residuals from cross-tabulations (Appendix F5 and F6) indicate a preference for 'like to like'.

9.3.3. Locomotor Mode and Support Use

9.3.3.1. *Indri indri*

To satisfy the requirement of the Chi-Squared test that no expected frequency should be less than 5 over more than 20% of the cells, bipedalism, two-handed suspension, four-handed suspension and drop were removed from analysis. All two-way pairings indicate an association (Table 9.7), although none is very strong.

Table 9.7. Pearson Chi-Squared (χ^2) and Cramér's *V* values for locomotor mode and support use in *I. indri*.

Category	*N*	χ^2	*Df*	*p* (2-sided)	*V*
LM/ISD	3896	202.841	12	0.000	0.132
LM/ISO	3896	552.312	12	0.000	0.217
LM/TSD	3373	344.341	3	0.000	0.320
LM/TSO	3373	178.704	3	0.000	0.230

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation

9.3.3.2. *Propithecus diadema*

To fulfil the minimal cell count requirements of the Pearson Chi-Squared test the locomotor mode categories assisted bipedal walk, two-handed suspension, quadrumanous suspension, drop and kangaroo hop were removed from analysis. Pearson correlation (Table 9.8) shows associations between locomotor mode and support use, although the relationships are not very strong.

Table 9.8. Pearson Chi-Square (χ^2) and Cramér's V values for locomotor mode and support use in *P. diadema*.

	N	χ^2	*df*	*p* (2-sided)	*V*
LM/ISD	5423	318.19	12	0.000	0.140
LM/ISO	5423	1210.21	12	0.000	0.273
LM/TSD	4510	230.04	3	0.000	0.226
LM/TSO	4510	309.06	3	0.000	0.262

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

9.3.3.3. *Hapalemur griseus griseus*

To fulfil the minimum cell requirements of the Pearson Chi-Squared test, the categories of foliage cross and hop were removed from analysis. Locomotor mode was found to be associated with all support categories (Figure 9.10).

Table 9.9. Pearson Chi-Square (χ^2) and Cramér's V values for locomotor data and support use in *H. g. griseus*.

	N	χ^2	*df*	*p* (2-sided)	*V*
LM/ISD	7743	256.241	16	0.000	0.091
LM/ISO	7743	2886.054	12	0.000	0.352
LM/TSD	4289	219.728	4	0.000	0.226
LM/TSO	4289	205.817	3	0.000	0.219

LM: locomotor mode, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

9.3.4. Raw Horizontal Distance Travelled

9.3.4.1. *Indri indri*

There are significant differences between mean raw horizontal distance travelled and locomotor mode (F [4, 3711] = 322.495, $p < 0.001$). Leaping as might be expected contributes most to raw horizontal travel distances (Table 9.10).

Table 9.10. Duncan post-hoc test between locomotor mode and raw horizontal distance travelled (m) for *I. indri*.

	N	Subsets		
		1	**2**	**3**
Vertical climb	374	0.35		
Cantilever	208	0.57		
Hop	53		1.06	
Quadrupedal	56		1.19	
Leap	3025			2.50
Subset significances		0.218	0.442	1.000

9.3.4.2. *Propithecus diadema*

There are significant differences between the raw horizontal distance travelled and locomotor mode (F [4, 737] = 141.631, $p < 0.001$). Leaping and quadrupedal walking contribute most (Table 9.11).

Table 9.11. Duncan post-hoc test between locomotor mode and raw horizontal distance travelled (m) for *P. diadema*.

	N	Subsets		
		1	**2**	**3**
Vertical climb	324	0.20		
Cantilever	61	0.46		
Hop	49		0.99	
Leap	294			1.63
Quadrupedal	14			1.76
Subset significances		0.126	1.000	0.458

9.3.4.3. *Hapalemur griseus griseus*

There are significant differences between raw horizontal distance travelled and locomotor mode (F [6, 7777] = 392.411, $p < 0.001$). The Duncan-post hoc (Table 9.12) indicates that the greatest horizontal distance is contributed by running and that there is no significant difference between distances covered by leaping and quadrupedal walking. This differs markedly from the case in both indriids.

Table 9.12. Duncan post-hoc test of raw horizontal distance travelled (m) in different locomotor modes for *H. g. griseus*.

	N	Subsets			
		1	**2**	**3**	**4**
Vertical climb	695	0.09			
Cantilever	538	0.22			
Foliage cross	18		0.47		
Hop	23		0.64		
Leap	3751			0.99	
Quadrupedal	2606			1.21	
Run	153				2.95
Subset significances		0.429	0.259	0.137	1.000

9.3.5. Raw Vertical Distance Travelled

One-way ANOVAs were used, together with the Duncan post-hoc test, to determine differences between locomotor mode and mean raw vertical distance travelled in a single bout. For *I. indri* and *P. diadema* observations did not fall evenly between a gain and loss of height, as would be expected. This is probably accountable for by observer bias in rough terrain. This was not evident for *H. g. griseus*, no doubt reflecting the flatter nature of their ranges.

9.3.5.1. *Indri indri*

The majority of locomotor bouts recorded no height change (60.23%, N = 3716). The remainder were split rather evenly between positive (16.60%) and negative (23.21%) height change. There are significant differences between the absolute vertical height change for locomotor modes (F [4, 3711] = 228.403, $p <$ 0.001). The greatest vertical height changes are obtained via vertical climbing (Table 9.13).

Table 9.13. Duncan post-hoc test between locomotor mode and absolute vertical height change (m) for *I. indri*.

	N	Subsets		
		1	**2**	**3**
Quadrupedal	56	0.24		
Cantilever	208	0.37		
Leap	3025	0.43		
Hop	53		1.10	
Vertical climb	374			2.14
Subset significances		0.202	1.000	1.000

A similar significant difference (*F* [4, 612] =14.482, $p < 0.001$) is found between locomotor mode and positive vertical height change. For positive changes, vertical climbing and hopping achieve the largest height change (Table 9.14). Significant differences are also found between negative height change and locomotor mode (*F* [3, 857] = 25.009, $p < 0.001$). However large negative height changes are obtained by leaping as well as vertical climbing (Table 9.15). Positive height changes are most often achieved via vertical climbing and negative height changes by leaping (Figure 9.4).

Table 9.14. Duncan post-hoc test between locomotor mode and positive vertical height change (m) for *I. indri*.

	N	**Subsets**		
		1	**2**	**3**
Cantilever	48	0.60		
Quadrupedal	11	1.07	1.07	
Leap	337	1.15	1.15	
Hop	41		1.42	1.42
Vertical climb	180			1.91
Subset significances		0.092	0.296	0.118

Table 9.15. Duncan post-hoc test between locomotor mode and negative vertical height change (m) for *I. indri*.

	N	**Subsets**	
		1	**2**
Vertical climb	194	-2.36	
Leap	607	-1.49	-1.49
Cantilever	58		-0.82
Quadrupedal	2		-0.75
Subset significances		0.237	0.343

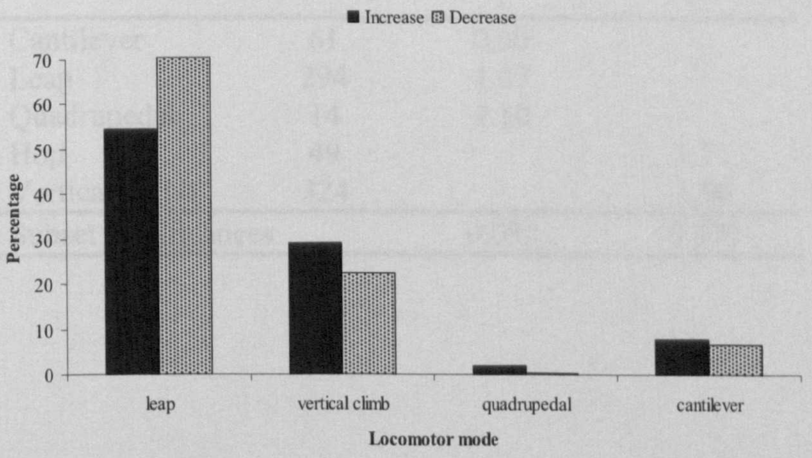


Figure 9.4. Percentage of total bouts recording an increase and decrease in vertical height for *I. indri*.

9.3.5.2. *Propithecus diadema*

The majority of locomotor bouts recorded no height change (63.07%, N = 5491). Positive height change (13.51%) is rarer than negative (23.42%) height change. There are significant differences in absolute vertical height change of locomotor modes (F [4, 5444] = 597.853, $p < 0.001$): as for *I. indri*, the greatest height changes are achieved through vertical climbing (Table 9.16 and Figure 9.5).

Table 9.16. Duncan post-hoc test of absolute raw vertical height change (m) for locomotor mode in *P. diadema*.

	N	**Subsets**		
		1	**2**	**3**
Quadrupedal	118	0.20		
Leap	4139	0.30		
Cantilever	403	0.31		
Hop	63		1.69	
Vertical climb	726			2.17
Subset significances		0.324	1.000	1.000

Significant differences are also apparent between the positive vertical height change of locomotor modes (F [3, 1268] = 75.693, $p < 0.001$). Again as for *I. indri*, hopping and vertical climbing accomplish the greatest positive height change (Table 9.17). Significant differences are also found between negative height change and locomotor mode (F [3, 1268] = 75.693, $p < 0.001$). Vertical climbing is used to achieve the most height loss (Table 9.18).

Table 9.17. Duncan post-hoc test of positive vertical height change (m) for locomotor mode in *P. diadema*.

	N	**Subsets**	
		1	2
Cantilever	61	0.60	
Leap	294	1.07	
Quadrupedal	14	1.10	
Hop	49		1.71
Vertical climb	324		1.96
Subset significances		0.092	0.379

Table 9.18. Duncan post-hoc test of negative vertical height change (m) for locomotor mode in *P. diadema*.

	N	Subsets	
		1	**2**
Vertical climb	402	-2.34	
Leap	746		-1.27
Quadrupedal	8		-1.00
Cantilever	116		-0.75
Subset significances		1.000	0.156

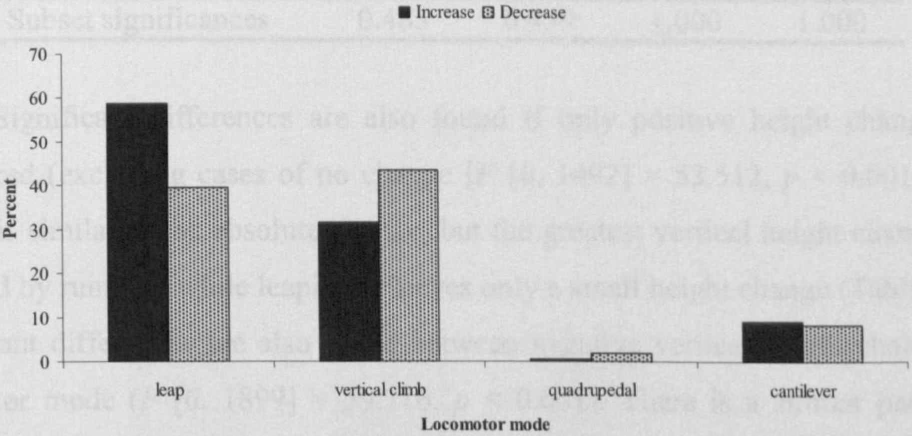


Figure 9.5. Percentage of total bouts recording an increase and decrease in vertical height for *P. diadema*.

9.3.5.3. *Hapalemur griseus griseus*

Over half the recorded bouts (58.67%, $N = 7784$) registered no vertical height change. The remainder were split rather evenly between positive (19.26%) and negative (22.07%) changes. There are significant differences between the vertical distance travelled for each locomotor mode ($F\ [6, 7777] = 271.353$, $p < 0.001$). The greatest absolute vertical height changes are obtained by vertical climbing and secondly by running, and the least by cantilevers, foliage crossing and leaping (Figure 9.6).

Table 9.19. Duncan post-hoc test of absolute vertical height change (m) in different locomotor modes for *H. g. griseus*.

	N	Subsets			
		1	2	3	4
Cantilever	538	0.10			
Foliage cross	18	0.15			
Leap	3751	0.17			
Quadrupedal	2606		0.41		
Hop	23		0.50		
Run	153			0.72	
Vertical climb	695				1.18
Subset significances		0.485	0.439	1.000	1.000

Significant differences are also found if only positive height changes are considered (excluding cases of no change [*F* [6, 1492] = 53.512, $p < 0.001$]). The pattern is similar to the absolute change, but the greatest vertical height changes are achieved by running, while leaping achieves only a small height change (Table 9.20). Significant differences are also found between negative vertical height change and locomotor mode (*F* [6, 1899] = 59.716, $p < 0.001$). There is a similar pattern as before, with the highest negative vertical changes being achieved by running (Table 9.21).

Table 9.20. Duncan post-hoc test of positive vertical height change (m) in different locomotor modes for *H. g. griseus*.

	N	Subsets		
		1	2	3
Cantilever	99	0.24		
Leap	497	0.53	0.53	
Foliage cross	4	0.55	0.55	
Quadrupedal	472		0.94	
Vertical climb	374		0.98	
Hop	11		0.98	
Run	42			2.06
Subset significances		0.205	0.079	1.000

Table 9.21. Duncan post-hoc test of negative vertical height change (m) in different locomotor modes for *H. g. griseus*.

	N	Subsets			
		1	2	3	4
Run	13	-1.79			
Vertical climb	320	-1.41	-1.41		
Quadrupedal	648		-0.98	-0.98	
Leap	780			-0.56	-0.56
Cantilever	128				-0.25
Foliage cross	5				-0.10
Hop	12				-0.09
Subset significances		0.157	0.116	0.116	0.092

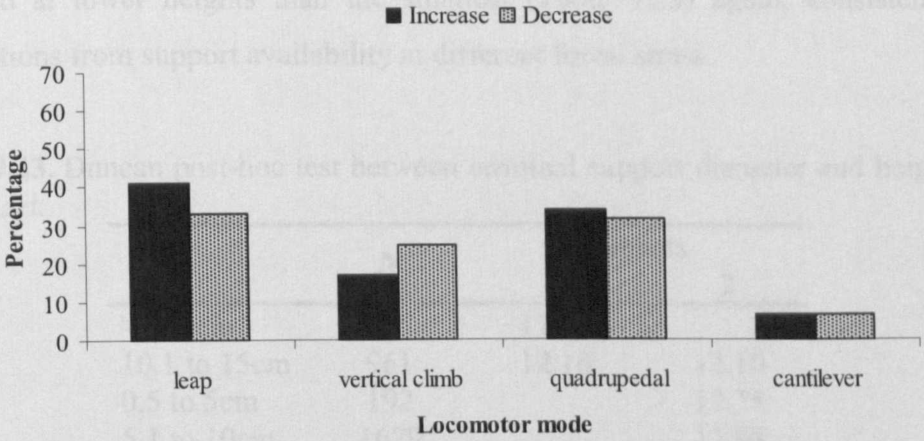


Figure 9.6. Percentage of total bouts recording an increase and decrease in vertical height for *H. g. griseus*.

9.3.6. Support Use and Raw Height

One-way ANOVAs were used, with the Duncan post-hoc test, to determine differences between support use and mean height. Only the initial recorded height was tested.

9.3.6.1. *Indri indri*

Significant differences were found between initial support orientation and height (F [3, 3677] = 4.807, $p < 0.001$). Duncan post-hoc testing indicates a tendency for larger supports to be used at lower heights than smaller supports (Table 9.22), consistent with expectations from support availability at different strata.

Table 9.22. Duncan post-hoc test between initial support diameter and height (m) for *I. indri*.

	N	**Subsets**	
		1	**2**
10.1 to 15cm	1093	12.16	
>15.1cm	447	12.25	12.25
0.5 to 5cm	269	12.74	12.74
5.1 to 10cm	1872		13.08
Subset significances		0.195	0.058

Similar significant differences exist for height and terminal support diameter (*F* [3, 3193] = 5.925, $p < 0.001$). The post-hoc test indicates that the largest supports are used at lower heights than the smallest (Table 9.23) again, consistent with expectations from support availability at different forest strata.

Table 9.23. Duncan post-hoc test between terminal support diameter and height (m) for *I. indri*.

	N	**Subsets**	
		1	**2**
>15.1cm	365	11.65	
10.1 to 15cm	961	12.10	12.10
0.5 to 5cm	192		12.78
5.1 to 10cm	1679		12.98
Subset significances		0.338	0.074

Significant differences were also found between initial support orientations and heights (*F* [3, 3677] = 61.710, $p < 0.001$). The same significant difference exists between terminal support orientations and heights (*F* [3, 3168] = 53.646, $p < 0.001$). Post-hoc testing indicates a clear separation of use of different support orientations, vertical supports being used lowest in the canopy and horizontals highest (Table 9.24), once again consistent with expectations from support availability at different forest strata.

Table 9.24. Duncan post-hoc test between initial and terminal support orientation and height (m) for *I. indri*.

	Initial support subsets					Terminal support subsets			
	N	1	2	3	4	*N*	1	2	3
Vertical	1494	11.24				1279	11.00		
Oblique	847		12.65			754		12.82	
Angle	866			13.50		771		13.51	
Horizontal	474				15.80	368			15.53
Subset significances		1.00	1.00	1.00	1.00		1.00	0.06	1.00

9.3.6.2. *Propithecus diadema*

Unlike the case in *I. indri*, no differences were found between initial support diameter and height (*F* [3, 5486] = 0.553, $p > 0.05$ns) or terminal support diameter and height (*F* [3, 4522] = 1.294, $p > 0.05$ns). However significant differences were observed between initial support orientation and height (*F* [3, 5473] = 161.154, $p < 0.001$) and terminal support orientation and mean height (*F* [3, 4508] = 196.118, $p < 0.001$). Post-hoc testing indicates that vertical supports tend to be used at lower heights than horizontal and oblique supports (Table 9.25), consistent with expectations from support availability.

Table 9.25. Duncan post-hoc test for initial support orientation and height (m) in *P. diadema*.

	Initial support subsets				Terminal support subsets			
	N	1	2	3	*N*	1	2	3
Vertical	2946	9.24			2480	8.75		
Angle	1006		11.20		860		11.15	
Horizontal	577			13.02	798			13.07
Oblique	948			13.02	374			13.44
Subset significances		1.000	1.000	0.999		1.000	1.000	0.182

9.3.6.3. *Hapalemur griseus griseus*

Groups One and Two were homogenous with respect to height (*U* =63647.500; $p > 0.5$ns) and have been pooled for this analysis. Significant differences were found between initial support diameter and height (*F* [4, 7825] = 131.203, $p < 0.001$). A similar significant difference exists between terminal support diameter and height (*F* [4, 4307] = 52.911, $p < 0.001$). Post-hoc testing indicates that larger supports are used lowest in the canopy, and smallest supports higher in the canopy

(Table 9.26). This is the same finding as for the indriids and consistent with expectations from support availability.

Table 9.26. Duncan post-hoc test between height (m) and initial and terminal support diameters in *H. g. griseus*.

	Initial support subsets						Terminal support subsets				
	N	1	2	3	4	5	*N*	1	2	3	4
>15.1cm	200	3.78					97	3.01			
5.1-10cm	2368		4.68				1298		4.27		
10.1-15cm	251			5.31			138		4.94		
0.6-5cm	4704				6.40		2617			5.70	
<0.5cm	307					7.29	162				6.52
Subset significances		1.00	1.00	1.00	1.00	1.00		1.00	0.05	1.00	1.00

There are significant differences between initial support orientation and height (*F* [3, 7789] = 377.770, p<0.001). Significant differences were also found between terminal support orientation and height (*F* [3, 4300] = 226.617, p<0.001). Duncan post-hoc testing indicates that vertical supports are used lower in the canopy and horizontal supports higher (Table 9.27).

Table 9.27. Duncan post-hoc test between height (m) and initial and terminal support orientation for *H. g. griseus*.

	Initial support subsets				Terminal support subsets			
	N	1	2	3	*N*	1	2	3
Vertical	2282	4.12			1744	3.80		
Oblique	1923		5.73		1048		5.57	
Angle	937		5.74		574		5.66	
Horizontal	2651			7.30	938			7.17
Subset significances		1.000	0.948	1.000		1.000	0.554	1.000

9.3.7. Between Species Comparisons

Following the general within-species description above we can now ask: what are the most important associations between species, locomotor mode, support and vertical spatial usage?

9.3.7.1. Comparison between *Indri indri* and *Propithecus diadema*

A: Log-Linear Modelling

Log-linear modelling was used to examine relationships between locomotor mode, support use and initial height in *I. indri* and *P. diadema*. Five significant models were found, all fulfilling the 'zero zero' cell count (Table 9.28 [for variable groupings see Appendix F7]). The most significant model, IP1, finds that locomotor mode and initial support diameter are the most strongly linked variables, to the exclusion of species. Model IP2 indicates that locomotor mode and terminal support diameter show strong links. This shows that locomotor mode is more important than species in determining support use. Model IP4, indicates that species, not locomotor mode, is the strongest correlate of height, confirming that the species are differentiated by stratum.

Table 9.28. Log-linear modelling significances and expressions comparing *I. indri*, and *P. diadema*.

Model	Model *p*	Model *df*	Model expressions	Partial χ^2	*df*	Standardized χ^2 (χ^2/df)
IP1	0.956	34	LM * ISD	111.667	2	55.83
			Sp * ISO * ISD	16.918	1	16.92
			Sp * IH * ISO	33.714	2	16.86
			Sp * LM	22.898	2	11.45
			IH * ISO * ISD	17.26	2	8.63
			Sp * IH * ISD	15.791	2	7.90
			LM * IH * ISO	11.469	4	2.87
IP2	0.892	36	LM * TSD	114.498	2	57.25
			Sp * IH * TSO	51.573	2	25.79
			Sp * IH * TSD	25.02	2	12.51
			Sp * LM	24.408	2	12.20
			Sp * TSO * TSD	9.386	1	9.39
			LM * IH * TSO	13.96	4	3.49
IP3	0.797	12	Sp * LM * ISD	14.412	4	3.60
			Sp * ISD * ISO	12.76	4	3.19
			LM * ISD * ISO	18.349	8	2.29
IP4	0.592	4	Sp * IH	181.568	2	90.78
			LM * IH	119.006	4	29.75
			Sp * LM	29.484	2	14.74
IP5	0.057	1	LM * TSO	297.716	1	297.72
			LM * TSD	135.982	1	135.98
			TSO * TSD	6.708	1	6.71

B. Leaping

Pearson Chi-Squared tests identified a correlation between species and support diameter and orientation during leaping for *I. indri* and *P. diadema* although low values for Cramér's V suggests that these correlations are fairly weak (Table 9.29).

Table 9.29. Pearson Chi-Squared (χ^2) and Cramér's V values for support use during leaping between *I. indri* and *P. diadema*.

	N	χ^2	*df*	*p* (2-sided)	*V*
Sp/ISD	7099	205.793	3	0.000	0.170
Sp/ISO	7099	156.352	3	0.000	0.148
Sp/TSD	7099	262.071	3	0.000	0.192
Sp/TSO	7099	173.297	3	0.000	0.156

Sp: species, ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

Standardized residuals from cross-tabulation (Appendix F8 to F11) for species against initial support diameter, indicates that *I. indri* leap from supports >10.1cm more often than expected and *P. diadema,* less often than expected. A similar pattern is observed for terminal support diameter, in that *I. indri* land on supports sized over 10.1cm more frequently than expected and *P. diadema* less often. *I. indri* leap from vertical supports less often than would be expected, while *P. diadema* leap from them more frequently than expected. A similar situation is observed for terminal support orientation, *I. indri* leaping onto vertical supports less often than expected and *P. diadema* more often than expected.

There is a significant difference between the horizontal distance *I. indri* and *P. diadema* travel during leaping ($U = 5324997, p < 0.001$); *I. indri* leap further than *P. diadema* (Table 9.30). Significant differences are also found between negative height changes (leaping from high to low [$U = 192075.5, p < 0.001$]); *I. indri* lose more height in leaping than *P. diadema*. There is a significant difference with a positive height change (leaps from low to high [$U = 40474, p < 0.001$]); *I. indri* gain more height in leaping than *P. diadema*.

Table 9.30. Values of raw horizontal distance travelled and raw positive and negative height change between *I. indri* and *P. diadema* while leaping.

	Species	***M* (m)**	***N***	***SD***	**Median (m)**
Raw horizontal distance travelled	*I. indri*	2.50	2977	1.42	2.40
	P. diadema	2.19	4122	1.15	2.00
	Total	2.32	7099	1.28	2.20
Negative vertical height change	*I. indri*	-1.42	599	0.88	1.00
	P. diadema	-1.23	742	0.76	1.00
	Total	-1.32	1341	0.82	1.00
Positive vertical height change	*I. indri*	1.15	326	0.63	1.00
	P. diadema	1.01	290	0.55	1.00
	Total	1.09	616	0.60	1.00

C. Vertical climbing

There is no correlation (χ^2 [3, 1101] = 3.240, $p > 0.05$ns) between species (*I. indri* and *P. diadema*) and initial support diameter in vertical climbing.

D. Quadrupedal Walking

There is no correlation between species and support diameter (χ^2 [2, 178] = 2.286, $p > 0.05$ns) or orientation (χ^2 [2, 178] = 3.654, $p > 0.05$ns) during quadrupedal walking. There is a significant difference however between the horizontal distance *I. indri* and *P. diadema* travel during quadrupedal walking (U = 2641.5, $p < 0.05$); *I. indri* travel further (Table 9.31). No significant difference was found for absolute vertical height change during quadrupedal walking (U = 3251.5, $p > 0.05$ns).

Table 9.31. Mean raw horizontal distance (m) of quadrupedal walking bouts for *I. indri* and *P. diadema*.

	***M* (m)**	***N***	***SD***	**Median (m)**
I. indri	1.1911	56	0.55899	1.00
P. diadema	1.5910	122	1.01843	1.40
Total	1.4652	178	0.91696	1.00

9.3.7.2. Comparison between *Indri indri*, *Propithecus diadema* and *Hapalemur griseus griseus*.

A. Log-Linear Modelling

Four significant models, all fulfilling the 'zero zero' cell count, were obtained during log-linear analysis to explain variable associations within the three species (Table 9.32 [for variable groupings see Appendix F12]). The most significant model, IPH1, indicates that the strongest association is between locomotor mode and initial support diameter and orientation (Table 9.32). This shows that for leaping and cantilevering (the only locomotor modes tested in this model), the mode of locomotion is more suitable in predicting support use than species. Model IPH2 indicates that the direct association between support use and height is more important than the association between species and support use and species and height. However IPH2, which includes vertical climbing, ranks the association between species and support use and locomotor mode most important. In Model IPH4, species forms the strongest association with terminal support diameter.

Table 9.32. Log-linear modelling significances and expressions comparing *I. indri*, *P. diadema* and *H. g. griseus*.

Model	**Model *p***	**Model *df***	**Model expressions**	**Partial χ^2**	***Df***	**Standardized χ^2 (χ^2/df)**
IPH1	0.892	4	LM * ISD * ISO	9.351	1	9.35
			Sp * LM * ISO	14.362	2	7.18
			Sp * ISD * ISO	10.792	2	5.40
IPH2	0.744	4	ISD * ISO * IH	26.087	2	13.04
			Sp * ISD * ISO	25.894	2	12.95
			Sp * ISO * IH	32.422	4	8.11
			Sp * ISD * IH	18.42	4	4.61
IPH3	0.114	6	Sp * ISO * LM	114.963	4	28.74
			Sp * ISO * ISD	29.913	2	14.96
			Sp * ISD * LM	23.563	4	5.89
IPH4	0.072	6	Sp * TSD	1456.227	2	728.11
			Sp * LM * TSO	13.863	2	6.93
			LM * TSD * TSO	4.056	1	4.06

LM: locomotor mode; ISD: initial support diameter; ISO: initial support orientation; Sp: species; IH: initial height; TSD: terminal support diameter; TSO: terminal support orientation.

B. Raw Horizontal Distance Travelled

A one-way ANOVA was performed to investigate possible differences in raw horizontal distances travelled by the three species. There are indeed significant differences (*F* (2, 16914) = 1434.374, $p < 0.001$). The Duncan post-hoc test (Table 9.33) indicates that mean travel distances achieved in each displacement are all significantly different from each other; *H. g. griseus* travel the least distance and *I. indri* the greatest.

Table 9.33. Duncan post-hoc test for the mean raw horizontal distance travelled (m) for *H. g. griseus*, *P. diadema* and *I. indri*.

	N	Subsets 1	 2	 3
H. g. griseus	7784	0.97		
P. diadema	5459		1.79	
I. indri	3674			2.13
Subset significances		1.000	1.000	1.000

There are significant difference in the mean heights of observation for each species (*F* (2, 16914) = 2720.083, $p < 0.001$). The post-hoc test (Table 9.34) indicates that mean initial heights are all significantly different from one species to another; *H. g. griseus* being seen at the lowest mean height and *I. indri* the highest.

Table 9.34. Duncan post-hoc test for initial height (m) during locomotion for *H. g. griseus*, *P. diadema* and *I. indri*.

	N	Subsets 1	 2	 3
H. g. griseus	7784	5.79		
P. diadema	5459		10.65	
I. indri	3674			12.70
Subset significances		1.000	1.000	1.000

C. Support Use

The larger bodied *I. indri* uses the largest supports and the smallest *H. g. griseus* the smallest supports (Figure 9.7). The association between species and initial support diameter is significant (χ^2 [6, 16917] = 5726.873, $p < 0.001$) and strong ($V = 0.411$). Species can predict diameter almost 20% of the time ($\tau = 0.193$), while diameter predicts species 15% of the time ($\tau = 0.150$).

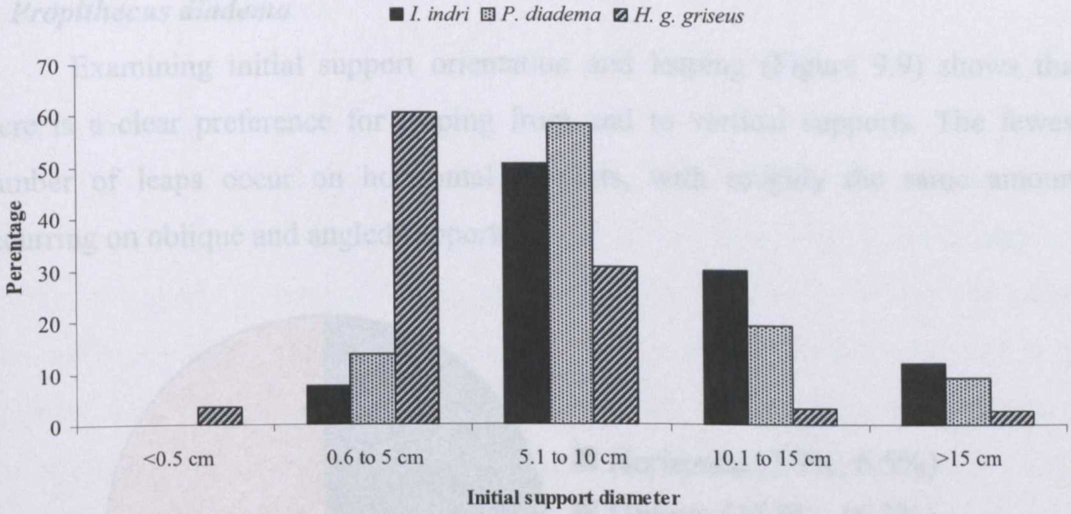


Figure 9.7. Initial support diameter usage for *I. indri*, *P. diadema* and *H. g. griseus*.

9.3.8. Support Use and the Mechanics of Leaping

Since leaping is the most frequently used form of locomotion for each species, in terms of both frequency and the mechanically effective distance travelled, a more detailed investigation is required into within-species support use, including which supports are associated with the greatest leap lengths.

9.3.8.1. Support Orientation

A. *Indri indri*

The most common support orientation for *I. indri* while leaping is vertical (Figure 9.8). Oblique and angled supports are used on roughly the same frequency, the fewest leaps beginning on horizontal supports. This is consistent with a preference for energetically optimal high trajectory leaping.

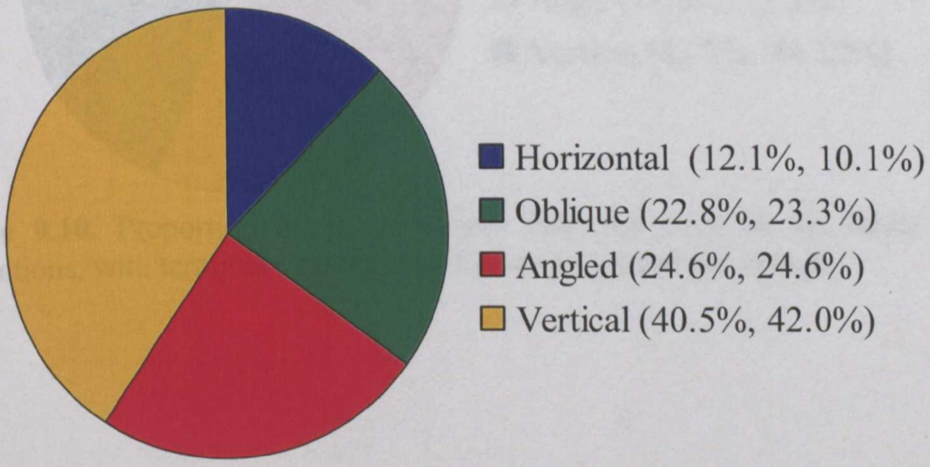


Figure 9.8. Proportion of *I. indri* leaps on each of the initial support orientations, with terminal support values given as second percentages.

B. *Propithecus diadema*

Examining initial support orientation and leaping (Figure 9.9) shows that there is a clear preference for leaping from and to vertical supports. The fewest number of leaps occur on horizontal supports, with roughly the same amount occurring on oblique and angled supports.

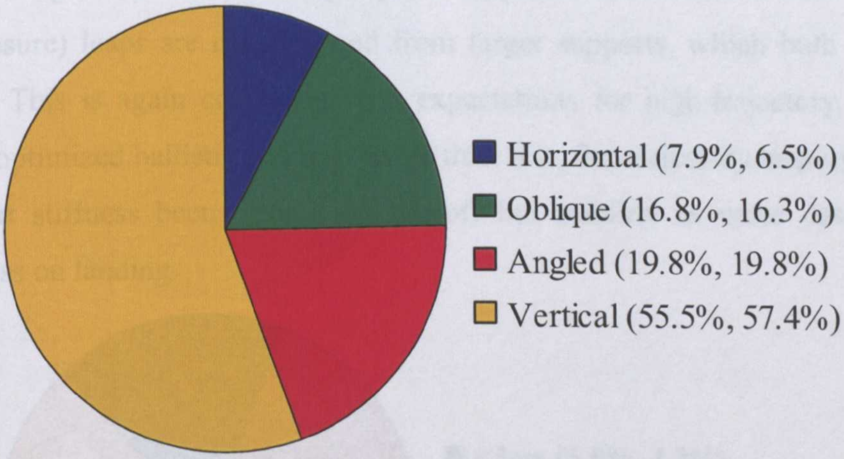


Figure 9.9. Proportion of *P. diadema* leaps on each of the initial support orientations, with terminal support values given as second percentage.

C. *Hapalemur griseus griseus*

Most leaps occur from and to vertical supports (Figure 9.9), the fewest from horizontal supports.

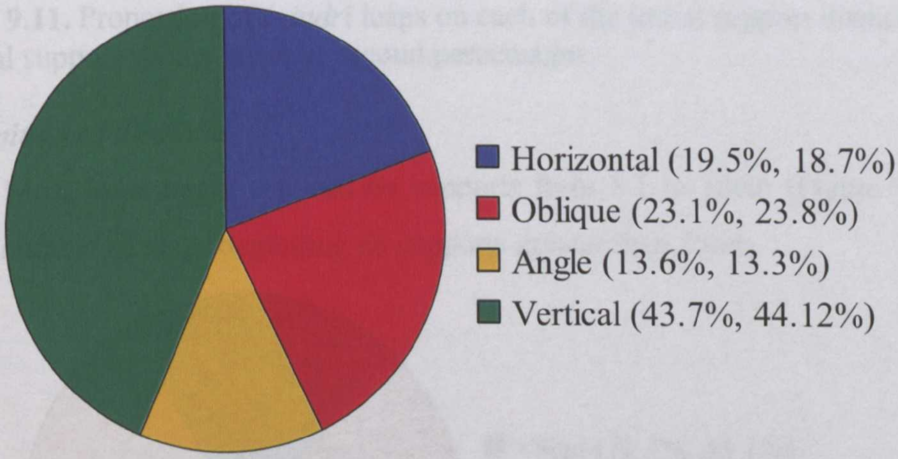


Figure 9.10. Proportion of *H. g. griseus* leaps on each of the initial support orientations, with terminal support values given as second percentage.

9.3.8.2. Support Diameter

A. *Indri indri*

This study found a clear preference for takeoff and landing supports sized from 5.1 to 10 cm (Figure 9.11) which would tend to support Demes and colleagues' (1995) finding of a preference for graspable supports. However, it is clear that longer (raw measure) leaps are made to and from larger supports, which both tend to be verticals. This is again consistent with expectations for high-trajectory, energy or distance-optimized ballistic leaping, rather than fast, flat-trajectory leaping and tends to support stiffness been desired on takeoff but stability as more desirable than energy loss on landing.

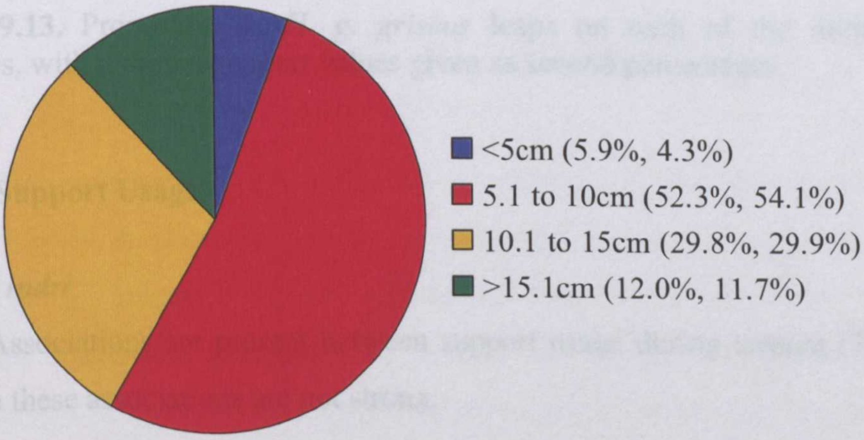


Figure 9.11. Proportion of *I. indri* leaps on each of the initial support diameters, with terminal support values given as second percentages.

B. *Propithecus diadema*

Most leaps begin and end on supports from 5.1 to 10cm (Figure 9.12), the fewest number of leaps beginning on supports greater than 15cm.

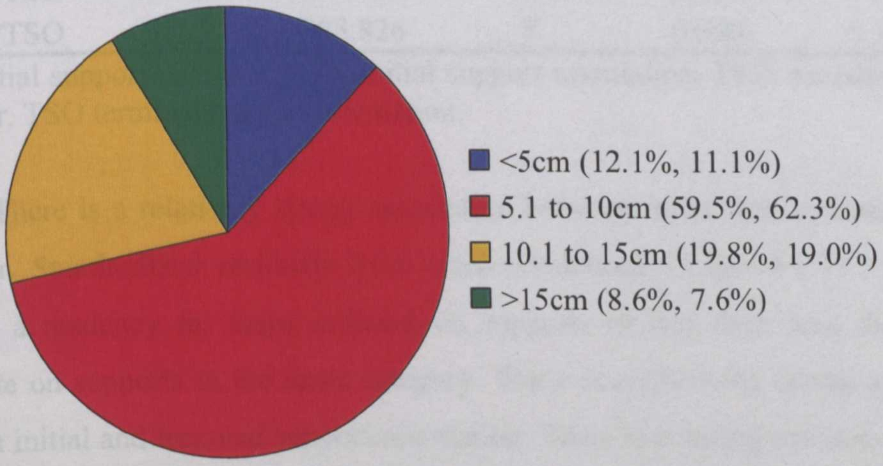


Figure 9.12. Proportion of *P. diadema* leaps on each of the initial support diameters, with terminal support values given as second percentage.

C: *Hapalemur griseus griseus*

Over half of all recorded leaps of H. g. griseus originate and terminate on supports 0.6 to 5cm in diameter (Figure 9.13).

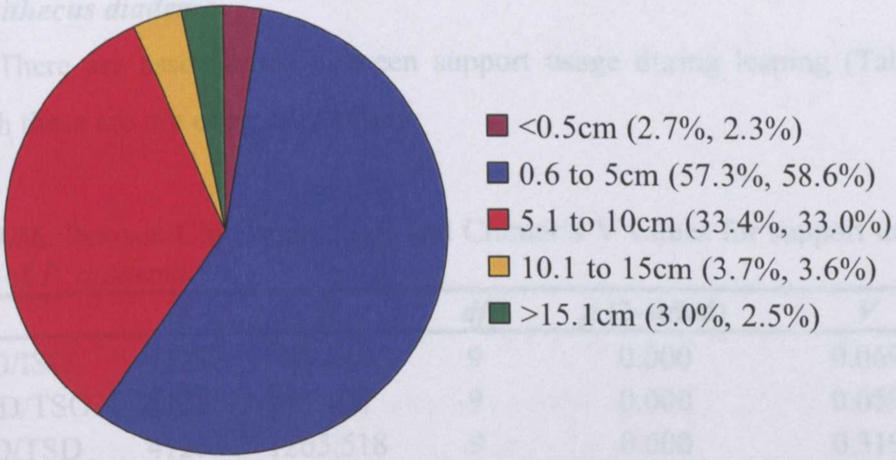


Figure 9.13. Proportion of *H. g. griseus* leaps on each of the initial support diameters, with terminal support values given as second percentages.

9.3.8.3. Support Usage

A. *Indri indri*

Associations are present between support usage during leaping (Table 9.35) although these associations are not strong.

Table 9.35. Pearson Chi-Squared (χ^2) and Cramér's V values for support use during leaping of *I. indri*.

Category	*N*	χ^2	*df*	*p* (2-sided)	*V*
ISO/ISD	3153	34.925	9	0.000	0.061
TSD/TSO	3153	36.329	9	0.000	0.062
ISD/TSD	3153	1236.748	9	0.000	0.362
ISO/TSO	3153	903.826	9	0.000	0.309

ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO terminal support orientation.

There is a relatively strong association between initial and terminal support diameter. Standardized residuals from cross-tabulations (Appendix F13 and F14) indicate a tendency for leaps initiated on supports of less than 5cm diameter to terminate on supports in the same category. There is a relatively strong association between initial and terminal support orientation. There is a strong tendency for leaps initiated on horizontal supports to terminate on horizontal supports, consistent with expectations for fast, flat-trajectory leaping.

B. *Propithecus diadema*

There are associations between support usage during leaping (Table 9.36) although these are not especially strong.

Table 9.36. Pearson Chi-Squared (χ^2) and Cramér's V values for support use during leaping of *P. diadema*.

	N	χ^2	*df*	*p* **(2-sided)**	*V*
ISD/ISO	4123	58.435	9	0.000	0.069
TSD/TSO	4123	43.104	9	0.000	0.059
ISD/TSD	4123	1265.518	9	0.000	0.319
ISO/TSO	4123	1088.87	9	0.000	0.297

ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO: terminal support orientation.

There is a strong association between initial and terminal support diameter during leaping. A relatively strong association is found between initial support orientation and terminal support orientation. Standardized residuals from cross tabulations (Appendix F15 and F16) indicate like to like; e.g. leaps initiated on horizontal supports are more likely to terminate on horizontal supports. This is again consistent with expectations for low-trajectory, fast leaps.

C. *Hapalemur griseus griseus*

To satisfy the minimum cell requirements of the cross-tabulations, the categories of '10.1 to 15cm' and '>15cm', were removed from the analysis of initial and terminal support diameter. There are associations between support use during leaping (Table 9.37), although these are not very strong.

Table 9.37. Pearson Chi-Squared (χ^2) and Cramér's V values for support use during leaping of *H. g. griseus*.

	N	χ^2	*df*	*p* **(2-sided)**	*V*
ISD/ISO	3751	137.807	12	0.000	0.111
TSD/TSO	3751	108.832	12	0.000	0.098
ISD/TSD	33329	1439.362	4	0.000	0.465
ISO/TSO	3751	1115.126	9	0.000	0.315

ISD: initial support diameter, ISO: initial support orientation, TSD: terminal support diameter, TSO: terminal support orientation.

There is a strong association between initial and terminal support diameter and a relatively strong association between initial and terminal support orientation. Standardized residuals from cross-tabulations (Appendix F17 and F18) indicate a strong preference for like to like.

9.3.8.4. Leap Length

A. ***Indri indri***

There is statistically significant differences between initial support orientation and average (raw) leap length (F [3, 3149] = 9.123, $p < 0.001$). A similar significant difference is observed for terminal support orientation (F [3, 3149] = 30.060, $p < 0.001$). The Duncan post-hoc test (Table 9.38) indicates that the longest leaps are achieved from (and to) vertical supports and the shortest from (and to) horizontal supports. This is consistent with a preference for energetically optimal high trajectory leaping.

Table 9.38. Duncan post-hoc test between initial and terminal support orientation and mean raw leap length (m) for *I. indri*.

	Initial support subsets				**Terminal support subsets**			
	N	**1**	**2**	**3**	*N*	**1**	**2**	**3**
Horizontal	381	2.28			318	2.12		
Oblique	720	2.37	2.37		734	2.25		
Angle	777		2.45		777		2.46	
Vertical	1275			2.60	1324			2.70
Subset significances		0.193	0.254	1.000		0.074	1.000	1.000

There is a significant difference between initial support diameter and leap length (F [3, 3149] = 27.544, $p < 0.001$). A similar difference is seen for terminal support diameter and leap length (F [3, 3149] = 21.691, $p < 0.001$). The Duncan post-hoc test (Table 9.39) indicates that the longest leaps are made from (and to) supports over 10.1cm in diameter. This suggests that support stability is more important than dissipation of energy on landing from long leaps and energy loss to the takeoff support is avoided for long leaps

Table 9.39. Duncan post-hoc test between initial and terminal support diameter and mean raw leap length (m) for *I. indri*.

	Initial support subsets				**Terminal support subsets**			
	N	**1**	**2**	**3**	*N*	**1**	**2**	**3**
<5cm	185	2.06			136	2.00		
5.1 to 10cm	1650		2.34		1707		2.36	
10.1 to 15cm	940			2.66	942			2.67
>15.1cm	378			2.79	368			2.68
Subset significances		1.000	1.000	0.127		1.000	1.000	0.894

B. *Propithecus diadema*

Minimum and maximum raw leap length was consistent across all orientation categories (0.2 to 7m), however significant differences are observed in the mean leap length of both initial (*F* [3, 4119] = 14.069, $p < 0.001$) and terminal (*F* [3, 4119] = 32.011, $p < 0.001$) support orientations. The Duncan post-hoc test (Table 9.40) indicates that longest leaps are achieved from and to vertical supports and the shortest from and to horizontal supports, consistent with ballistic expectations.

Table 9.40. Duncan post-hoc test between initial and terminal support orientation and mean raw leap length (m) for *P. diadema*.

	Initial support subsets				**Terminal support subsets**			
	N	**1**	**2**	**3**	*N*	**1**	**2**	**3**
Horizontal	326	1.96			267	1.77		
Oblique	693		2.08		674		2.04	
Angle	817		2.11		815		2.07	
Vertical	2287			2.28	2367			2.32
Subset significances		1.000	0.651	1.000		1.000	0.613	1.000

The one-way ANOVA (*F* [3, 4119] = 33.407, $p < 0.001$) indicates significant differences between initial support diameter and leap length. The Duncan post-hoc test (Table 9.41) shows that longer leaps are achieved from supports over 10.1cm in diameter, consistent with a requirement for minimizing energy loss to compliant takeoff supports on long leaps. A similar difference is observed for terminal support diameter (*F* [3, 4119] = 25.703, $p < 0.001$). Here the longest leaps occur onto supports from 10.1 to 15 cm (Table 9.41) again suggesting that support stability is more important than dissipation of energy.

Table 9.41. Duncan-post hoc between initial and terminal support diameter and mean raw leap length (m) for *P. diadema*.

	Initial support subsets				Terminal support subsets			
	N	1	2	3	*N*	1	2	3
<5 cm	498	1.87			459	1.91		
5.1 to 10cm	2452		2.15		2568		2.16	
>15.1cm	356			2.37	313		2.21	
10.1 to 15cm	817			2.44	783			2.45
Subset significances		1.000	1.000	0.237		1.000	0.392	1.000

C. *Hapalemur griseus griseus*

There is a significant difference between the raw horizontal distance travelled in leaping and initial support diameter (F [4, 3746] = 19.701, $p < 0.001$). The Duncan post-hoc test (Table 9.42) indicates that longer leaps are achieved from larger initial supports (>5.1cm), consistent with the case in the indriids and expectations for energy saving.

Table 9.42. Duncan post-hoc test of initial support diameter and raw horizontal distance travelled (m) for leaping in *H. g. griseus*.

	N	Subsets		
		1	2	3
<0.5cm	100	0.78		
0.6 to 5cm	2148		0.92	
>15.1cm	111		0.99	0.99
10.1 to 15cm	140			1.11
5.1 to 10cm	1252			1.12
Subset significances		1.000	0.375	0.082

A similar difference is found between the horizontal distance travelled and terminal support diameter (F [4, 3746] = 20.517, $p < 0.001$) although the post-hoc test indicates a less straightforward relationship (Table 9.43); the shortest leaps occur onto the smallest and largest supports categories, the longest leaps are associated with landing supports sized from 5.1 to 15cm.

Table 9.43. Duncan post-hoc test for terminal support diameter and raw horizontal distance travelled (m) for leaping in *H. g. griseus*.

	N	Subsets 1	Subsets 2	Subsets 3
<0.5cm	85	0.76		
>15.1cm	92	0.87	0.87	
0.6 to 5cm	2199		0.93	
5.1 to 10cm	1239			1.11
10.1 to 15cm	136			1.21
Subset significances		0.166	0.394	0.182

There is also a significant difference between the horizontal distance travelled during leaping and the initial support orientation (*F* [3, 3747] = 76.772, $p < 0.001$); longer leaps are achieved when leaping from angled and vertical supports, the shortest from horizontal supports (Table 9.44). This is again consistent with use of high trajectories in longer leaps. A similar difference is shown between the horizontal distance travelled during leaping and terminal support orientation (*F* [3, 3747] = 122.373, $p < 0.001$). Here is there is a clear trend for shorter leaps to land on horizontal and longer leaps on vertical supports (Table 9.44), again consistent with ballistic expectations if high-angle takeoff supports enable higher-angle trajectories.

Table 9.44. Duncan post-hoc test between initial and terminal support orientation and mean raw horizontal distance travelled (m) for leaping in *H. g. griseus*.

	Initial support subsets				Terminal support subsets				
	N	1	2	3	*N*	1	2	3	4
Horizontal	733	0.70			703	0.66			
Oblique	868		0.94		893		0.88		
Angle	511			1.09	500			1.01	
Vertical	1639			1.13	1655				1.19
Subset significances		1.000	1.000	0.251		1.000	1.000	1.000	1.000

9.3.9. Locomotor Mode and Activity

This section describes any within-species differences in locomotor mode with regards to activity type. Previous studies (Crompton & Andau, 1986) have shown differences in locomotor behaviour during foraging and travel so: **Hypothesis 9.6: different locomotor modes will be employed by *I. indri*, *P. diadema* and *H. g. griseus* during feeding and travel.** Activity was recorded with regards to the apparent behavioural context purpose of the locomotor mode. For example if a locomotor mode terminated in resting, the mode was considered 'rest'.

9.3.9.1. *Indri indri*

Locomotor modes are not used evenly across the different activity categories (Figure 9.14). This difference is significant (χ^2 [8, 3713] = 528.157, $p < 0.001$), although the association is not especially strong ($V = 0.267$). Leaping is observed more often than expected during travel and less often during feeding, as predicted by Hypothesis 9.6. All other locomotor modes are less often observed during travel.

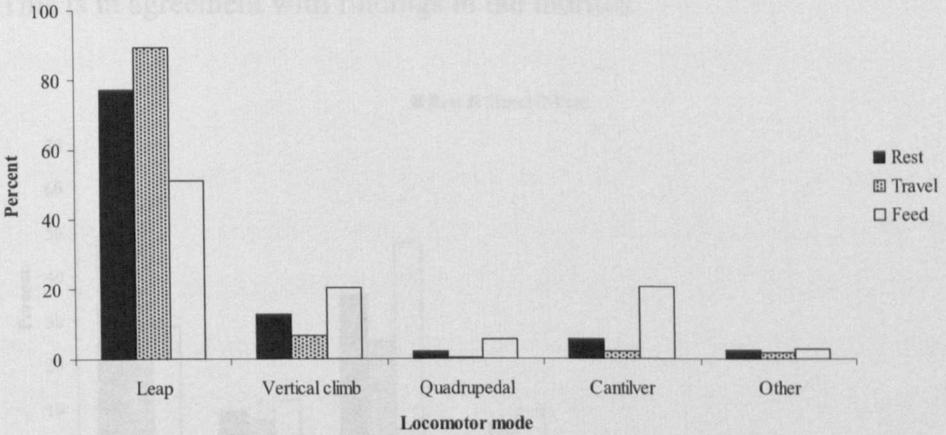


Figure 9.14. Frequency of locomotor modes used in each activity category for *I. indri*.

9.3.9.2. *Propithecus diadema*

As can be seen in Figure 9.15, locomotor modes are not used by *P. diadema* evenly for each activity. The association between locomotor mode and activity is significant (χ^2 [8, 5444] = 429.506, $p < 0.001$), although the association is not very strong ($V = 0.199$). Leaping was observed more during travel and less often during feeding, while all other locomotor modes were less common during travel. This finding is very similar to that for *I. indri*,

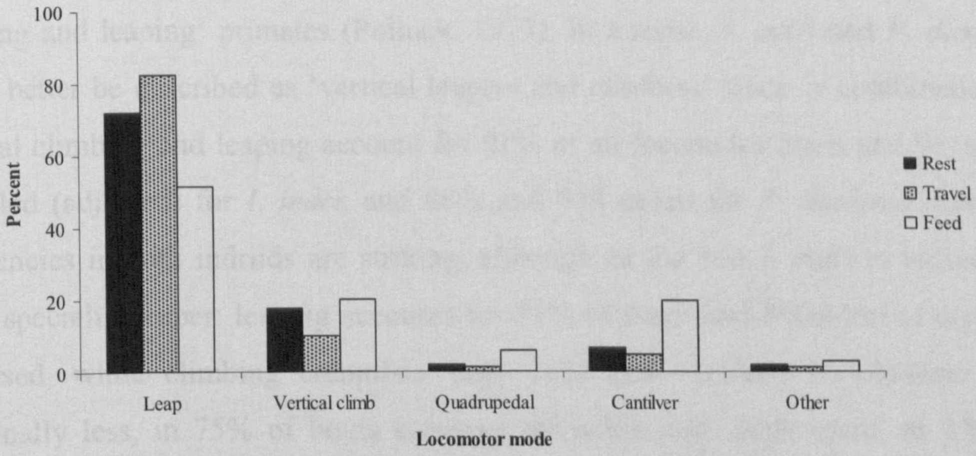


Figure 9.15. Frequency of locomotor modes for each activity category for *P. diadema*.

9.3.9.3. *Hapalemur griseus griseus*

As can be seen in Figure 9.16 locomotor modes are not used by *H. g. griseus* evenly for each activity. The association between locomotor mode and activity is significant (χ^2 [12, 7725] = 669.526, $p < 0.001$), although the association is not very strong ($V = 0.208$). Leaping and running were observed more during travel and less often during feeding, while all other locomotor modes were less common during travel. This is in agreement with findings in the indriids

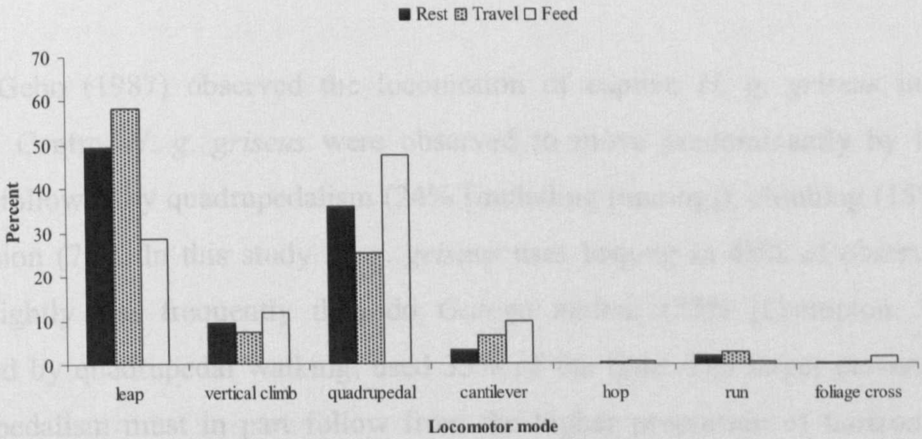


Figure 9.16. Frequency of locomotor modes used during each activity in *H. g. griseus*.

9.4. Discussion

9.4.1. Overall Locomotor Frequencies and Distances Travelled in Different Modes (m/km)

I. indri have long been regarded as the most specialised of the extant 'vertical clinging and leaping' primates (Pollock, 1977). In a sense, *I. indri* and *P. diadema* could better be described as 'vertical leapers and climbers' since a combination of vertical climbing and leaping account for 91% of all locomotor bouts and 961m/km travelled (adjusted) for *I. indri*; and 88% and 938 m/km for *P. diadema*. Leaping frequencies in both indriids are striking, although of the two *I. indri* is indeed the more specialist leaper: leaping accounts for 81% of bouts and 870m/km of distance traversed, while climbing comprises only 10% and 91m/km. *P. diadema* leap marginally less, in 75% of bouts covering 801m/km and climb more, in 13% of bouts, covering 137m/km travelled. The frequencies exceed even those in *Tarsius* species; *Tarsius spectrum* (the spectral tarsier) were observed to leap in 63% of all bouts (MacKinnon & MacKinnon, 1980) and *T. bancanus* in 66% (Crompton & Andau, 1986).

Bipedal hopping on the ground has been recorded for *I. indri* (Napier & Walker, 1967; Walker, 1979). Although no *I. indri* was observed hopping on the ground during this study, this was observed once, for a brief period, during a preliminary study visit to Mantadia (personal observation). The lack of such observations during the study period draws attention to difficulties in recording rare (but potentially important) methods of locomotion during even long-term field studies.

Gebo (1987) observed the locomotion of captive *H. g. griseus* in Duke Primate Centre. *H. g. griseus* were observed to move predominantly by leaping (56%), followed by quadrupedalism (24% [including running]), climbing (15%) and suspension (7%). In this study *H. g. griseus* uses leaping in 48% of observations, only slightly less frequently than do *Galago moholi* (53% [Crompton, 1984]), followed by quadrupedal walking, used 33% of the time. The larger percentage of quadrupedalism must in part follow from the higher proportion of horizontal and oblique supports in the mid-storey in the ranges of *H. g. griseus* (Chapter 2), resulting from a higher incidence of liana vine and also from the structure of *Cathariostachys madagascariensis* (giant bamboo) which dominates *H. g. griseus* diet: with vertical shoots which grow vertically until they buckle under their own weight and thus, together, produce a horizontal layer.

9.4.2 Within Species Support Use and its Interactions with Locomotor Mode

P. diadema used verticals more than do *I indri* (55.4% vs. 40.5%) and of course *H. g. griseus* (12.7%) and indeed more frequently than do *Lepilemur edwardsi* (42.5%). Although both indriids in the present study used vertical supports more frequently than the smallest indriid *Avahi occidentalis* (37% [Warren & Crompton, 1997a]) and *Galago moholi* (16% [Crompton, 1984]), but less than *Tarsius bancanus* (72.4% [Crompton & Andau, 1986]). Compare also, *T. spectrum* (65% [MacKinnon & MacKinnon, 1980]) and *G. alleni* (73% [Charles-Dominique, 1977]), but both MacKinnon and McKinnon (1980) and Charles Dominique (1977) used only three support categories and it is possible that in their studies the category 'vertical' included what would be classed 'angled' in the present study. If this were the case, we can conflate the two categories in this study, in which case *I. indri* would have used vertical/angled supports in 64.1% of displacements while *P. diadema* used this category in 72.16% of cases: this produces percentages more comparable figures to those in MacKinnon and McKinnon (1980) and Charles Dominique (1977).

9.4.3 Relationships between Support Use, Locomotion and Height

For all species there is a clear preference for motion between similar initial and terminal supports, but only weak association between diameters and orientations of initial and terminal supports. Discounting terminal supports, log-linear modelling found locomotor mode and initial support diameter the most significant expression (examining mode, initial support use and initial height). Categorical (Log-Linear) Modelling found that in *I. indri* and *P. diadema,* locomotor mode and initial support diameter interact to influence the horizontal distance travelled. For *P. diadema* the strongest association was found between locomotor mode and terminal orientation. Similarly, locomotor mode has a stronger correlation with terminal support use than initial support use in *I. indri.* Since cantilevering nearly always starts and finishes on the same support, initial diameter and orientation are especially important during cantilevering: horizontal and oblique supports smaller than 5cm in diameter are preferred. Since cantilevering is used most commonly during feeding (see Activity, below) this indicates that feeding is often carried out on small terminal branches.

9.4.4 Horizontal Distance Travelled and Locomotion

For *I. indri* the greatest individual horizontal displacements are achieved via leaping, as might be expected from it constituting their main mode of travel. *P. diadema* achieve the greatest horizontal distances from leaping *and* quadrupedal walking. However quadrupedal walking comprises only a small percentage of their locomotor repertoire (2%). Although *P. diadema* and *I. indri* make their longest leaps from and to vertical supports greater than 10.1cm in diameter, they leap from these supports only 17% of the time, indicating they do not, or cannot, always select the ideal supports for optimum leap length.

The furthest horizontal distances in *H. g. griseus* are achieved, by contrast during running. Distances travelled by quadrupedal walking and leaping are not significantly different. The longest leaps are achieved on vertical to angled supports from 5.1 to 15cm in diameter (although leaping is commonest on angled to vertical supports sized 0.6 to 5cm, which may simply reflect availability). Overall 24.2% of leaps occur from supports suitable for achieving the greatest leap length. However, such a small-bodied primate (800g) could not be expected to gain any benefit from landing-support compliancy on supports of 15cm in diameter.

9.4.5. Vertical Height Change and Locomotion

The greatest vertical height changes were achieved through vertical climbing in both *I. indri* and *P. diadema*. For *I. indri* leaping is proportionally more likely to be used to reduce height than to vertical climbing. However, for *P. diadema* leaping is proportionally more likely to be used to achieve a height increase than vertical climbing. The reasons for this are at present unclear.

In *H. g. griseus* vertical climbing and running achieve the greatest vertical height changes and leaping is responsible for only slight vertical height changes. It is unclear why running, and not quadrupedal walking, is used most frequently to achieve a height change.

9.4.6. Species, Stratum, Locomotion and Support Use

There is frequently a correlation between support use and body size: larger species may need larger supports to sustain their weight, and increased diameter may make it easier to maintain the centre of gravity above the support (Fleagle & Mittermeier, 1980), for example, for South and Central American platyrrhines, both Fleagle and Mittermeier (1980) and Boinski, (1989) noted that larger animals used larger supports, regardless of locomotor type. However, in a study of African catarrhines, all species, regardless of size, preferred medium sized supports (Gebo & Chapman, 1995). A comparison between bout lengths in all three species in the present study indicates that *I. indri* are found on average highest in the canopy and yet travel the furthest in an individual bout; *H. g. griseus* lowest yet travel the shortest distance in a bout. This might appear to correlate best with body size, larger animals living higher and travelling further than smaller animals. In this study, as in studies on platyrrhines (Boinski, 1989; Fleagle & Mittermeier, 1980), the largest bodied species (in this case *I. indri*) used larger supports than did the smallest bodied (in this study *H. g. griseus*.) Indeed some have argued that suspensory postures increase in frequency with size, as it might be easier for a large animal to hang from, rather than balance on top of a branch (Fleagle & Mittermeier, 1980). However Thorpe *et al.* (2007) show that this does not hold true for the largest arboreal primate, the orang-utan. And in this study, body size does not appear to be a determinant of locomotor mode (cf. Preuschoft *et al.* [1998]).

The log-linear modelling studies indicate on the one hand that the study species are separated by stratum, *I. indri* being found the highest, then *P. diadema*, and *H. g. griseus* the lowest, but on the other that locomotor mode is more important than species in determining support usage, and that support use is determined by height, underlining the importance of forest structure in the understanding of locomotion. This would suggest that forest structure determines support availability, which in turn elicits the required locomotor mode. While a relatively simple means whereby niche separation can be achieved might be possible for primate species with different locomotor repertoires, whereby predominantly quadrupedal species will be likely to travel in the upper canopy where there are more horizontal supports, and smaller discontinuities, leaping species to travel lower where there are more vertical supports and larger discontinuities (Fleagle & Mittermeier, 1980; Fleagle *et al.*, 1981. Crompton, 1984) the present study suggests a more subtle relationship between support availability and use, stratum and locomotor capabilities, residing perhaps in detail of the biomechanical characteristics of leaping, such as a development of greater long-distance leaping capacity in *I. indri* at the expense of control over landing, which prevents this genus from selecting more compliant landing supports. Consideration of leap length as a means of efficient crossing of forest zones with more long discontinuities recalls the facts that valleys in the study area were characterised by open spaces and large discontinuities (Chapter 2) and that *I. indri* are denizens of the valleys to a greater extent than are *P. diadema.* Further as discussed in Chapter 8 *I. indri* utilise leaping lower in the canopy than any other locomotor mode (10.7m for leaping with a mean overall height of 11.3m) and during leaping they are closer in height to *P. diadema* (10m for leaping with a mean overall height of 10.6m). This suggests that *I. indri* move lower in the canopy to leap to make greater use of larger discontinuities.

9.4.7 Substrate Use and the Mechanics of Leaping

9.4.7.1 Support Diameter

In this study, although both *I. indri* and *P. diadema* display a preference for supports sized 5.1 to 10cm in diameter, *I .indri* use these supports less (50.5% of all bouts) than *P. diadema* (58.1%), a significant difference. *I. indri* use supports greater than 10.1cm more, *P. diadema* use them less. *I. indri* show a clear preference for takeoff and landing supports sized from 5.1 to 10cm. In contrast over half of all recorded leaps of *H. g. griseus* originate and terminate on supports 0.6 to 5cm in diameter. Indriid hands are long, primarily due to elongation of the phalanges (Napier & Walker, 1967 and see Figure 9.17). Further *I. indri* and *P. diadema* have a pincer-like arrangement between the first digit and the rest of the hand, superficially at least, resembling an opposable thumb. This high degree of prehensility aids them to support their weight when vertically clinging. Thus *I. indri* may need to use larger supports than *P. diadema* simply due to their larger size and thus, larger grip, so that results would tend to support Demes and colleagues' (1995) finding of a preference for graspable supports.

Figure 9.17. A: Hand of adult female *H. g. griseus*. **B:** Hand of sub-adult male *P. diadema* **C:** Foot of sub-adult male *P. diadema*. Photographs: Mary Blanchard, January 2005.

9.4.7.2 Support Diameter during Leaping

In *I. indri* there was a relatively strong association between initial and terminal support diameter, leaps initiated on supports of less than 5cm diameter tending to terminate on similar-sized supports, and also between initial and terminal support orientation, with a strong tendency for leaps initiated on horizontal supports to terminate on horizontal supports. Similarly, in *P. diadema* initial and terminal support diameter showed linkage, but orientations were associated relatively strongly, initial and terminal orientations tending to be the same: leaps initiated on horizontal supports are more likely to terminate on horizontal supports. Results for both species are consistent with expectations for fast, flat-trajectory leaping (horizontal to horizontal) and efficient, high-trajectory leaping (vertical to vertical) respectively. Similarly, there were associations between initial and terminal support diameter, and more strongly, initial and terminal support orientation in *H. g. griseus*, and these were again like to like. Thus, while Hypothesis 9.1 held that the large bodied indriids would use small, compliant, supports for landing leaps to absorb energy and would use larger, less compliant, supports for take-off to minimise energy loss, initial and terminal supports tended to be the same in all three species, consistent with requirements for high-trajectory and low-trajectory leaps, but also with expected support availability in different strata. Similarly, Hypothesis 9.2 held that *H. g. griseus* should use smaller landing, but larger take off supports compared to *I. indri* and *P. diadema* during leaping, but no difference was observed between support use during landing and take-off, although *H. g. griseus* did use smaller supports during leaping overall than did the indriids.

Demes *et al.* (1995) found that in leaping of wild *I. indri* and *P. diadema* there was a preference was 'small' diameter, (vertical) initial and terminal supports. Small supports swayed with the forces of take-off and landing. On takeoff support compliance results in loss of energy compared to leaping from stiff supports, but while disadvantageous in takeoff, this loss of energy to the support is advantageous on landing (Demes *et al.*, 1995). In this study, although both *I. indri* and *P. diadema* display a preference for supports sized 5.1 to 10cm in diameter, *I. indri* use these supports less (50.5% of all bouts) than *P. diadema* (58.1%). *I. indri* use supports greater than 10.1cm more, than *P. diadema*. This is opposite to expectations based on raw height of observation (Chapter 8) and support availability (Chapter 2); and findings in previous reports of other species: Crompton (1984); Warren (1997) and Warren & Crompton (1997a) found that the species which moved lower in the forest used larger supports. *I. indri* tend to be found 2m higher in the canopy than *Propithecus* where *smaller* supports are more available. It follows that *I. indri* select to leap from and to larger supports. On the other hand, *P. diadema* utilised vertical supports more frequently (53.8% of all bouts) than *I. indri* (40.6%). Similarly *I. indri* use vertical supports less than expected compared with *P. diadema*. This finding is consistent with height differentiation between the species (Chapter 8) and the greater availability of vertical supports lower down (Chapter 2). However, both species tend to use vertical supports when lower in the forest, as do *Avahi occidentalis* (western woolly lemur); *Lepilemur edwardsi* (Milne-Edward's sportive lemur [Warren &

Crompton 1997a]), and *Galago moholi* and *Otolemur crassicaudatus* (Crompton, 1984).

9.4.7.3 Support Orientation in Leaping

The most common support orientation for both *I. indri* and *P. diadema* leaping is vertical (Figure 9.8). Oblique and angled supports are used on roughly the same frequency, the fewest leaps beginning on horizontal supports. This is consistent with a preference for energetically optimal high trajectory leaping. Even in *H. g. griseus*, most leaps occur from and to vertical supports (Figure 9.9), the fewest from and to horizontal supports. Hypothesis 9.3 held that *I. indri* and *P. diadema* would use vertical supports for leaping more than the (presumed) less specialist *H. g. griseus*, but during leaping *I. indri* used vertical supports least frequently (40.5%) and *P. diadema* most frequently (55.5%), with *H. g. griseus* falling in the middle (43.7%). The hypothesis is not upheld as stated, as it applies only to comparison of the results for *P. diadema* and *H. g. griseus*. Again, Hypothesis 9.5 held that as the supposedly more specialized leaper, *I. indri* would use vertical take-off, and perhaps landing, supports more than *P. diadema*, to permit ballistically optimal, more efficient leaps, with an orthograde body posture and hence the centre of gravity located along a ballistic trajectory from the hindlimb, and force directed along the more stable long axis of the support. In fact, *I. indri* used vertical supports less often for leaping (40.5%) than *P. diadema* (55.5%) which may be accounted for in terms of support availability in *Indri*'s higher stratum of occupation.

9.4.7.4 Support Use and Leap Length

In *I. indri* the longest leaps are clearly achieved from (and to) vertical supports and the shortest from (and to) horizontal supports. This is consistent with a preference for energetically optimal high trajectory leaping. Similarly, initial support diameter tends to increase with leap length: the longest leaps are made from (and to) supports over 10.1cm in diameter. A similar relationship is seen for terminal support diameter and leap length. This suggests that support stability is more important than dissipation of energy on landing from long leaps and energy loss to the takeoff support is avoided for long leaps. In *P. diadema*, the longest leaps are achieved from and to vertical supports and the shortest from and to horizontal supports, consistent with ballistic expectations. Longer leaps are achieved from supports over 10.1cm in diameter, consistent with a requirement for minimizing energy loss to compliant takeoff supports on long leaps, and again the longest leaps terminate on supports from 10.1 to 15cm (Table 9.41), again suggesting that support stability is more important than dissipation of energy. In *H. g. griseus* longer leaps are achieved from larger initial supports (>5.1cm), consistent with the case in the indriids and expectations for energy saving. Longer leaps are also achieved when leaping from angled and vertical supports, the shorter from horizontal supports (Table 9.44). This is again consistent with use of high trajectories in longer leaps, but less clearly so than with the indriids. The leap-length/terminal diameter relationship is less straightforward: the shortest leaps occur onto the smallest and largest supports categories, the longest leaps are associated with landing supports sized from 5.1 to 15cm. For all three species

In all three species longer (raw measure) leaps are made from larger supports, which both to be verticals. This is again consistent with expectations for high-trajectory, energy or distance-optimized ballistic leaping, rather than fast, flat-trajectory leaping and tends to indicate that stiffness is desirable in takeoff supports but (in the indriids) stability as more desirable than energy loss on landing. Hypothesis 9.4 held that for all three species longer leaps would use larger, more stable, terminal supports. This is upheld for *I. indri*, which landed on supports >10.1cm for their longest leaps. It is in part upheld for *P. diadema* which achieved longest leaps onto supports sized between 10.1 to 15cm, but *not* onto those >15.1cm, and in part upheld for *H. g. griseus* who used supports between 5.1 to 15cm to land their longest leaps and *not* those over >15.1cm. *I. indri* select larger-diameter supports for take-off and landing, achieving their longest leaps on supports greater than 10.1cm in diameter, but *P. diadema* only for take-off, consistent with selection of stiff takeoff supports by both species, but more stable support for landing in *I. indri* but more compliant supports, which can dissipate the shock of landing, by *P. diadema*. Similarly, Crompton *et al.* (1993) found that *Galago moholi* used larger diameter initial supports for its longest leaps, *Tarsius bancanus* larger diameter terminal supports. The present result is considerably more unequivocal in its mechanical implications for these larger leapers. The suggestion of Demes *et al.* (1995) that compliant supports were selected by *I. indri* for takeoff and landing is contradicted by the present findings. Apparent selection of less compliant takeoff and landing supports suggests that energetic efficiency and stable landing supports are more important for *I. indri* than any potential benefit to be derived from compliancy of takeoff or landing supports, and the earlier finding on all locomotor modes might suggest that of these two, stability of the terminal support is more vital. For both *I. indri* and *P. diadema* the longest leaps were achieved from vertical supports, and landed on vertical supports. An apparent preference for vertical supports for takeoff and landing on the longest leaps can be interpreted 1. in terms of an advantage of aligning the centre of gravity with a relatively high leap trajectory on both takeoff (for effective acceleration) and landing (for effective deceleration) 2. in terms of an advantage in directing forces along the stiffest axis of the support: for takeoff this might be attributed to a need for energetic efficiency, but for landing the benefit of a secure landing target may be more important.

9.4.8 Activity

I. indri, *P. diadema* and *H. g. griseus* all use leaping and vertical climbing as their primary modes for travel. (*H. g. griseus* also uses running during bouts of travel). Other modes of locomotion (quadrupedal walking etc.) are used not for travel but to negotiate smaller distances during foraging. Hypothesis 9.6 held that: different locomotor modes will be employed by *I. indri*, *P. diadema* and *H. g. griseus* during feeding and travel. This is upheld: *I. indri*, *P. diadema* and *H. g. griseus* utilised leaping more frequently during travel and all other modes less frequently, while during feeding leaping was used less frequently and all other modes more frequently. Differences have been often been found between modes of locomotion during bouts of travel and bouts of feeding. Fleagle and Mittermeier (1980) suggest that this is because during travel, the end point is general, while in feeding it is more specific often requiring access to relatively "small" terminal branches. In South American platyrrhines, as in African strepsirrhines, less leaping and more climbing and suspension/cantilevering have been were observed during bouts of feeding compared to travel (Fleagle & Mittermeier, 1980; Crompton, 1984; Gebo & Chapman, 1995). This agrees with findings in Malaysian and African strepsirrhines and Central American platyrrhines, where larger (horizontal) supports were used during locomotion than during feeding (Fleagle, 1978; Boinski, 1989; Gebo & Chapman, 1995). During feeding and foraging leaping often decreases and climbing and quadrupedalism increase (Dagosto, 1995).

9.4.9 Predation

Many researchers have considered the importance of predation in locomotor choice and evolution (Gebo *et al.*, 1994; McAdam & Kramer, 1998; Hatle *et al.*, 2002; Sherratt *et al.* 2004; Crompton & Sellers, 2006; Fichtel, 2007). An association has been noted between locomotion and predation in *Lepilemur ruficaudatus* (red-tailed sportive lemur [Fichtel, 2007]): play-back of *Cryptoprocta ferox* (fossa) calls elicited an escape response from *L. ruficaudatus*; calls of *Polyboroides radiatus* (Madagascar harrier hawk) however elicited a cryptic response: staying still and scanning the sky. Fichtel (2007) suggested this was related to the different hunting strategies displayed by *C. ferox* and *P. radiatus*. *P. radiatus* use stealth, so remaining motionless allows *L. ruficaudatus* an opportunity to locate the silent predator; *C. ferox* are noisier while hunting and an escaping *L. ruficaudatus* could use this sound to locate and hence avoid them.

Differences in locomotor behaviour have been observed between normal movement, and movement due to a heightened predation risk in *Colobus badius* (red colobus [Gebo *et al.*, 1994]). While fleeing from either terrestrial or avian 'predators' *C. badius* displayed an increased frequency of leaping and vertical bounding. Leaping occurred at a rate of 33.4% during normal travel but increased to 47.5% in response to terrestrial predation and 52.9% in response to an avian predator. For avian predators the horizontal distance travelled during leaping increased from a mean of 1.82 to 2.5m. Selection pressures surrounding fleeing from predation would of course be elevated. Gebo and colleagues suggest that the anatomical features of limbs would therefore evolve more under selection for the requirements of leaping away from predators than under selection operating on the combination of modes used in a normal travel situation.

Speed of movement in prey species has been linked to predation. Unprofitable prey (those that are unpalatable or have stings, venom etc.) usually move slower and more predictably than profitable prey with no defence mechanisms (Hatle *et al.*, 2002). Models designed by Sherratt *et al.* (2004) confirmed that unprofitable species evolved slower movements than profitable prey, indicating that although metabolic costs played a part, profitable prey evolved rapid movement despite its higher metabolic costs.

In some species, locomotion is broken by pausing; this inevitably increases the energetic costs of locomotion by adding costs of acceleration and deceleration, and increased travel time (McAdam & Kramer, 1998). It is logical to assume that the potential benefits of pausing, such as prey searching, improved endurance, increased detection of prey, and reduced detection or attack by predators must in these cases outweigh its costs (McAdam & Kramer, 1998). Moving animals are more liable to be attacked than stationary ones, possibly due to easier detection, so pausing may decrease detection. However by increasing travel time, an animal increases the time in which it can itself be detected. McAdam and Kramer's (1998) study of vigilance in *Sciurus carolinensis* (grey squirrel) and *Tamias striatus* (eastern chipmunk) found that *S. carolinensis* used pausing to improve anti-predator vigilance, although this behaviour was not observed in *T. striatus*.

Crompton and Sellers (2006) have theorised that for prosimian primates classed as 'solitary foragers', leaping might be a prime predator-avoidance strategy. They suggest that leaping could be as important for 'solitary foragers' as vigilance is for predator-avoidance in non-solitary prosimians. Field studies have shown that mean leap length is far below the maximum achievable. For *Galago moholi* and *Tarsius bancanus*, while leaps greater than 4m have been recorded, mean leap lengths were 0.69 and 1.12m respectively (Crompton & Andau, 1986). Crompton and Sellers (2006) suggest that this discrepancy between mean and maximum leap distances can be attributed to predator avoidance; if an animal were to leap greater distances than is normal, a predator would be confused.

All three species in the present study use high energy leaping as their primary way of travelling within their home ranges, but predation risk appears to substantially differ. The small bodied *H. g. griseus* are at great risk from a range of predators: avian, mammalian and reptilian. They are capable of leaping up to 4m, yet their mean leap length is only 1m. However they were not observed to employ leaping as method of predator avoidance. Rather, the presence of raptors induced a cryptic response; individuals would slowly lower in the canopy and remain quiet and still until the threat had subsided. Terrestrial predators, *Galidia elegans* (ring-tailed mongoose), observers, dogs, caused a mobbing response; individuals would remain facing the potential predator loudly alarm-calling.

Both *I. indri* and *P. diadema* had maximum leap lengths far outweighing their mean; *I. indri* were could leap at least 10m but their mean leap was only 2.5m and *P. diadema* could leap 7m, but their mean was 2.2m. It is difficult to assess the predation risk for the two largest indriids. According to Powzyk, (1997) an eleven month old *I. indri* predated by *Cryptoprocta ferox* but such accounts are rare. *C. ferox* is however known to prey heavily upon the similarly sized (5 to 6.5kg) *P. edwardsi.* Predation attempts of *C. ferox* on both species were witnessed by Powzyk (1997) and attempts by raptors on infant *I. indri* have been observed (Powzyk, 1997; personal observation). According to Powzyk, (1997) *P. diadema* and *I. indri* appear to move towards raptors rather than away from them; and the presence of *C. ferox* does not cause *P. diadema* to flee, rather remaining in the same location and alarm-calling. As with cases of *C. ferox* predation on *P. edwardsi*, the 11 month old *I. indri* noted as predated by Powzyk was apparently taken by *C. ferox* during the night, when an ability to 'out-run' *C. ferox* would be less relevant.

Of course the problem is complicated by extinct predators (Chapter 10). Remains of extinct large bodied *Aquila* (eagle) and *Cryptoprocta* (fossa) have been found on Madagascar. Even extant forms of *Aquila* can carry prey up to 10kg, and the extinct *Cryptoprocta* species, *C. spelea* could probably have taken prey larger than the extant *C. ferox.*

While this study has indicated a discrepancy between maximum achievable and usual leap length for each species there is no clear single cause for this phenomenon. It would seem that only a strong selection pressure is likely to act on maximum leap length and predation is such a force in other primate species. However, the observed responses towards predation did not include long leaps for any of the species, although the absence of observations does not mean that they do not occur. Leaping may well have evolved in small-bodied prosimians as means of predator avoidance, but it is also possible that the potential of producing longer leap lengths compared to the mean evolved as a means of crossing large discontinuities. As was previously shown (Chapter 2) valleys in the study area were characterised by open spaces and large discontinuities. Potentially it may be more efficient, energetically, to cross such large gaps in a single long leap, than to make a diversion which requires many smaller leaps.

9.5. Summary

Hypothesis 9.1 held that: the (large bodied) indriids would use small, compliant, supports for landing leaps to absorb energy and would use larger, less compliant, supports for take-off to minimise energy loss.

This is not upheld. Initial and terminal supports usage showed no difference. This suggests that support availability is more important than minimising energy costs.

Hypothesis 9.2 held that: the relatively higher take-off and landing forces predicted to be incurred by *H. g. griseus* should result in the use of smaller landing, but larger take off supports compared to *I. indri* and *P. diadema* during leaping.

This is in part upheld: *H. g. griseus* did use smaller supports during leaping compared to the indriids, however no difference was observed between support use during landing and take-off.

Hypothesis 9.3 held that: *I. indri* and *P. diadema* would use vertical supports more than the (presumed) less specialized *H. g. griseus*.

This is not upheld. During leaping *I. indri* used vertical supports least frequently (40.5%) and *P. diadema* most frequently (55.5%), with *H. g. griseus* falling in the middle (43.7%).

Hypothesis 9.4 held that: that as the supposedly more specialized leaper (Oxnard *et al.*, 1990) *I. indri* will use vertical take-off, and perhaps landing, supports more than *P. diadema*, to permit ballistically optimal, more efficient leaps, where an orthograde body posture both locates the centre of gravity located along or near a ballistic trajectory from the hindlimb, and also directs force along the more stable long axis of the support.

This is not upheld: *I. indri* used fewer vertical supports (40.5%) for leaping from and to compared to *P. diadema* (55.5%).

Hypothesis 9.5 held that: for all three species longer leaps will end on larger, more stable supports to provide a safer landing.

This is upheld for *I. indri*, who landed on supports >10.1cm for their longest leaps. This is in part upheld for *P. diadema* who achieved longest leaps onto supports sized between 10.1 to 15cm, but *not* onto those >15.1cm. This in part upheld for H. g. griseus who used supports between 5.1 to 15cm to land their longest leaps and *not* those over >15.1cm.

Hypothesis 9.6 held that: different locomotor modes would be employed by *I. indri*, *P. diadema* and *H. g. griseus* during feeding and travel.

This is upheld: *I. indri*, *P. diadema* and *H. g. griseus* utilised leaping more frequently during travel and all other modes less frequently, while during feeding leaping was used less frequently and all other modes more frequently.

Chapter 10 Predation

This chapter reviews the literature of predation on all lemur species. A brief description of extinct Malagasy predators and their potential role in forming present day predator avoidance tactics is included. The role of predation risk as a factor in habitat choice, social grouping and dynamics is also discussed as are descriptions of predation observed and inferred during the study.

10.1 Predation in Lemurs

Predation and its effects on prey is difficult to measure. It is rare for an observer of a prey species to witness predation: the observers' presence makes it less likely that a wild, unhabituated predator will attack. Much knowledge of predation originates from examining predators' scats and by finding remains of animals with injuries that can be attributed to predation. It is also possible to study how an animal responds to potential predators and use this to infer which animals they perceive to be threats. This evidence strongly suggests that primates are subject to a substantial predation risk (Miranda *et al.*, 2006).

Accounts of predation in the literature are often anecdotal, observed only once. Given a lack of quantitative evidence, it is easy to assume that any one observed event is indicative of a general predation pattern: '*Cryptoprocta ferox* (fossa) was seen predating upon *Propithecus*, therefore *C. ferox* always predate upon *Propithecus*'.

In a similar way, a study of citations of tool-use anecdotes showed that most anecdotes are misrepresented in the literature (Sarringhaus *et al.*, 2005). When researchers cite a study, they often use a single event as evidence that the entire population does the same (Sarringhaus *et al.*, 2005). On occasion this is later proved correct, but often the tool-use remains the preserve of the one initial individual (Sarringhaus *et al.*, 2005). Sarringhaus *et al.* (2005) ask for caution, not in the reporting of anecdotes, but in their citation.

The small nocturnal lemurs of the family *Cheirogaleidae*, especially *Microcebus* spp. (mouse lemurs) have the most diverse range of documented predators of all lemurs (Goodman *et al.*, 1993a). *Accipiter henstii* (Henst's goshawk [Karpanty, 2003]), *Tyto alba* (barn owl [Goodman *et al.*, 1993a; 1993b]), *Tyto* *soumagnei* (Madagascar red owl [Goodman & Thorstrom, 1998]), *Asio madagascariensis* (Madagascar long eared owl [Goodman *et al*., 1993a; 1993c; Rasoloarison *et al*., 2000]), *Polyboroides radiatus* (Madagascar harrier hawk [Karpanty, 2003; Karpanty & Goodman, 1999]), *Aviceda madagascariensis* (Madagascar cuckoo falcon), *Vanga curvirostris* (hooked-billed vanga), *Ithycyphys miniatus* (colubrid snake), *Sanzinia madagascariensis* (Madagascar tree boa), *Cryptoprocta ferox*, *Mungotictis decemlineata* (narrow-striped mongoose), and *Galidia elegans* (ring-tailed mongoose) are all known to prey upon *Cheirogaleidae* (Goodman *et al*., 1993a; Goodman, 2003a; Goodman *et al*., 2003).

10.1.1. *Cryptoprocta ferox*

Cryptoprocta ferox (fossa) is a viverrid carnivore endemic to Madagascar, found in undisturbed dry and wet forests (Hawkins, 2003). *C. ferox* is solitary except in the mating season, October to December, when males and females can be seen together (Hawkins *et al*., 2005). It is the largest terrestrial animal in Madagascar: males have a mean body weight of 7.4kg and females 6.1kg (Hawkins, 1998). *C. ferox* is not only terrestrial: the species is adapted to the arboreal environment, combining excellent climbing skills with the ability to make controlled, head-first descents (Iwaniuk *et al*., 2000).

Figure 10.1. *Cryptoprocta ferox* (fossa) in Vakona Park. Photograph: Mary Blanchard, 29 August 2005.

The diet of *C. ferox* contains a higher proportion of primates than any other mammalian predator (Hawkins & Racey, 2005). *C. ferox* predation on genus *Eulemur* has been documented for *Eulemur coronatus* (crowned lemur) at Ankarana

(Wilson *et al.*, 1989) and *Eulemur fulvus* (common brown lemur) at Ranomafana (Goodman *et al.*, 1993a). *C. ferox* predation has been described for *Propithecus verreauxi* (Verreaux's sifaka) near Morondava, at Beza and for *Propithecus deckeni* (Decken's sifaka) near Bongolava (Goodman *et al.*, 1993a). At Kirindy, near Morondava, *P. verreauxi* constitutes a major part of the diet of *C. ferox* (Rasoloarison *et al.*, 1995). It appeared that this large lemur was taken preferentially, *C. ferox* removing 29% of the yearly population growth (Rasoloarison *et al.*, 1995). At Kirindy lemurs comprised 57% of the predated biomass and over half of the individual prey items (Rasoloarison *et al.*, 1995). The presence of *Cheirogaleus medius* (fat-tailed dwarf lemur) in scats at a period when the lemur was hibernating shows that *C. ferox* is capable of removing the lemur from hibernation (Rasoloarison *et al.*, 1995).

The remains of at least two *Cheirogaleus major* (greater dwarf lemur) were recovered from twenty *C. ferox* scats examined from Andringitra National Park, specifically from the Plateau d'Andohariana (Goodman *et al.*, 1997). In addition at least one *Lepilemur mustelinus* (weasel sportive lemur) was also found (Goodman *et al.*, 1997).

C. ferox predation accounted for five out of seven deaths in thirteen released *Varecia variegata* (black-and-white ruffed lemur) in Betampona Reserve, eastern Madagascar (Britt *et al.*, 2001; 2003). This high rate was hypothesised to be due to the naivety of captive bred lemurs to *C. ferox*. Britt *et al.* (2001; 2003) knew of no wild *V. variegata* taken during the study. Four of the five deaths occurred during a six month period. Britt *et al.* (2001; 2003) suggested that a single *C. ferox* could have specialised in the easy-to-catch released *V. variegata*.

This opportunistic nature of *C. ferox* kills has been noted in the eastern fragmentary forest at Tsinjoarivo, where an episodic bout of predation on *P. diadema* was thought to be attributable to just one individual *C. ferox* (Irwin, pers. comm. to Colquhoun, 2006).

During 1998 remains of two *Eulemur albifrons* (white-fronted brown lemur [fur, tail and stomach contents]) were found in Betampona, both attributed to *C. ferox* kills (Britt *et al.*, 2001). In 2001 two *C. ferox* were disturbed feeding from an *E. albifrons* in the same forest (Britt *et al.*, 2001).

An old *Eulemur rubriventer* (red-bellied lemur) female was found predated upon by *C. ferox* in southwest Madagascar (Overdorff, 1995). The female was radio-collared as part of an ongoing study. It appeared that the *C. ferox* had consumed most of the lemur, including internal organs, leaving only the radio-collar, fur, distal tail portion and skull.

A substantial study of *C. ferox* predation has been carried out for *Propithecus edwardsi* (Milne-Edward's simpona [Wright, 1998; Wright *et al.*, 1997]). Eight *C. ferox* faecal samples were collected over ten years at Ranomafana (Wright *et al.*, 1997). All samples were found to contain lemur remains (Wright *et al.*, 1997). Remains were found of four large diurnal lemurs, all over 2kg, suggesting a preference for larger prey; *P. edwardsi*, *Eulemur rufus* (red-fronted brown lemur), *E. rubriventer* and *Prolemur simus* (greater bamboo lemur [Wright *et al.*, 1997]). Remains of the 5.3 to 6.3kg *P. edwardsi* (Kappeler, 1991) and 2.5kg *E. rufus* (Kappeler, 1990) were found in more than one scat (Wright *et al.*, 1997). A preference for larger prey is shown in other mammalian carnivores outside Madagascar: *Panthera pardus* (leopard) most often preys upon large-bodied individuals (Zuberbühler & Jenny, 2002).

The same study observed groups of *P. edwardsi* to assess potential predation (Wright, 1998). Seven cases of predation by *C. ferox* were confirmed, with no preference for age and sex (Wright, 1995; Wright *et al.*, 1997; Wright, 1998). Twelve other *P. edwardsi* disappeared, possibly as a result of *C. ferox* predation, although three of these could have emigrated to different groups (Wright, 1998). Three of the known kills occurred at night, while *P. edwardsi* were sleeping, also coinciding with the darkest phase of the moon (Wright 1995; 1998). All verified kills occurred between July and September (Wright, 1998). This is the dry season, when *P. edwardsi* infants are one to three months old (Wright, 1998). Individuals were taken from groups with four to six individuals, suggesting there was no link between low predation risk and large group size (Wright, 1995). Wright (1995) suggests that *C. ferox* is an 'ambush' predator, in which case more 'eyes and ears' are not of particular benefit to a prey species. No cases of predation by raptors were observed during this study (Wright, 1998).

Powzyk (1997) observed a joint attempt by a male and female *C. ferox* to catch *P. diadema*. This occurred in October, during the *C. ferox* mating season. Each *C. ferox* approached from opposite directions, the female on the ground and the male moving agilely towards them in the trees. The group had not noticed the male, focussing entirely on the female. It appeared to Powzyk (1997) that the male was waiting for the *P. diadema* to move in its direction prior to attacking. However the group moved off in the other direction and no attack was forthcoming. Powzyk (1997) attributed this rare observation to the fact that the *C. ferox* had become habituated to the observers' presence.

It appeared to Powzyk (1997) that *C. ferox* made a successful attempt on an eleven month old *I. indri*. The infant disappeared overnight in June (19 June 1994) and in the morning the adult female was found 500m from her rest spot of the previous night, a rare occurrence in *I. indri*. The adult male rejoined the female later in the day following a 'long-call'. Although no remains were found, Powzyk (1997) believed that *C. ferox* was the only nocturnal predator capable of taking an eleven month *I. indri*, especially as *C. ferox* were known to inhabit the study area. This occurred between a first quarter moon (16 June 1994) and new moon (23 June 1994 [www.timeanddate.com]). This is not the darkest phase of the moon, as was the case of the *P. edwardsi* predations in Ranomafana and is prior to the July to September period in which all known kills occurred.

10.1.2. *Viverricula indica*

The small *Viverricula indica* (Indian civet) is an introduced predator to Madagascar (Goodman *et al.*, 2003). *V. indica* has been observed preying upon an infant *Lemur catta* (ring-tailed lemur [M. Enafa pers. comm. to Goodman *et al.*, 1993a]). The *V. indica,* lying flush to the ground, waved its tail, which is similar in appearance to that of the *L. catta*. *L. catta* approached the familiar looking tail, at which point the civet attacked an infant by grabbing its muzzle.

10.1.3. *Felis catus* and *Canis lupus familiaris*

Felis catus (domestic cat) and *Canis lupus familiaris* (domestic dog) are introduced to Madagascar, and feral examples are common (Goodman *et al.*, 2003). Bones of *Lemur catta* have been found at feral *F. catus* dens, indicating they predate upon lemurs (P. Rakatomanga pers. comm. to Goodman *et al.*, 1993a). *C. l. familiaris* are thought to prey upon *Propithecus verreauxi*. A carcass found at Beza Mahafaly Special Reserve, southern Madagascar, had bite wounds at the base of the spine consistent with a canine predator (Sauther, 1989).

10.1.4. *Crocodilus niloticus*

One of the more unusual Malagasy predators must be *Crocodilus niloticus* (Nile crocodile). In Madagascar *C. niloticus* can reach 4.5m in length and could once be found throughout much of the island (Kuchling *et al.*, 2003). Although no cases of predation have were observed, Wilson *et al.* (1989) suggested that the *C. niloticus* might prey on *Eulemur coronatus* at Ankarana.

10.1.5. *Acrantophis madagascariensis*

Three species of boa are found on Madagascar: *Acrantophis madagascariensis* and *Acrantophis dumerili*, both ground boas, and *Sanzinia madagascariensis*, the tree boa (Raxworthy, 2003). *A. madagascariensis* and *S. madagascariensis* are both known to take lemurid prey (Raxworthy, 2003). An *A. madagascariensis* (Madagascar ground boa) was observed swallowing an adult *Eulemur albifrons* (2 to 2.6kg) on Nosy Mangabe (A. Peyrieras pers. comm. to Goodman *et al.*, 1993a). Boas have also been observed eating *H. g. griseus* in Ranomafana (R. Rakoto pers. comm. to Goodman *et al.*, 1993a) and at the Station Foresteière de Tampolo (Rakotondravony *et al.*, 1998).

It is not only smaller lemur species that are at risk from predation from snakes. A large *A. madagascariensis* was observed constricting an adult female *Propithecus coquereli* (Coquerel's sifaka) near the Anjohibe caves, north western Madagascar (Burney, 2002). An adult female *P. coquereli* approximately weighs 3.8kg (Kappeler, 1991). The *A. madagascariensis* was estimated at 3m in length, with a girth of 25cm, far larger than most *A. madagascariensis* seen (Burney, 2002). The *P. coquereli*, finally released by human intervention from the *A. madagascariensis'* grip, was noticed to be lactating. A slight bulge high in the *A. madagascariensis* oesophagus, suggested that the female's infant had already been eaten.

10.1.6. *Asio madagascariensis, Tyto alba* and *Tyto soumagnei*

Asio madagascariensis (Madagascar long-eared owl) is the largest species of owl in Madagascar, females weighing 770g (Rene de Roland & Goodman, 2003). *A. madagascariensis* are found throughout Madagascar, including urban areas (Rene de Roland & Goodman, 2003). Remains of either an adult *H. g. griseus* or *Avahi laniger* (eastern woolly lemur) were found in a pellet from *A. madagascariensis* in the

Bezavona Forest, eastern Madagascar (Goodman *et al.*, 1993a). In Kirindy forest, remains of four lemur species were found in pellets of *A. madagascariensis*: *Microcebus* spp., *Cheirogaleus medius*, *Mirza coquereli* (Coquerel's dwarf lemur) and *Lepilemur mustelinus* (Rasoloarison *et al.*, 1995). These four lemurs range in size from the 30g *Microcebus* spp. to the 600g *L. mustelinus* (Kappeler, 1990). In the same forest *Microcebus murinus* (grey mouse lemur) was preyed upon by *Tyto alba* (barn owl [Rasoloarison *et al.*, 1995]). Studies in the Ihazoara Valley have shown that *Microcebus griseorufus* (reddish-grey mouse lemur) and *M. murinus* are both prey for *A. madagascariensis*, the former far more commonly (Rasoloarison *et al.*, 2000). *Microcebus rufus* (brown mouse lemur) is prey for *Tyto soumagnei* (Madagascar red owl) on the Masoala Peninsula (Goodman & Thorstrom, 1998). A minimum of three individuals were found in pellets over two years; no *M. rufus* were found in pellets from a third year (Goodman & Thorstrom, 1998).

10.1.7. *Accipiter henstii*

The endemic *Accipiter henstii* (Henst's goshawk) is the largest of the Malagasy *Accipiter* spp. (Rene de Roland & Thorstrom, 2003). Found throughout Madagascar, males weigh around 600g and females 1kg (Rene de Roland & Thorstrom, 2003) and they are approximately 52 to 62cm in height (Morris & Hawkins, 1998). Karpanty (2003; 2006) found in a study on raptor nest sites in Ranomafana National Park that *A. henstii* preyed upon seven lemur species: *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *H. g. griseus*, *Eulemur rufus*, *Eulemur rubriventer* and *Varecia variegata editorum* (southern black-and-white ruffed lemur). The largest of its prey is *V. v. editorum* weigh on average 3.5kg (Kappeler, 1990); *E. rufus* weighing 2.4kg (Kappeler 1991) and *E. rubriventer* 2kg (Kappeler, 1990). The percentage of the Ranomafana lemur population killed each year by *A. henstii* was calculated by Karpanty (2006). The medium rates of predation for each species preyed on by *A. henstii* were: *M. rufus* 1.55%; *C. major* 2.16%; *A. laniger* 3.26%; *H. griseus* 42.31%; *E. rufus* 5.80%; *E. rubriventer* 7.17% and *V. v. editorum* 3.48% .

Together with *P. radiatus*, the potential total yearly median rate of predation for *H. griseus* was 69.74%, with a minimum of 15.12% and a maximum of 100% (Karpanty, 2006). Karpanty (2006) suggests that the highly unlikely maximum figure resulted from the survey being conducted during the nesting season. Other prey may be easier to catch at different times of the year (Karpanty, 2006). Karpanty (2006) found a distinct seasonal pattern to raptor predation: no predation being recorded during the incubation period of nesting or during observations made outside of the nesting season.

A. henstii also preys upon *Eulemur sp.* and *Avahi laniger* (Goodman *et al.*, 1998; Karpanty, 2003). In the dry forest of Kirindy, in western Madagascar, *A. henstii* has been observed carrying off *E. fulvus* (Schwab, 1999). Predation of a juvenile male *A. laniger* by *A. henstii* was observed at Ranomafana (E. Balko pers. comm. to Goodman *et al.*, 1993a). At midday the *A. henstii* swooped down, hit the resting *A. laniger* and carried the animal to the ground before feeding. The *A. laniger* weigh 0.5kg without its head, which had been eaten. *A. laniger* made up 65.4% of the diet of *A. henstii* in the Masoala Peninsula, northeastern Madagascar (Goodman *et al.*, 1993a).

10.1.8. *Polyboroides radiatus*

Endemic to Madagascar, *Polyboroides radiatus* (Madagascar harrier hawk) is found in primary and degraded forests (Thorstrom *et al.*, 2003). Larger than *A. henstii*, *P. radiatus* is approximately 68cm in height (Morris & Hawkins, 1998). In a study of nest sites at Ranomafana, *P. radiatus* was found to prey upon four species: *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger* and *H. g. griseus* (Karpanty, 2003). The percentage of the lemur population killed each year by *P. radiatus* was calculated and median rates of predation were: *M. rufus* 2.7%, *C. major* 1.12%, *A. laniger* 8.34%, *H. griseus* 27.43% (Karpanty, 2006).

Interestingly, in Karpanty's (2006) study, there was no predation by either *A. henstii* or *P. radiatus* on *Propithecus edwardsi*. Although fully grown adults (5.8kg) are probably too heavy -studies show that *A. henstii* and *P. radiatus* can carry prey of up to 4kg, infants and juveniles would be viable prey (Karpanty, 2006). *A. henstii* do kill adult *V. v. editorum*, which weigh 3.5kg (Karpanty, 2006). The largest prey *P. radiatus* was found to capture at Ranomafana was the 800g *H. griseus* (Karpanty, 2006), although it has been observed taking larger prey elsewhere.

A *P. radiatus* was observed seizing an adult female *Propithecus verreauxi* which was nursing a small infant, along the Onilahy River, southwest Madagascar (J.M. Rasoanindrainy pers. comm. to Goodman *et al.*, 1993a). The *P. radiatus* appeared to have difficulty flying while carrying the adult female; the infant, releasing its grip from its mother, fell. Adult *P. verreauxi* weigh 3.6kg (Kappeler 1990; 1991). Studies of *P. radiatus* in Berenty and Bealoka private reserves showed that *P. verreauxi* comprised 48.4% of the total mass of *P. radiatus'* diet, including infants and adults (Karpanty & Goodman, 1999). The *P. verreauxi* were taken during the courtship stage of the *P. radiatus* breeding season (Karpanty & Goodman, 1999). This agrees with findings in Ranomafana, where high levels of lemur predation by raptors are thought to coincide with courtship and the pre-fledgling stage (Karpanty, 2003). For *P. radiatus* at Berenty and Bealoka Reserves in southeastern Madagascar, courtship begins in August (Karpanty & Goodman, 1999).

Three failed attempts of *P. radiatus* predation on adult *P. verreauxi* have been observed at Beza Mahafaly Special Reserve (Brockman, 2003). Also at Beza, a *P. radiatus* has been observed carrying off a young *Lemur catta* (Goodman *et al.*, 1993a). Juvenile and adult *L. catta* bones were found beneath a *P. radiatus* nest site at Lac Tsimanampetsotsa, south-eastern Madagascar (Goodman *et al.*, 1993a). An adult *L. catta* weighs 2.5kg (Kappeler, 1991).

In Kirindy an *Avahi occidentalis* (western woolly lemur) was observed being taken from its sleeping tree by *Polyboroides radiatus* (Schülke & Ostner, 2001). The *P. radiatus* clung to the tree, attacking the *A. occidentalis* in its sleeping hole, using its beak. The *P. radiatus* continued to tear pieces from the lemur until it was disturbed. *P. radiatus* also prey upon *Cheirogaleus medius* (Gilbert & Tingay, 2001).

Powzyk (1997) twice observed *P. radiatus* close to groups of *P. diadema.* On both occasions alarm calls were issued and adult females chased the *P. radiatus* until they flew off. In the same study an attempt of a *P. radiatus* to take an eight month old *I. indri* was observed (Powzyk, 1997). The infant was feeding three metres above its mother when a *P. radiatus* flew in to attack. The female raced up the tree and reached out to the bird of prey, almost grabbing it in her hands and forcing it to veer away. The infant jumped onto its mothers back and the pair moved down into a dense thicket, remaining quiet as the *P. radiatus* circled above. The male *I. indri* remained high in the canopy giving predator alarm calls.

10.1.9. *Buteo brachypterus*

Buteo brachypterus (Madagascar buzzard) is endemic to Madagascar, and common throughout the island (Thorstrom *et al.*, 2003). Individuals weigh up to 680g (Ravokatra *et al.*, 2003). A *B. brachypterus* was seen feeding on an adult male

Propithecus verreauxi 80km north of Morondava (C. Cassel pers. comm. to Goodman *et al*., 1993a). On the Masoala Peninsula, northeastern Madagascar, studies of *B. brachypterus* have shown no evidence of lemurid prey (Berkelman, 1997).

10.1.10. Predation by *Eulemur rufus*

There is evidence of predation on a *Lemur catta* newborn by a sympatric *Eulemur rufus* at Berenty (Pitts, 1995). As *E. rufus* are not native to the reserve, introduced in 1972, the sympatry is artificial (Jolly, pers. comm. to Pitts, 1995). This observation remains significant, nevertheless as *E. rufus* are sympatric with a large number of similarly sized lemurs throughout their natural range. However, it must be considered that this incident may have resulted from unique man-made conditions. A weak new born infant *L. catta* fell from its mother and was immediately picked up by a female *E. rufus* who was then observed to eat the infant in its entirety (Pitts, 1995). A further case was recorded at Berenty, when a *L. catta* mother had semi-abandoned her infant. She remained within close distance and watched (Jolly *et al*., 2000). An *E. rufus* female descended from a tree, grabbed the infant and was seen to bite it and tear it apart before running off with it (Jolly *et al*., 2000).

Figure 10.2. *Eulemur rufus* (red-fronted brown lemur), Kirindy Forestry Reserve. Photograph: Mary Blanchard, 11 May 2005.

Although this would appear to be abnormal behaviour, there is an account of *Eulemur fulvus* killing and eating a *Terpsiphone mutata* (Madagascar paradise flycatcher) nestling (Mizuta, 2002). Although this was observed on only one occasion, similar damage to other *T. mutata* nests, suggested to Mizuta (2002) that predation by *E. fulvus* was fairly common. Mobbing by an adult *T. mutata* of *H. g.*

griseus in Mantadia (01 December 2004), might also suggest that the birds consider lemurs a threat. *E. fulvus* have also been observed consuming eggs from nests of *Ploceus sakalava sakalava* (Sakalava weaver) in Ankarafantsika (Nakamura, 2004). Attempts were made on three consecutive days, eggs being successfully eaten on two of these (Nakamura, 2004).

10.1.11. Alarm Calling and Anti-Predator Tactics

A study in Ranomafana examined how different lemur species respond to diurnal raptor calls (Karpanty & Grella, 2001). The lemurs were tested with vocalisations from three species: *Accipiter henstii*, *Polyboroides radiatus* and *Eutriorchis astur* (Madagascar serpent eagle). *H. g. griseus* reacted to calls from all three raptors. Calls from *P. radiatus* made them look at the source and search the sky. Vocalisations from *E. astur* gave a stronger reaction, in addition to scanning they gave predatory alarm calls, dropped down in the canopy and fled from the source. The response to *P. radiatus* was similar, but they moved away from the source on even more occasions.

Powzyk (1997) found that *P. diadema* alarm called in the presence of aerial predators daily (1.03 calls per day, per group), while alarm calls due to ground predators were less common (0.19 calls per day, per group). A similar pattern was observed for *I. indri*. Aerial predator alarm calls were heard at a rate of 0.84 calls per day, per group, and ground predators alarm called 0.20 calls per day, per group (Powzyk, 1997). This led Powzyk (1997) to suggest that both *P. diadema* and *I. indri* were under greater threat of predation by raptors than they were by *Cryptoprocta ferox*. However, more frequent observation of aerial predators, and more alarm calling in their presence does not necessarily mean they are the greatest threat. It is possible that although aerial predators are more common, ground predators are actually the greater or more effective threat.

Karpanty (2006) noted that the anti-predator tactics of *H. g. griseus* are opposite to those of the less-preyed-upon *Eulemur* and *Varecia*. Under threat of predation, Grassi (2001) found *H. g. griseus* became cryptic and huddled into a sleeping, yet vigilant group. However *Eulemur* and *Varecia* both act aggressively in predator encounters (Karpanty & Grella, 2001).

10.2 Extinct Malagasy Predators

In addition to extant predatory species, there are recently-extinct predators which may have shaped lemur anti-predatory behaviour. Reasons behind these extinctions are unclear, but appear connected to the arrival of humans on the island. The date of first human arrival on Madagascar is a contentious issue. The first settlements appear around A.D. 80 on the coast of south-western Madagascar near Tulear (Dewar & Wright, 1993). Earlier evidence of human occupation comes in the form of human-modified *Hippopotamus* bones (MacPhee & Burney, 1991). MacPhee and Burney (1991) dated these bones to around 2000 B.P, placing them before the first settlements.

Since human arrival the environment in Madagascar has altered, resulting in extinction of most of the large native animals (Burney *et al.*, 1997). There is difficulty in separating human impact from concurrent climate-change. The environment on Madagascar appears to have been changing for more than 40,000 years (Burney, 1997), much longer ago than any evidence of human arrival has been reported. Despite this on-going climate change it would still appear that the mega-fauna has died out within the 2,000 year time frame of human habitation (Burney, 1997). Burney *et al.* (1997) found that in caves with only a recent record of human activity, many of the mega-fauna existed for longer than in other areas.

An extinct and larger form of *Cryptoprocta* was found on Madagascar during the Holocene (Goodman *et al.*, 2004). This form, known only from sub-fossil records, has been named as *Cryptoprocta spelea* (Goodman *et al.*, 2004). Goodman *et al.* (2004) suggest that the massive jaw and large carnassial teeth, used to shear meat, of *C. spelea* are indicative that it could take larger prey than can *C. ferox*.

At least two species of the genus *Aquila* (eagle) now extinct on Madagascar were once found on the island (Goodman & Rakotozafy, 1995). In the early part of the last century a collection of bones were found in Mitoho Cave, on the Mahafaly Plateau, southwest Madagascar (Goodman, 1994). Eggshell found in this assemblage, has been dated to 4030 ± 70 radiocarbon years (Goodman, 1994). A bone attributed to an unidentifiable form of the large eagle *Aquila* has been found in this assembly (Goodman, 1994). Bones of *Lemur catta* and *Propithecus verreauxi*, found in the Mahafaly region, have been found in the cave along with bones of the extinct *Megaladapis edwardsi* (estimated at an approximate 50 to 100kg body weight

(Jungers, 1978; Goodman, 1994). Remains of *Aquila* have also been collected from Ampasambazimba, situated on the central highland plateau (Goodman & Rakotozafy, 1995). Similar sized extant forms of *Aquila* are diurnal, can carry animals weighing up to 10kg and are capable of killing prey up to 40kg (Goodman, 1994). Remains of a smaller *Aquila* species have been found at Ampasambazimba, western Madagascar (Goodman & Rakotozafy, 1995).

10.2.1. Predator Removal and Re-introduction

Gil-da-Costa *et al.* (2003) studied the behaviour of *Alouatta palliata* (mantled howler monkey) following the re-introduction of *Harpia harpyja* (harpy eagle) to Barro Colorado Island, Panama. *A. palliata* had not been prey to *H. harpyja* for at least 79 years prior to the re-introduction. Despite this, call playback experiments showed they rapidly learnt to recognise the call of *H. harpyja* and to initiate escape. This response continued for at least one year after removal of *H. harpyja* from Barro Colorado Island for environmental reasons. Control experiments were conducted on *A. palliata* in Gigante, Panama, where *H. harpyja* has been lost as a predator 50 to 100 years ago with no recent reintroduction (Gil-da-Costa *et al.*, 2003). This population did not react to calls of *H. harpyja* and did not develop a reaction, even after repeated playbacks. It should be noted that the *A. palliata* in Gigante were not at risk of predation from mammals, birds or snakes during the absence of *H. harpyja* (Gil-da-Costa *et al.*, 2003). A similar situation was found in relation to *Alces alces* (moose) exposed to predator recolonisation (Berger *et al.*, 2001). Gil-da-Costa *et al.* (2003) suggested that 50 to100 years was long enough for prey to lose an ability to react to a lost predator, although only a short re-exposure of time was required to re-learn the response.

Studies in Taï National Park, Ivory Coast have examined the relationship between human predators and their prey, *Cercopithecus diana* (Diana monkey [Bshary, 2001]). Humans have traditionally mimicked the calls of *Stephanoaetus coronatus* (crowned hawk eagle) and the distress calls of *Cephalophus* spp. (duiker) caught by *Panthera pardus* to initiate a mobbing response in *C. diana*, allowing the humans to locate them, killing up to 10,000 monkeys a year. Outside the research areas, it was found that *C. diana* had evolved a separate response to the human imitations: rather than mobbing they would silently move away. Poaching has been eliminated from the areas of research and in these areas *C. diana* did not discriminate between human and non-human calls, mobbing in both cases. As poaching occurred in these areas until recently, this discrimination has presumably been lost in less than two decades, equivalent to the lifespan of one monkey. Studies of other groups in the same reserve indicate that discrimination was lost within four years of the cessation of poaching, equivalent to one monkey generation (Bshary, 2001).

Alteration of behaviour has been observed for *Rattus norvegicus* (Norway rat) in relation to *Vulpes vulpes* (red fox [Fenn & Macdonald, 1995]). A population of the usually nocturnal *R. norvegicus* was found to be diurnal, and this behaviour modification appeared to be associated with the presence of the nocturnal predator, *V. vulpes*. Fenn and Macdonald (1995) removed one population of diurnal *R. norvegicus* keeping them in an enclosure free of *V. vulpes*. This sub-population of *R. norvegicus* then reverted back to nocturnal behaviour.

10.3. Predation as a Controller of Ecology and Behaviour

10.3.1. Predation and Habitat Choice

From a predation view point, the 'best' habitats can of course be either those with a decreased risk of predators or those where there is an increase in the ability to avoid predators (Enstam & Isbell, 2004). Therefore, differences in potential predator species, predator density and habitat structure all affect the predation risk of any habitat (Enstam & Isbell, 2004). Habitat may indeed have a very strong bearing on rates of predation. Cheney and Wrangham (1987) compared predation rates on *Chlorocebus aethiops* (vervet monkey) in different studies. They noticed that estimated predation rates in Sambura, Kenya, (Whitten, 1983) were half those at Amboseli, Kenya, (Cheney *et al.*, 1981), despite the same social structure (Cheney & Wrangham, 1987).

Structural differences that can affect the perceived and actual predation risk include: the availability and distance of refuges such as cliffs, burrows, trees and protective cover, and the height and density of obstructive cover such as tall grass (Enstam & Isbell, 2003). Prey animals may prefer habitats that provide more refuges, increased protective cover or increased predator visibility (Enstam & Isbell, 2003).

Erythrocebus patas (patas monkey) in Kenya preferentially utilise taller trees within their overall home range (Enstam & Isbell, 2004). In the tallest trees female *E.*

patas scanned more often and appeared to detect predators only from the taller trees. Enstam and Isbell (2004) proposed that the use of taller trees decreased predation risk by increasing ability to detect predators. No evidence of increased food availability or reduced predator presence was noticeable amongst the taller trees. In *Callithrix flaviceps* (buffy-headed marmoset) individuals were more vigilant when higher in the canopy and during periods of scarce leaf cover (Ferrari & Ferrari, 1990).

A change in ranging behaviour followed a change in habitat visibility in *Chlorocebus aethiops* (Enstam & Isbell, 2002). A bush fire decreased available habitat for potential felid predators, and increased visibility for *C. aethiops*. Following the fire *C. aethiops* ranged further into the burnt area, presumably as they had better predators visibility.

It has also been suggested that behavioural differences exist between the same species of primates in fragmented, disturbed, forest and undisturbed forest (Goldberg *et al.*, 2006). Male *Procolobus tephrosceles* (red colobus) in fragmented forest in Uganda displayed extreme anti-predator behaviour towards a *Glaucidium perlatum* (pearl-spotted owlet [Goldberg *et al.*, 2006]). The males, having previously reacted to the presence of a large raptor, killed the owlet, whose small size posed no threat to the colobus. This level of aggression has never been observed in red colobus living in undisturbed forest (Goldberg *et al.*, 2006).

Age has been found to change habitat usage during foraging in *Saimiri sciureus* (squirrel monkey [Stone, 2007]). Wild populations of *S. sciureus* were presented with feeding platforms with differing degrees of vegetation cover. Adults used platforms all year, regardless of cover and food availability. Juveniles used all platforms in the dry season, but did not feed from exposed platforms during the wet season when food was more plentiful. This suggested to Stone (2007) that juveniles felt at a higher risk of predation than adults, taking the greater risk only when overall food resources were low.

10.3.2. Predation and Group Dynamics

Group structure and dynamics have long been related with predation risk. For many primates, and animals in general, it has been considered the role of males to detect predators and to defend the group (Van Schaik & Noordwijk, 1989). Studies of *Cebus albifrons* (white-fronted capuchin) and *Cebus apella* (tufted capuchin) confirmed the importance of males in predator detection and defence (Van Schaik & Noordwijk, 1989). Van Schaik and Noordwijk, (1989) suggested this was because males lead group progressions, and see a predator first. Therefore the more males in a group, the better predator detection and defence will be. However this is only effective in male-dominated groups. Following a study of African monkeys Treves (1999) concluded that patterns of social behaviour within groups do not predict antipredator behaviour, as predation is not a uniform selective pressure.

10.3.3. Predation and Group Size

Studies have arrived at conflicting conclusions as to whether larger group size protects from predation. Shultz *et al.* (2004) found that in Africa, lower rates of predation were associated with large group size. However, Zuberbühler and Jenny (2002) found that African leopards most often predated upon individuals from larger groups. They suggest that this is because it is easier for leopards to locate large groups, and that this outweighs any benefit from increased vigilance and dilution. The same study found that larger-bodied individuals were preyed upon more frequently than smaller-bodied individuals. Zuberbühler and Jenny (2002) concluded that leopard predation increased the behavioural flexibility of primates and triggered complex cognitive processes.

Two theories link monogamous groups with rates of predation. The first suggests that monogamous pairs form when predation rates are exceptionally low, favouring smaller groups (Rutberg, 1983). The second theory is the opposite, suggesting that high predation rates favour smaller more cryptic groups (Rutberg, 1983).

Some South American platyrrhines and African strepsirrhines form mixed-species groups. It has been suggested that this is to increase vigilance for early detection of predators, without the costs usually associated with large groups (for example, increased foraging pressures [Terborgh, 1990]). In Africa long term associations between *Chlorocebus aethiops*; *Papio cynocephalus* (yellow baboon [Moynihan, 1976]); *Cercopithecus ascanius* (red-tailed guenon), and *Cercopithecus mitis* (blue monkey [Cords, 1990]), have been shown to have a benefit against predation as have associations between *Saguinus fuscicollis* (saddle-backed tamarin) and *Saguinus labiatus* (red-bellied tamarin [Pook & Pook, 1982; Buchanan-Smith, 1990]) in South America. Absence of large mixed-species groups in Madagascar led in the past to belief that predation rates there are low.

It has been suggested that the type of behaviour displayed by a predator, stalking or opportunistic, should determine group and individual behaviour (Cresswell *et al.*, 2003). When predators use 'sit-and-wait' stalking methods, it is better to have more vigilant behaviour, even if the overall group size is smaller. An individual would need to spend less time foraging, and there would be lower intra-group competition so it could spend the extra time scanning for predators. When predators are opportunistic it is better to have larger groups. Although an individual will have less time to scan for predators as a result of the increased time required for foraging, due to higher intra-group competition, this does increase its predation risk (Cresswell *et al.*, 2003).

10.4. Predation in Andasibe Mantadia National Park

10.4.1. Mammals

A *Galidia elegans* was observed climbing a tree near *Hapalemur* by Sabine Day and Joseph Rasolofoniaina (21 November 2004) during observations of *H. g. griseus* Group One. The *H. g. griseus* had been alarm calling prior to this observation and the assumption was that this calling was a response to the presence of the *G. elegans*. *G. elegans* is endemic to Madagascar and weighs up to 960g (Goodman, 2003). Although not known to predate upon *H. g. griseus* it is possible they could capture even an adult.

There was no evidence of *Cryptoprocta ferox* in the study area and the only other observed mammalian predators were *Canis lupus familiaris*. Villages were situated only 4km away in either direction along the mine road and *C. l. familiaris* were frequently seen and heard around the camp, often stealing food supplies. On the night of 25 March 2005 alarm calls of *H. g. griseus* close by the tents led to observations at midnight. There was a full moon and no cloud, and silhouettes of *H. g. griseus* were visible. The group of *H. g. griseus* appeared agitated and were leaping around at the tops of the trees, 10m high. About 15m away a small mammal was observed running on the ground. The animal appeared to be a small dog, although it is possible, that it was a small native carnivore. The alarm calling and movement continued for roughly 20 minutes before the group became quiet.

10.4.2. Snakes

There were a number of reptiles seen in the forest including many species of snake. Two species of boa seen were *Sanzinia madagascariensis* (Madagascar tree boa) and *Acrantophis madagascariensis* (Madagascar ground boa). Boas were frequently observed during the summer months, before hibernation in winter.

In February (19 February 2005) a case of predation involving *S. madagascariensis* was observed. At 07:20 (S18°48.749, E46°286.863) a '*H. g. griseus*' tail was seen in an eight-metre-high tree on a valley slope. The lemur was observed to plummet to the ground. On reaching the lemur it became apparent that what had fallen was a *S. madagascariensis* tightening itself around what was assumed to be a juvenile *H. g. griseus* (Figure 10.3). The lemur was still alive; calling and struggling to escape. Using a stick attempts were made to pry the *S. madagascariensis* from the lemur. The *S. madagascariensis* was lifted up on the stick so it had to support itself together with the full weight of the lemur. After this, at approximately 07:30, the *S. madagascariensis* began to slowly release the lemur. It then became apparent that the lemur was a *Cheirogaleus major*. The *C. major* scrambled along the ground for 6m before climbing straight up into a tree. The *S. madagascariensis* remained on the ground (Figure 10.4). It was estimated to be 1.5m in length with a maximum body diameter of 4.5cm. The *C. major* appeared large and was probably near the largest size for its species.

Figure 10.3. *Cheirogaleus major* (greater dwarf lemur) predated by *Sanzinia madagascariensis*. Photograph: Mary Blanchard, 19 February 2005.

Figure 10.4. *Sanzinia madagascariensis* after releasing *Cheirogaleus major*. Photograph: Mary Blanchard, 19 February 2005.

10.4.3. Birds

Predatory birds were frequently heard and seen. At night *Asio madagascariensis* (long-eared owl) and the smaller *Otus rutilus* (Scops' owl) were heard. *O. rutilus* is a tiny owl, weighing only 100g (Ravokatra *et al*., 2003) and is too small to be a threat to lemur species in this study. The larger *A. madagascariensis* is capable of taking *H. g. griseus*, but is too small to take the two larger lemur species. Diurnal raptors present were *Polyboroides radiatus*, *Buteo brachypterus* and smaller *Accipiter francesii* (Madagascar goshawk). All three were seen and heard frequently throughout the home ranges of all groups including around the camp. *A. francesii* weigh up to 150g (Ravokatra *et al.*, 2003) and are not recorded as feeding on any lemur species (Rene de Roland & Thorstrom, 2003). The larger *B. brachypterus* are also not known to feed on lemurs however *P. radiatus* is.

In July (16 July 2005) a dead *Avahi laniger* was found on a trail (S18°48.853, E48°26.309) around 07:30 (Figure 10.5 and Figure 10.6). The individual was male and may have been one of the pair seen previously (13 December 2005) only 30m away (S18°48.853, E48°26.309). The largely defleshed head (muzzle fur remained) was lying detached from the body, approximately 60cm away (Figure 10.5). The eyes had been removed. The intestines (partly eaten) and stomach were lying by the head (Figure 10.6). The left arm had been removed (one bone lying alongside the body) and eaten. The *A. laniger* torso had been torn open, some of the internal organs removed and eaten (Figure 10.5). The remains were collected and returned to camp for weighing and measuring (Appendix G1). The remains weighed 750g, although the actual body weight would have been greater.

Feathers were found attached to the body of the *A. laniger* strongly suggesting predation by a raptor. A local guide identified the feathers as *Accipiter henstii*. Lack of smell suggested that the *A. laniger* had only recently been killed, probably a few hours earlier the same morning.

Figure 10.5. Dead *Avahi laniger* torso, note arm bone in top right corner. Photograph: Mary Blanchard, 16 July 2005.

Figure 10.6. Dead Avahi laniger skull and intestines. Photograph: Mary Blanchard, 16 July 2005.

Rakotonodravelo Alfred observed *Polyboroides radiatus* capture a juvenile *H. g. griseus* at the Special Reserve some time prior to this study. The attack was during the day and the *P. radiatus* ate its eyes followed by the intestines, leaving the rest of the body.

10.4.4. Humans

There was evidence of human predation on lemurs in the study area. This is illegal under Malagasy law and capture of offenders by police can involve a prison sentence and fine. Unfortunately it is notoriously difficult to prove and most perpetrators avoid detention.

On arrival in camp (November 2004) a guide, Joseph, and Jules Medard, a CAFF/CORE official, found and dismantled an old lemur trap. CAFF/CORE is the Malagasy committee that grants permission for research permits and oversees research in Madagascar. An official visits each project to ensure adherence to research permits. Joseph thought this trap was probably used for trapping *Eulemur fulvus*. This is traditionally the most commonly caught and eaten lemur in the area. Joseph described the trap at a later date and said that it used bait to attract the lemur. When the lemur ate the bait a stake would drop, impaling the individual. Joseph added that in his time as a guide he has found and dismantled 3 traps; traps found recently are old and show no signs of use.

On 29 May 2005 while following H. *g. griseus* Group Two, it was noticed that the collared adult female was missing. She was present in the group during previous observations in April (28 April 2005). The collar was tracked to a small area of road at the entrance to camp, although at this time the collar could not be found. At a later date (05 August 2005) the collar was retrieved from this area (S18°48.810, E48°25.795). It was beneath ground cover but on top of the earth. It showed significant deformation (Figure 10.7) and evidence of cut marks that could only have been caused by human involvement. The black plastic on the collar covers a brass inner core that is circular to fit round the neck of the lemur. This would require significant pressure to deform. It appears that when she was caught the perpetrators, on noticing the collar panicked, and tried to cut it off before pulling it from her neck and throwing it away. This female presumably ended up in the cooking pot.

Figure 10.7. Biotrack collar from adult female *H. g. griseus* retrieved from the road. Photograph: Mary Blanchard, 05 August 2005.

10.4.5. Disappearances and Anti-Predator Behaviour

At the end of June (22 June 2005) it was noticed that an adult female *H.* g. *griseus* had disappeared from Group One. The female was present earlier in June (07 June 2005). There was no evidence as to the cause of her disappearance, and initial assumptions were that it had been taken by humans. However, later in the day, a call from a raptor identified by the guide as *Polyboroides radiatus* was heard. The *H.* g. *griseus* descended from the tops of the trees, where they were feeding, to lower levels in the canopy. They remained still and quiet for roughly 20 minutes. By this time the *P. radiatus* could not be heard and the *H.* g. *griseus* continued as normal. It is therefore possible that the female could have been taken by a raptor.

Subsequent to this a similar reaction to birds of prey was observed (20 August 2005). While following *H.* g. *griseus* Group One a small bird of prey, probably *Accipiter francesii*, flew by, although it showed no interest in the *H. g.*

griseus. *A. francesii* are small birds of prey, no taller than 35cm (Morris & Hawkins, 1998). The adjacent lemurs stopped feeding and moved down, remaining quiet for about 5 minutes before returning to feed.

While following *I. indri* (20 February 2005) *Buteo brachypterus* flew by. The adult female alarm called and her infant moved closer to her. The adult male, which was feeding slightly away also from the group moved closer to the adult female and infant.

In May (31 May 2005) an infant *I. indri* was found to be missing, although it had been present on the previous follow earlier in May (18 May 2005). As *I. indri* are protected by local 'fady' it is probable that either the infant died naturally or fell prey to natural predation. With no evidence of *C. ferox* in the study area it was assumed this predation was by raptor. An *I. indri* infant also disappeared in Powzyk's (1997) study, with no obvious cause.

In September (05 September 2005) the *I. indri* group moved relatively early (08:22) to a position lower in the canopy. This movement was possibly caused by *Polyboroides radiatus* observed flying overhead, despite no infant being present in the group at this time.

The infant *P. diadema* also disappeared; this was noticed in October (01 October 2005) and the infant had last been seen alive in September (17 September 2005 [Chapter 2]). It is impossible to know if this infant was killed by a predator or died from injury or illness. However on 17 September 2005 the group alarm-called in the presence of a *Buteo brachypterus* flying overhead. In August (13 August 2005) *P. diadema* appeared to alarm call in the presence of a bird, but this was not a raptor. Powzyk (1997) noted that a six month old *P. diadema* disappeared during observations, with no known cause. Remains of a juvenile *P. diadema* were found, with no apparent cause of death (Powzyk, 1997).

10.5. Discussion

It has been suggested that lemurs display residual behaviour evolved to protect them from extinct predators, especially in the case of raptors. However studies suggest that without reinforcement, primates and other animals quickly lose anti-predator responses, within a few generations. This would suggest that if lemurs display anti-predator behaviour towards raptors, it is because extant raptors enforce great enough predation pressure to reinforce this behaviour. The other possibility is that rates of predation of other extant predators, mammalian and reptilian, have been enough to reinforce the unnecessary anti-predator behaviour. However, this appears the least likely situation. If lemurs respond with anti-predator behaviour to extant raptors, it is because extant raptors still pose a significant threat.

It is unclear as to the extent of predation on the two larger study species, *P. diadema* and *I. indri*. No adults of either species were found to disappear during this study or during Powzyk's (1997) nineteen month study and in a review of predation in lemurs Goodman (2003b) could find no documented cases of actual predation in *I. indri*. Young animals disappeared from groups of both species during both studies. Infants and juveniles are at greater risk of predation than adults of the same species due to their smaller size. It must be remembered that until fully developed young are at greater risk from illness and lack of experience in locomotion puts them at greater risk of falls and injuries.

The largest mammalian predator, *Cryptoprocta ferox*, appears to preferentially take larger lemurid prey and appears highly adapted to arboreal environments (Iwaniuk *et al.*, 2000). *C. ferox* is responsible for a large number of *P. edwardsi* deaths in Ranomafana, eats *P. verreauxi*. and is known to take *P. diadema* and probably infant *I. indri*. It would appear that *C. ferox* has the potential to be a predator on adult *I. indri*, although at 7.3kg the female *I. indri* is larger than a female *C. ferox* and approximately the same size as a male. It is probably correct to say that adult *I. indri* are at very small risk of predation by *C. ferox*, while the slightly smaller adult *P. diadema* are likely to be at a greater risk. Infants of both species are highly vulnerable to *C. ferox*.

The largest lemurid prey known to have been taken by any snake is an adult *Propithecus coquereli* predated by a large *Acrantophis madagascariensis* although in this example the adult female was released by human intervention (Burney, 2002). At an average weight of 3.8kg an adult female *P. coquereli* is 1.5kg lighter than the adult male *P. diadema* in the present study and almost three kilograms lighter than an adult female *I. indri*. As the *A. madagascariensis* in question was thought to be an especially large individual, it is highly unlikely that adult *P. diadema* or *I. indri* could be taken by *A. madagascariensis*. Considering size alone it is entirely possible that *A. madagascariensis* could constrict an infant or juvenile of either species. It seems unlikely that an infant sleeping with and being carried by its mother could be taken by *A. madagascariensis*, although a slightly older infant, sleeping on its own could be at risk.

Asio madagascariensis has not been known to take lemurid prey larger than 600g and *Tyto alba* no prey larger than 30g. Both have only been recorded as predating upon nocturnal lemurs. This would remove them as potential predators for either infant or adult *P. diadema* and *I. indri.*

Accipiter henstii regularly takes lemurid prey, up to 3.5kg in body weight and can carry prey up to 4kg (Karpanty, 2003). However, they have never been observed taking any *Propithecus* and as such would appear little threat to adult *P. diadema* or *I. indri*. It is however possible that if an opportunity arose *A. henstii* would be capable of taking infants of either species. *P. diadema* and *I. indri* frequently feed at the tops of trees, although *P. diadema* are on average found 2m lower in the canopy ($U = 34089652$; $p = 0.000$). The propensity of both species to feed while exposed in the upper canopy suggests that aerial predators are not a large threat to adults.

Polyboroides radiatus take substantial numbers of *Propithecus verreauxi*, which at 3.6kg are comparable to the largest known prey taken by *A. henstii*, but it has never been observed capturing larger rainforest *Propithecus* species (Karpanty, 2006). Despite this Powzyk (1997) did observe a predation attempt by *P. radiatus* on an infant *I. indri* and saw evidence of significant anti-predator behaviour by both *I. indri* and *P. diadema,* leading her to conclude that avian predators posed a greater threat to both species than did ground predators.

As a consequence of their body weight and size adult *I. indri* have a reduced threat of predation by all types of predator compared to other lemurid species. This is suggested by the life-history of the species, where the adult male and female pair for life, are long-lived with a long birth-interval and low reproductive rates. This life-history is not suggestive of an animal at high risk of predation. Despite this young are at risk, and this threat is recognised by the adults. Their defence towards avian predators appears to be confrontational, if necessary attacking the predator. It is debatable whether *P. radiatus* or *C. ferox* pose the greater threat to *I. indri.* Greater densities of *P. radiatus*, combined with the distance a raptor can travel daily, mean that *I. indri* are potentially exposed to *P. radiatus* more regularly than *C. ferox*.

Adult *P. diadema* are only slightly smaller in body weight than *I. indri.* However, differences in body weight of 1kg will be crucial for a predator when its prey is near the upper limit in body weight of prey it can catch. *P. diadema* adults are unlikely to be at high risk of predation from either *C. ferox* or *P. radiatus*, but this risk could be higher than that for an adult *I. indri* since the multi-male, multi-female group composition and larger group size of *P. diadema*, suggests that the predation risk is greater than that of *I. indri*.

The predation risk for *H. g. griseus* is entirely different. The smallest of all diurnal lemurs, *H. g. griseus* is at high risk from mammalian, reptilian and avian predators. Between the two study groups, a total of 13 individuals, two adult females, one infant and one juvenile disappeared.

At least one of the adult females was probably hunted and killed by local people. Hunting by locals might be expected to be a high risk for both groups. The territories of both groups bordered the miners' road and they often fed in *Clidemia hirta* (mazambody), a low growing shrub, growing alongside. This road was extensively used by locals, and walking along it, it was easy to spot multiple groups of *H. g. griseus*. Unfortunately the very process of habituation led both study groups to tolerate the presence of people. This combination put both groups at high risk of human predation. It is always easier to consider actions with the power of hindsight, but in future studies it would be preferable not to habituate any groups which already had such a precarious relationship with *Homo sapiens*.

Despite this, it is highly unlikely that all the individuals that disappeared ended up 'in the cooking pot'. The reaction of Group One to raptors strongly indicates that *H. g. griseus* perceive raptors as a threat. Alarm calling directed towards *Galidia elegans* and possibly towards domestic dogs during the night indicates that mammalian predators are also a risk.

Different reactions were observed when *H. g. griseus* were exposed to mammalian, or to avian predators. Avian predators drew a cryptic response: the *Hapalemur* moved low down or stayed still and remain silent, until after the point at which the raptor was no longer a threat. Mammalian predators however elicited copious alarm calling and agitation; adults leaped around, not away from, the predator.

Zuberbühler and Jenny (2002) suggest that future work on primate predation should compare groups within a species that have both single and multi-male groups. *H. g. griseus* would be an interesting test-case as they appear to have a variety of social groupings in different regions, although the same predators are present. In addition the small size of *Hapalemur* puts them at risk from a range of predators.

Chapter 11 Discussion

This chapter summarizes findings on whether the hypotheses laid out in each results chapter have been sustained by the evidence of the data collected. It then discusses evidence relating to the two Key Hypotheses presented in Chapter 1, including vertical spatial usage and seasonality, and the major theme of ecological specialism versus generalism, and addresses the issues raised by the contrasts between the findings of this study and that of Powzyk (1997), performed in the same reserve.

11.1 Review of Hypotheses

Hypothesis 5.1 held that: *I. indri* and *P. diadema* as larger bodied folivores will be diurnal; *H. g. griseus* as a much smaller folivore will be cathemeral.

Data from this study upheld the first part of hypothesis 5.1; *I. indri* and *P. diadema* were diurnal during the course of this study. The second part of this hypothesis is not upheld; *H. g. griseus* in Mantadia are not cathemeral. Their activity pattern would more correctly be termed crepuscular; a peak of activity at dawn and dusk and a lull mid-day.

Hypothesis 5.2 held that: *I. indri*, *P. diadema* and *H. g. griseus* will be more active in summer months (long hours of daylight) compared to winter months (short hours of daylight)

Hypothesis 5.2 was upheld for *I. indri* and *P. diadema* but not for *H. g. griseus*. The length of the daily active period in *I. indri* and *P. diadema* correlated with hours of daylight: they spent significantly longer active on days during the summer opposed to the winter. No correlation was observed between hours of daylight and active period for *H. g. griseus*.

Hypothesis 5.3 held that: the start and end of the active period will run parallel to sunrise and sunset for the diurnal *I. indri* and *P. diadema*

This hypothesis was upheld for *I. indri*: *I. indri* start their active period later in the morning and end it earlier in the evening in accordance with sunrise and sunset. It was not upheld for *P. diadema*; although they did alter the start and end of their active period with the progression of sunrise and sunset the difference between sunrise/sunset and start/end of activity is not constant.

Hypothesis 5.4 held that: for *I. indri*, *P. diadema* and *H. g. griseus* resting (during the active period) will increase in the austral winter, when availability of good-quality food should be relatively low, while travelling and indeed feeding will proportionately decrease.

For *I. indri* this hypothesis was rejected: length of daily feeding shows no correlation with daylight, while length of daily rest and travel periods decreases. This hypothesis can be rejected for *P. diadema*: the rest and travel periods during the active period decreases in winter while the feeding time increases. No correlation was found for rest, travel or feed periods with hours of daylight, hence the hypothesis is rejected. This hypothesis can in-part be rejected for *H. g. griseus*: feeding time did not alter seasonally, while rest and travel increased slightly during the austral winter.

Hypothesis 6.1 held that: niche differentiation between *I. indri* and *P. diadema* occurs by adoption of quantitatively different diets.

This hypothesis is not upheld; Schoener's index gives a dietary overlap of 0.42 (equivalent to 42%), ranging from 0.15 in April to 0.53 in July. This indicates that up to 50% of specific diets overlap; considerably more than the maximum 0.12 (equivalent to 12%) overlap found by Powzyk (1997).

Hypothesis 6.2 held that: *I. indri*, as proposed by Powzyk (1997) is a more specialized feeder on low quality food, and *P. diadema* a generalist, eating higher quality food.

This is partially upheld; *P. diadema* did have a more diverse diet compared to *I. indri*.

Hypothesis 6.3 held that: as a more specialized feeder *I. indri* will have fewer and longer feeding bouts each day compared to *P. diadema* (Powzyk, 1997 [and see also e.g. Crompton, 1984 for *Galago moholi* and *Otolemur crassicaudatus*]).

This hypothesis is upheld; the mean length of feeding bouts for *I. indri* was 1508 seconds, for *P. diadema* it is 998 seconds. *I. indri* had a mean of 8 feeding bouts per day, compared to a mean of 14 bouts per day for *P. diadema*.

Hypothesis 6.4 held that: females of each species will take better-quality food from more diverse sources.

This hypothesis is not upheld for *I. indri* or *P. diadema*: observations show that males have a more diverse diet. However this result could be attributed to sampling bias. The hypothesis is however upheld for *H. g. griseus*: females have the more diverse diet.

Hypothesis 6.5 held that: if all three species will show strong seasonality in diet.

This hypothesis is upheld; each species relied on young leaves, but used other resources as and when they were available.

Hypothesis 7.1 held that: following Sussman (1977) since *P. diadema* are more frugivorous they will have the largest home range. All other things being equal, the more folivorous *I. indri* and *H. g. griseus* will have smaller home ranges; but solely on a body size basis the expectation is that *I. indri* will have a larger home range than *H. g. griseus*.

This hypothesis is upheld; *P. diadema* had the largest home range (27ha), followed by *I. indri* (13ha), while *H. g .griseus* had the smallest home ranges (3.5 and 5.4ha).

Hypothesis 7.2 held that: following Warren and Crompton (1997b) *P. diadema* as a more selective feeder will use a larger proportion of its home range daily and monthly.

This hypothesis is upheld: on average *P. diadema* utilised 14% of their total home range daily and 53% monthly, while *I. indri* utilised 10% daily and 42% monthly.

Hypothesis 7.3 held that: *P. diadema* will have longer daily path lengths than *I. indri*.

This hypothesis is upheld: *P. diadema* had significantly longer daily path lengths; a mean of 902m, compared to 482m in *I. indri*.

Hypothesis 7.4 held that: daily path lengths in *I. indri* and *P. diadema* will be shorter in the austral winter.

This hypothesis is upheld: the daily path length in *I. indri* and *P. diadema* were found to positively correlate at the 0.01 level with hours of daylight; decreasing daylight in the austral winter leads to shorter path lengths.

Hypothesis 7.5 held that: since *H. g. griseus* are seasonally frugivorous they will be expected to have longer daily path lengths and monthly home ranges in the season when fruit is most commonly consumed.

This hypothesis is not upheld: although fruit was consumed from February to July, no seasonal effect of ranging or path length could be found for *H. g. griseus*.

Hypothesis 8.1 held that: niches of *I. indri* and *P. diadema* will be differentiated in part by height or stratum

This is upheld: *I. indri* were found significantly higher (12.62m) compared to *P. diadema* (10.55m).

Hypothesis 8.2 held that: *P. diadema* will travel lower down in the canopy, where discontinuities are larger but fewer, to maximize travel speed.

This is upheld; *P. diadema* travelled at a mean height of 9.75m, while *I. indri* travelled at a mean height of 12.20m.

Hypothesis 8.3 held that: *H. g. griseus* will occupy a lower stratum than either of the indriids.

This is upheld: *H. g. griseus* were found at a mean height of 7.78m, lower than that of both *I. indri* (12.62m) and *P. diadema* (10.55m).

Hypothesis 8.4 held that: all three species will be found lower in the canopy during the summer to avoid excessive heat.

This is not upheld: No seasonal trend was found in height utilisation for any species. Differences in heights of *I. indri* over time are most likely due to the presence (or absence) of the infant and not due to seasonal effects.

<u>Hypothesis 9.1</u> held that: the (large bodied) indriids would use small, compliant, supports for landing leaps to absorb energy and would use larger, less compliant, supports for take-off to minimise energy loss.

This is not upheld. Initial and terminal supports usage showed no difference. This suggests that support availability is more important than minimising energy costs.

<u>Hypothesis 9.2</u> held that: the relatively higher take-off and landing forces predicted to be incurred by *H. g. griseus* should result in the use of smaller landing, but larger take off supports compared to *I. indri* and *P. diadema* during leaping.

This is in part upheld: *H. g. griseus* did use smaller supports during leaping compared to the indriids, however no difference was observed between support use during landing and take-off.

<u>Hypothesis 9.3</u> held that: *I. indri* and *P. diadema* would use vertical supports more than the (presumed) less specialized *H. g. griseus*.

This is not upheld. During leaping *I. indri* used vertical supports least frequently (40.5%) and *P. diadema* most frequently (55.5%), with *H. g. griseus* falling in the middle (43.7%).

<u>Hypothesis 9.4</u> held that: that as the supposedly more specialized leaper (Oxnard *et al.*, 1990) *I. indri* will use vertical take-off, and perhaps landing, supports more than *P. diadema*, to permit ballistically optimal, more efficient leaps, where an orthograde body posture both locates the centre of gravity located along or near a ballistic trajectory from the hindlimb, and also directs force along the more stable long axis of the support.

This is not upheld: *I. indri* used fewer vertical supports (40.5%) for leaping from and to compared to *P. diadema* (55.5%).

<u>Hypothesis 9.5</u> held that: for all three species longer leaps will end on larger, more stable supports to provide a safer landing.

This is upheld for *I. indri*, who landed on supports >10.1cm for their longest leaps. This is in part upheld for *P. diadema* who achieved longest leaps onto supports sized between 10.1 to 15cm, but *not* onto those >15.1cm. This in part upheld for H. g. griseus who used supports between 5.1 to 15cm to land their longest leaps and *not* those over >15.1cm.

<u>Hypothesis 9.6</u> held that: different locomotor modes would be employed by *I. indri*, *P. diadema* and *H. g. griseus* during feeding and travel.

This is upheld: *I. indri*, *P. diadema* and *H. g. griseus* utilised leaping more frequently during travel and all other modes less frequently, while during feeding leaping was used less frequently and all other modes more frequently.

11.2. Vertical Spatial Usage

Height is controlled by a range of factors including diet (Ganzhorn, 1989; Chapter 6), stratum availability (Fleagle *et al.*, 1981; Chapter 2), locomotion (Fleagle & Mittermeier, 1980; Chapter 9) and predation (Ferrari & Ferrari, 1990; Enstam & Isbell, 2004; Chapter 10).

Height within the canopy was found to act as a niche separator between all three species (Chapter 8): *H. g. griseus* 5.8m, *P. diadema* 10.6m and *I. indri* 12.7m. This is especially important for *I. indri* and *P. diadema* which shared a similar diet, with up to 53% overlap during July (Chapter 6). Ganzhorn (1989) suggests that sympatric primates whose niche is differentiated by height do not substantially differ in the chemical content of their diet. *I. indri* feed at a mean height of 13.0m and *P. diadema* at 11.2m, and if Ganzhorn (1989) is correct we should expect that *I. indri* and *P. diadema* do not differentially select plant parts based on chemical content. However this assumption is in sharp contrast to findings by Powzyk (1997) where differences were indeed found in the chemical content of plants consumed by each species, despite no statistically significant difference in stratum.

Upwards movement requires high energy expenditure to do work against gravity and for some species, it is possible to feed and travel in the upperstorey, a habit shown by *Eulemur fulvus* (common brown lemur [Sussman, 1977]). The mean height of travel for *I. indri* is 12.2m and for *P. diadema* 9.8m (Chapter 8); 1m lower than they both feed. A similar pattern is observed for *H. g. griseus*; feeding occurs at 6.5m and travel at 5.9m. Forest structure (Chapter 2) shows that *I. indri*, *P. diadema* and *H. g. griseus* travel in the midstorey and feed in the upperstorey. The food of *I.*

indri and *P. diadema*, leaves, fruit, flowers, will occur in the crown where trees branch. Saplings and smaller trees will produce leaves lower down, but there is an argument that lack of light for photosynthesis will decrease lead quality (Ganzhorn, 1988). Thus, both indriids and *H. g. griseus* select lower, more discontinuous strata for travelling.

The most common form of locomotion during bouts of travel is leaping (*I. indri* 90%; *P. diadema* 82%; *H. g. griseus* 58%); leaping was used less during feeding (*I. indri* and *P. diadema*: 50%; *H. g. griseus* 29%).

For the indriids leaping preferentially occurred from and to vertical supports sized between 5.1 and 10cm. For *H. g. griseus* leaps occurred preferentially on vertical supports sized 0.6 to 5cm in diameter. Vertical supports are found most commonly in the midstorey, as tree trunks, prior to their branching (Chapter 2). Trunks are found from the ground up, but within the understorey there is a tangle of low growing shrubs and herbaceous plants with almost no open spaces. The lower mid-storey also contains a tangle of larger shrubs coupled with the branches of saplings and small trees; there are no gaps between suitable verticals through which to leap. The upper mid-storey, above the branching height of small trees and below that of the larger trees, has the vertical supports coupled with open spaces and discontinuities large enough to allow minimization of the number of leaps required to cross a given distance. Of course it is the very suitability of this stratum for leaping, devoid of branches, that makes it unsuitable for feeding. Therefore the mode of travel, leaping, determines the height of travel, and a preference for energy/distance optimized high trajectory leaps is facilitated by use of vertical take off and landing supports. Thus while the indriids and *H. g. griseus* use an energetically expensive method of travel, leaping (Walton & Anderson, 1988) they minimize its costs by travelling lower down than they feed.

Crompton *et al.* (2007) compared the energetics of the three study species with four other prosimian primates: *Tarsius bancanus* (western tarsier), *Galago moholi* (southern lesser bushbaby), *Lepilemur edwardsi* (Milne-Edward's sportive lemur), and *Avahi occidentalis* (western woolly lemur). *I. indri* and *P. diadema* leap more frequently than any other species. The kinetic energy cost of leaping was calculated for each species and compared to the cost of climbing down to the ground, crossing the ground and climbing up to the same height. Expressed as a percentage of the mechanical energy costs of the work done against gravity, *I. indri* and *A.*

occidentalis gain the most from leaping, as leaping as a means of crossing between trees is approximately 13% of the cost of vertical climbing, and *P. diadema* only slightly less, ratio of 14.7%). The ratio for *H. g. griseus* (21.8%) is only marginally higher than for *L. edwardsi* (19.1%) and lower than for *G. moholi* (32%). This indicates that it is not energetically efficient for any of the study species to cross between trees via the ground when a leap is possible. So if support availability at the feeding height is not suitable for leaping, it is almost certainly cheaper to move down to a stratum at which supports more optimal for efficient leaping can occur.

Predation risk has an affect on stratum usage; the higher in the canopy the greater the risk from aerial predation, the lower in the canopy the higher the risk from terrestrial predation. Both *I. indri* and *P. diadema* adult female with infants were significantly lower in the canopy. This suggests they perceive the greatest threat on infants to be from aerial predation and adjust their stratum usage accordingly even when, in the case of diet, it may prove detrimental; Ganzhorn (1989) found leaf chemical quality decreased with decreasing height in the canopy, potentially as a result of diminished sunlight.

Thus, **Key Hypothesis 1.1: That in all three sympatric species a relationship exists between support use, locomotion and stratum on the one hand and between stratum and dietary preference and predation risk on the other** is upheld for all three species

11.3. Seasonality

Even in eastern rainforests, Madagascar is a strongly seasonal country, and seasonality will drive lemur ecology (Pochron & Wright, 2003). The effects of seasonality on prosimians is however complicated by the fact that prosimians have the lowest basal metabolic rates (BMR) of all primates and maintain low body temperatures (Müller, 1985).

Seasonality is linked to day length, ambient temperature, humidity, precipitation and food abundance (Morland, 1993; Wright, 1999). Temperatures within Mantadia varied very substantially seasonally, the maximum range encompassing; a low of 5°C in July and a high of 34°C in January. The length and time of the daily active period for *I. indri* and *P. diadema* correlates and appears influenced by the hours of daylight and time of sunrise and sunset. This trend is observed in many endothermic species (Daan & Aschoff, 1975) including *P. verreauxi* (Erkert & Kappeler, 2004). The present study found that the active period in both *I. indri* and *P. diadema* decreases with decreasing hours of daylight and maximum temperature. However the species have adapted different strategies for coping with the changing conditions. *I. indri* decreases the active period evenly, resting both longer in the morning and earlier in the evening. *P. diadema* on the other hand take relatively longer to rise in the morning compared to ending their activity in the evening. *P. diadema* also decrease activity in rain, a pattern not observed for *I. indri.*

Decreased activity periods indicate that both species are conserving energy in colder winter months presumably due to the increased requirements of maintaining internal body temperature. However *P. diadema* appear to require longer time on colder days to become active and are less active during rain. It would therefore be expected that *P. diadema* are the least efficient at maintaining body temperature and have the higher metabolic rate. In Chapter 6 and especially in previous work by Powzyk (1997), *P. diadema* were found to consume a higher energy diet, since it contains more fruit and less young leaves, and this again is consistent with P. *diadema* having the higher metabolic rate. But *I. indri* are less active than *P. diadema* and may have reached a lower limit for the minimum activity required to provide their basic energetic needs. In addition dietary differences in winter months suggest that seasonally, *I. indri* may acquire more energy than *P. diadema* from its food.

A peculiarity of lemur social systems, compared to other primate societies, is that groups either contain equal numbers of males or females or have a higher ratio of males (Kappeler, 2000b), and suggests that this phenomenon may be related to thermoregulation by social huddling. Thermoregulation in *Eulemur rufus* (red-fronted brown lemur) is indeed aided by social huddling (Ostner, 2002). A higher ratio of adult males to females has been observed for *P. diadema* than *I. indri,* and ad-hoc observations suggest that *P. diadema* huddle more in winter months compared to summer, which could well aid in thermoregulation.

Differences between the species extend into their seasonal use of their active periods for travelling, feeding and resting. During winter months *I. indri* travel and rest less during their active period but maintain the same duration of feeding. *P. diadema* also travel less during colder winter months, but they spend more time feeding and resting during their active period. That *P. diadema* spend longer feeding in winter suggests that either their energetic requirements are higher or that the quality of their food decreases. The two are of course not mutually exclusive. Energetic requirements are decreased by lowering costs of travel but increased by the costs of maintenance of body temperature. Unfortunately without metabolic information, the balance of these cannot be known. For *I. indri* the question is rather, does decreased travel time in winter compensate for their increased metabolic needs in maintaining body temperature? If this were the case the reason they do not seasonally change time spent feeding may be that overall their energy requirements remain stable. From comparing total activity time, the suggestion has already been made that *I. indri* are the more efficient in temperature regulation during colder months, and less affected by low environmental temperatures. However their diet too may well decrease in nutritional quality so that they must maintain the same period of feeding time to sustain lower energetic costs. Again, the lack of metabolic data makes it impossible to resolve the issue.

A different situation exists for *H. g. griseus*, where less seasonality is observed with regards to activity and ranging than in the indriids. Although a seasonal pattern was observed with regards to monthly ranging behaviour, daily path lengths were found to correlate with observation time, which suggests the results may be in part artifactual. Seasonal ranging patterns cannot therefore be stated with any degree of confidence, but there was a weak correlation of longer rests and less travel during colder winter months. However during colder months they continued to be active early and, unlike the indriids, did not appear to need a period of time to 'warm up' following the night.

Thus, **<u>Key Hypothesis 1.2</u>, that: in all three sympatric species seasonality will be apparent in activity, feeding and ranging and that it will be especially marked in the small-bodied *H. g. griseus*** is not upheld for *H. g. griseus*: seasonality was found to exert, at most, only a week effect on *H. g. griseus* ecology. However, it is upheld for *I. indri* and *P. diadema* where marked seasonality was found in activity, diet and ranging.

11.4. Comparison with Powzyk (1997)

Results of this field study are in many ways different from previous work (Powzyk, 1997) despite the similarity in their location. In this study home ranges for *I. indri* were over 60% smaller and for *P. diadema* at least 20% smaller than reported by Powzyk; activity budgets indicate different patterns, and dietary content differs, especially for *P. diadema.*

Temporal and spatial ecological variation has been described in a range of primate species: *Procolobus badius* (western red colobus [Chapman *et al.*, 2000]), *Cercocebus albigena* (grey-cheeked mangabey [Waser, 1977]) and *Gorilla gorilla beringei* (eastern mountain gorilla [Fossey & Harcourt, 1977]). It is not possible, however, to determine what temporal or spatial effects may lie at the heart of the distinctions between the present study and that of Powzyk from the available data. The only way to determine temporal variation would be to return to the two sets of study groups and observe them continually for a number of years. To investigate spatial differences however the groups in this study and that of Powzyk would need to be observed simultaneously. While these exercises might be achievable in a future study, for the present we can only assess the possible alternative sources of the behavioural distinctions between the two studies on the basis of, and within the limits of, available information.

Home range sizes seem unlikely to have undergone variation over time. Intra-species aggression was low and ranges appeared stable during the study period.

However habitat differences have been found to lead to intraspecific variation in ranging behaviour (Oates, 1987) and Powzyk (1997) commented that, for *I. indri*, patterns of long-calling indicated higher group densities existed in other areas of Mantadia. Higher group densities could however be associated either with overlapping home ranges or smaller home ranges. At Betampona, Glessner and Britt, (2005) reported that only very limited overlap occurred in border regions of *I. indri* ranges. Therefore it is probably more likely that higher densities of *I. indri* would be associated with smaller home ranges. In this case, distinctions in home ranges at Mantadia between those reported by Powzyk and those reported here could be the consequence of spatial differences. It might be expected that ranges of *P. diadema* would follow a similar pattern.

The next question is then why home ranges of *I. indri* and *P. diadema* in one area of Mantadia should be substantially smaller compared to those in another. Home range size can controlled by body size, diet, group size and resource availability (Harvey & Clutton-Brook, 1981; Milton & May, 1976; Oates, 1987). Body weights of the female *I. indri* observed in this study (6.7 and 7.3kg) are comparable to those collected by Powzyk (6.7 and 7.5kg [1997]) and well within the generally accepted range for the species (6 to 9.5kg [Mittermeier *et al.*, 2006]). However weights of the *P. diadema* in this study (5.1 and 5.3kg) are lower than those reported by Powzyk (6 to 7.3kg [1997]) and lower also than the accepted range for the species (6 to 8.5kg [Mittermeier *et al.*, 2006]). Although the weights are within the range Irwin *et al.* (2007) found for individuals within Tsinjoarivo, there is speculation that the Tsinjoarivo *P. diadema* are a separate variant; in part due to their low body mass. Therefore, there is evidence that the body weight of the study males was smaller than 'normal' for non-Tsinjoarivo *P. diadema*. However, is the small body size the reason for smaller range size, or rather a product of it? Unless we wish to describe a new sub-species, it seems likely that the low body weights of the study group are a consequence of ecology, i.e. a product of small range size and not a cause of it.

Group size could be expected to affect home range size both in respect of defendability and resources required. However, the group sizes of the study group *I. indri* (2 adults and offspring) and *P. diadema* (7 adults and sub-adults) do not differ from findings reported by Powzyk (1997). Therefore we can expect that there is no difference in either the resources required or potential defendability of the ranges.

A group's range must include enough dietary resources to ensure survival of group members. Thus; in areas of high productivity of suitable food resources home ranges could indeed be smaller and yet support equal-sized groups. The *I. indri* in the present study however are of 'normal' body weight and yet have a smaller territory, although they travel the same distance daily as did Powzyk's groups which have larger home ranges. Their small territory must therefore provide them with enough food to sustain their body weight, and it may reasonably be concluded that their home range exhibited high productivity.

Is this also likely for *P. diadema*? The smaller body weight of the study group compared to those within Powzyk's study might indicate that they are not ingesting enough food to fulfil all their energetic requirements. Opposite to the case in *I. indri*, they maintained not only smaller home ranges but shorter daily path lengths.

Unfortunately this could be interpreted in either of two conflicting ways: either that their ranges are so productive that they need to travel less to find the same amount of food, or that their ranges are so unproductive that they do not have the same energy available to expend on travel. If, as is likely in *I. indri*, small ranges are linked to higher productivity, the same might be expected to apply to *P. diadema* since diets and body weights are similar, although not identical.

Indeed dietary differences exist between this study and Powzyk's for both species, but more so for *P. diadema*. Powzyk observed *P. diadema* to eat fruit on every study day, but in the present study consumption of fruit was not observed at all during May and June. It would seem likely, given their propensity for fruit-eating in other studies, that the study *P. diadema* would have eaten a greater percentage of fruit if it had been available to them. Unfortunately a lack of phenological data for the present study means we cannot say so with certainty.

Home ranges of frugivores are usually larger than that of folivores as fruit distributions are patchy (Sussman, 1977). Therefore the lack of fruit in the diet of the crowned simpona study group can reasonably confidently be linked with their small home range size. That their home range provides enough food to sustain the group is not under question, but it seems likely that their home range does not provide enough suitable, high energy, food to sustain a large group at the maximum possible body weight. So the study group appear to be sacrificing potential maximum body weight for smaller home range, as we would expect the study group to have had a larger home range so as to encompass areas of high fruit productivity. No immediate benefit appears to attach to smaller home range per se, so it appears likely that there are constraints on home range size.

A species unchecked will grow in number until it reaches saturation within the environment, after which point its numbers are unsustainable (Stacey, 1979; Stacey & Ligon, 1991). However, there is likely to be a population density at which individuals can survive, but with depressed health (and perhaps body mass).. This case has indeed been demonstrated for *P. diadema* in Tsinjoarivo, where male individuals from groups living in fragmented forest are smaller in body mass and skeletal size compared to those from continuous forest (Irwin *et al.*, 2007). The authors suggested that this was linked to female dominance (females did not differ in size), reduced food quality and increased parasitic infection. Therefore it can be said that with reduced available food quality male *P. diadema* will be lower in body weight than with high available food quality.

The forest inhabited by the *P. diadema* study group, although close to the miners' road was in primary rainforest, and although it was subject to human interference, the effect was minimal, so it would appear unlikely that human disturbance would affect condition. However their territory is certainly on the edge of the forest, the miners' road acting as a barrier between the two segments of Mantadia. It is therefore conceivable that there is a decreased possibility of dispersal within and around in the study area. A male from the study group had evidently previously been radio-collared and it was assumed that this was one of the animals collared by Powzyk (1997), since two sub-adults and one juvenile male were collared between December 1992 and October 1993. The distance between the two study sites is unclear, but it is likely to be less than 3km, indicating that one of the sub-adults or the juvenile dispersed from his natal group to the study group. Thus dispersal does occur. However it is possible that the road acts as a barrier to east/west or west/east dispersal which could lead to a higher density of individuals, and therefore groups with smaller ranges. Groups of *I. indri* in Analamazoatra are known to be larger than usual due to the lack of suitable forest into which offspring can disperse (Powzyk, 1997).

This suggests that the small home ranges observed in this study in *I. indri* and *P. diadema* are not consequences of the same constraints. *I. indri* appear to live successfully in small home ranges, while the condition of *P. diadema* suffers when the size of their home range decreases.

Home range was not the only ecological variable to differ: activity and diet also differ from Powzyk's findings. In the present study both *I. indri* and *P. diadema* were found to spend a higher percentage of the day travelling and feeding and less time resting than reported in Powzyk's study. The trend in both species in the two studies remains the same: in both, both species feed for a similar amount of time, but *I. indri* rest more and *P. diadema* travel more. It is difficult to explain the differences, which are quantitative rather than qualitative, ecologically and it is possible that differing definitions coupled with omissions of some months in this study have caused the differences between the two studies.

The indriids' diet in the present study is more similar than in Powzyk's study: specifically *P. diadema* eat less fruit and more leaves than Powzyk reported. This could well be a reflection of smaller *P. diadema* home range.

11.5. Specialist versus Generalists

Despite its small physical size (around 800g) the geographic range of *H. g. griseus* is the largest of all three study species, substantially greater than other *Hapalemur* and *Prolemur* spp. and indeed one of the largest geographic ranges of all diurnal lemur species (Mittermeier *et al.*, 2006). Both study groups lived in disturbed forest and were observed living in close proximity to human habitation. An ability to live in disturbed forest is particularly important with a continual increase of anthropogenic influences on primary rainforest. Other studies (Irwin, 2005; 2006) indicate that *P. diadema* can also live in fragmented forests, although for males at least experiencing decreased condition. Although *I. indri* are found in the small forest area of Analamazoatra, there is less evidence however to suggest that *I. indri* can tolerate disturbed conditions.

Onderdonk and Chapman (2000) have suggested that it is impossible to make generalisations about which primates are capable of living in fragmented forest. However, it is certain that some species are capable of tolerating disturbed, fragmented forest more than are others (Chiarello, 1993; Tutin *et al.*, 1997; Onderdonk & Chapman, 2000; Mandujano *et al.*, 2004; Irwin, 2005; Lehman *et al.*, 2006; Irwin, 2006b).

For a species to live in fragmented forest it appears that they must either be able to tolerate small home ranges or be able to travel between fragments (Onderdonk & Chapman, 2000). This study has shown that although *H. g. griseus* ranges can reach 20ha in some locations (Overdorff *et al.*, 1997) they are capable of living in very small home ranges, as little as 3.5ha [Chapter 7]). The large indriids can also be found occupying very different sized home ranges: *P. diadema* ranges can reach 60ha (Irwin, 2006b) but in this study lived in a range less than half that area (Chapter 7); while home ranges in *I. indri* at Mantadia vary from 13ha (Chapter 7) to 40ha (Powzyk, 1997). Therefore adaptability in required range size alone does not necessarily imply an ability to survive in disturbed forest.

A second apparent key to success in disturbed areas is dietary: either a result of a species' own adaptability or benefit arising external to the animal, from the altered ecological conditions themselves. For example, species can benefit from secondary growth in disturbed areas (Chiarello, 1994; Onderdonk & Chapman, 2000). For example (Chapter 4), *Alouatta fusca* (brown howler monkey) in southeastern Brazil benefit from forest-fragmentation and secondary growth due to a proliferation of lianas, one of their main foods (Chiarello, 1994). *A. fusca* were found at higher-than-average densities in disturbed forest, but with smaller-than-average home ranges, probably as a result of increased food resources, due both to forest disturbance and the overall dietary flexibility of *A. fusca.*

We have seen that although primarily a bamboo specialist *H. g. griseus* consume a large proportion of fruit and are highly adaptable in their choice of bamboos. Depending on availability they can base their diet on *Cathariostachys madagascariensis* (giant bamboo [Chapter 6; Tan, 1999]) or *Cephalostachyum* cf. *pierreri* (vine bamboo [Overdorff *et al.*, 1997; Grassi, 2002; personal observations]). In primary rainforest vine bamboo species such as *C. cf. perrieri* predominate (Glander *et al.*, 1989; Grassi, 2002; Wright *et al.*, 1989) but density is low and home ranges of *H. g. griseus* are up to 20ha (Overdorff *et al.*, 1997). In secondary forest, such as in this study, *C. madagascariensis* grows in high density and home ranges are smaller (Tan, 1999; Chapter 7). The highest proportion of *C. madagascariensis* in the study area was in the area adjacent to the miners' road, in the groups' home ranges. At certain seasons, both groups spent up to (approximately) 82% of their total feeding time on *C. madagascariensis,* while at other seasons up to 40% was spent on fruit of *Clidemia hirta* (mazambody), which grew at high densities alongside the miners' road. Therefore although *H. g. griseus* have a restricted and specialized diet, disturbed conditions can create a proliferation of plant growth (*C. madagascariensis* and *C. hirta*) suited to their needs. This allows not only *H. g. griseus* to survive in disturbed forest, but to exist at high densities.

However this utilisation of disturbed, fragmented habitat by *H. g. griseus* is not without a risk. Predation risk is known to alter, and indeed potentially increase in disturbed forest (Irwin, 2005; Ludwig *et al.*, 2007). Secondary growth in *H. g. griseus* ranges has lead to a more open canopy (Chapter 2), resulting in an increased risk from aerial predation. Further the open forest and proximity to the miners' road have made it easier for human hunting.

P. diadema live in fragmented forest and display dietary diversity, consuming from 44.4% foliage (Powzyk, 1997) to 83.9% foliage (Chapter 6). Fruit consumption ranges from 23.9% (Irwin, 1997) to 7.6% (Chapter 6). Further dietary diversity appears linked to home range size and plant availability (Irwin, 1997; this study). Therefore it is the adaptability of diet within *P. diadema* rather than external factors (as is the case in *H. g. griseus*) which allows them to survive in fragments.

Although dietary breadth and regional variation exist for *I. indri*, their diet rather specialised on low-energy young leaves. This allows them to be very tolerant of short-term seasonal stress; indeed they appear to have out-performed the *P. diadema* subjects in this study during the austral winter. However their high degree of specialism makes them ill-suited to long-term stress and therefore it is unlikely that *I. indri* are a species that will react well to disturbed conditions. Further the extended length of required habituation time suggests that they react 'badly' to human presence (which appeared to disturb the two other species less) and they also exhibit long interbirth intervals (Chapter 3; Mittermeier *et al.*, 1994), which also puts them at risk from disturbance.

This has important implications for conservation. Although health, body mass and reproductive performance may decrease, *H. g. griseus* and *P. diadema* can adapt well to changing conditions, but it is unlikely that *I. indri* is able to do so. Therefore it is of particular importance to protect areas inhabited by *I. indri*, which can act as a 'flagship species' which by protection of its habitat can extend protection to all sympatric species.

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Appendix A: Taxonomy and Vernacular Names of Mammals, Birds and Reptiles Included in this Thesis

Class: Mammalia

Taxonomy based on Wilson and Reeder (2005a; 2005b) Volumes One and Two.

Family Cheirogaleidae				
	Allocebus			**Hairy-eared Dwarf Lemurs**
		trichotis		Hairy-eared dwarf lemur
	Cheirogaleus			**Dwarf Lemurs**
		major		Greater dwarf lemur
		medius		Fat-tailed dwarf lemur
	Microcebus			**Mouse Lemurs**
		griseorufus		Reddish-grey mouse lemur
		murinus		Grey mouse lemur
		rufus		Brown mouse lemur
		lehilahytsara		Goodman's mouse lemur
	Mirza			**Giant Mouse or Dwarf Lemurs**
		coquereli		Coquerel's dwarf lemur
	Phaner			**Fork-Marked Lemurs**
Family Lemuridae				
	Eulemur			**True Lemurs**
		albifrons		White-fronted brown lemur
		coronatus		Crowned lemur
	fulvus			Common brown lemur
		macaco macaco		Black lemur
		mongoz		Mongoose lemur
		rubriventer		Red-bellied lemur
		rufus		Red-fronted brown lemur
	Hapalemur			**Bamboo or Gentle Lemurs**
		alaotrensis		Alaotran bamboo lemur
		aureus		Golden bamboo lemur
		griseus		Eastern lesser bamboo lemur
		occidentalis		Western lesser bamboo lemur
		meridionalis		Southern lesser bamboo lemur
	Lemur			**Lemurs**
		catta		Ring-tailed lemur
	Prolemur			**Greater Bamboo Lemurs**
		simus		Greater bamboo lemur
	Varecia			**Ruffed Lemurs**
		rubra		Red-ruffed lemur
		variegata		Black-and-white ruffed lemur
			variegata	Black-and-white ruffed lemur
			editorum	Southern black-and-white ruffed lemur
Family Lepilemuridae				
	Lepilemur			**Sportive Lemurs**
		mustelinus		Weasel sportive lemur
		microdon		Small-toothed sportive lemur
		leucopus		White-footed sportive lemur

ruficaudatus	Red-tailed sportive lemur
edwardsi	Milne Edwards's sportive lemur
Family Indridae	
Avahi	**Woolly Lemurs**
laniger	Eastern woolly lemur
occidentalis	Western woolly lemur
Propithecus	**Sifakas, Simponas**
verreauxi	Verreaux's sifaka
deckeni	Decken's sifaka
coronatus	Crowned sifaka
coquereli	Coquerel's sifaka
tattersalli	Tattersall's sifaka
diadema	Diademed simpona
edwardsi	Milne-Edward's simpona
candidus	Silky simpona
perrieri	Perrier's simpona
Family Daubentoniidae	
Daubentonia	**Aye-aye**
madagascariensis	Aye-aye
Family Loridae	
Loris	**Loris'**
tardigradus	Slender loris
Family Galagonidae	
Euoticus	**Needle-Clawed Bushbabies**
Galago	**Bushbabies**
alleni	Allen's squirrel bushbaby
moholi	Southern-lesser bushbaby
senegalensis	Senegal or lesser bushbaby
Galagoides	**Bushbabies**
zanzibaricus	Zanzibar bushbaby
Otolemur	**Greater Bushbabies**
crassicaudatus	Thick-tailed greater bushbaby
garnettii	Garnett's greater bushbaby
Family Tarsiidae	
Tarsius	**Tarsiers**
bancanus	Western tarsier
spectrum	Spectral tarsier
Family Cebidae	
Callithrix	**Marmosets**
flaviceps	Buffy-headed marmoset
emiliae	Emilia's marmoset
Saguinus	**Tamarins**
fuscicollis	Saddle-backed tamarin
weddelli	Weddell's saddle-backed tamarin
mystax	Moustached tamarin
geoffroyi	Red-crested tamarin
labiatus	Red-bellied tamarin
Cebus	**Capuchin Monkeys**
apella	Tufted capuchin
albifrons	White-fronted capuchin

capucinus	White-throated capuchin
Saimiri	**Squirrel Monkeys**
sciureus	Squirrel monkey
Aotus	**Night Monkeys**
azarai	Azara's night monkey
Family Pitheciidae	
Calicebus	**Titis**
personatus	Masked titi monkey
Pitheca	**Saki's**
albicans	Buffy Saki
Family Atelidae	
Aloutta	**Howler Monkeys**
seniculus	Red howler monkey
caraya	Black-and-gold howler monkey
fusca	Brown howler monkey
palliata	Mantled howler monkey
Ateles	**Spider Monkeys**
geoffroyi	Geoffroy's spider monkey
Lagothrix	**Woolly Monkeys**
lagotricha	Woolly monkey
Family Cercopithecidae	
Cercocebus	**Mangabeys**
albigena	Grey-checked mangabey
Cercopithecus	**Guenons**
mitis	Blue monkey
diana	Diana monkey
ascanius	Red-tailed guenon
petaurista	Lesser spot-nose guenon
campbelli	Campbell's guenon
cephus	Moustached guenon
nictitans	Greater spot-nosed guenon
pogonias	Crowned guenon
Chlorocebus	**Vervet Monkeys**
aethiops	Vervet monkey
Macaca	**Macaques**
fascicularis	Long-tailed macaque
fuscata	Japanese macaque
mulatta	Rhesus monkey
silenus	Lion-tailed macaque
Papio	**Baboons**
cynocephalus	Yellow baboon
Colobus	**Colobus**
guereza	Black-and-white colobus
badius	Red colobus
Presbytis	**Langurs**
johnii	Nilgiri langur
thomasi	Thomas' langur
Procolobus	**Colobus**
badius	Western red colobus
tephrosceles	Red colobus

Pygathrix	**Langurs**
nemaeus	Red-shanked douc langur
Rhinopithecus	**Langurs**
bieti	Black-and-white snub-nosed monkey
Trachypithecus	**Langurs**
delacouri	Delacour's langur
hatinhensis	Hatinh langur
Erythrocebus	**Patas Monkeys**
patas	Patas monkey
Family Hylobatidae	
Hylobates	**Gibbons**
lar	White-handed gibbon
Family Hominidae	
Pongo	**Orang-Utans**
abelii	Sumatran orang-utan
Gorilla	**Gorillas**
gorilla	
beringei	Eastern mountain gorilla
Pan	**Chimpanzees**
troglodytes	
verus	West African
Family Felidae	
Felis catus	Domestic cat
Puma concolor	Cougar
Panthera pardus	Leopard
Family Viverridae	
Viverricula indica	Indian civet
Family Eupleridae	
Cryptoprocta ferox	Fossa
Cryptoprocta spelea	Extinct
Eupleres goudotii	Falanouc
Fossa fossana	Fanaloka
Galidia elegans	Ring-tailed mongoose
Galidictis fasciata	Broad-striped mongoose
Mungotictis decemlineata	Narrow-striped mongoose
Family Caniformia	
Canis lupus familiaris	Domestic dog
Canis lupus	Wolf
Vulpes vulpes	Fox
Family Hippopotamidae	
Hippopotamus	Hippopotamus
Family Cervidae	
Alces alces	Moose
Family Bovidae	
Bos primigenius indicus	Zebu
Cephalophus	Duiker
Family Sciuridae	
Sciurus carolinensis	Grey squirrel
Tamias striatus	Eastern chipmunk
Family Muridae	

Rattus norvegicus	Norway rat

Class: Aves

Taxonomy based on Morris and Hawkins (1998).

Family Accipitridae	
Aviceda madagascariensis	Madagascar cuckoo falcon
Eutriorchis astur	Madagascar serpent eagle
Polyboroides radiatus	Madagascar harrier hawk
Accipiter henstii	Henst's goshawk
Accipiter francesii	Madagascar goshawk
Buteo brachypterus	Madagascar buzzard
Harpia harpyja	Harpy eagle
Stephanoaetus coronatus	Crowned hawk eagle
Aquila	Eagle
Family Tytonidae	
Tyto soumagnei	Madagascar red owl
Tyto alba	Barn owl
Family Strigidae	
Otus rutilus	Scops' owl
Asio madagascariensis	Madagascar long eared owl
Glaucidium perlatum	Pearl-spotted owlet
Family Vangidae	
Vanga curvirostris	Hooked-billed vanga
Family Monarchidae	
Terpsiphone mutata	Madagascar paradise flycatcher
Family Ploceidae	
Ploceus sakalava sakalava	Sakalava weaver

Class: Sauropsida

Taxonomy based on Glaw and Vences (2007).

Family Crocodylidae	
Crocodilus niloticus	Nile crocodile
Family Iguanidae	
Iguana iguana	Green iguana
Family Polychrotidae	
Anolis	Lizards
Family Boidae	
Sanzinia madagascariensis	Madagascar tree boa
Acrantophis madagascariensis	Ground boa
Acrantophis dumerili	Ground boa
Family Colubridae	
Ithycyphys miniatus	Colubrid snakes

Appendix B: Supporting Information for Chapter 2

Appendix B1. Sightings of Non-Study Lemur Species

A pair of *A. laniger* were observed 18 April, 2005 disturbed by *P. diadema* (S18°48.962, E48°26.056). A solitary *Microcebus* sp. was observed on 11 December 2004, disturbed by Group One *H. g. griseus* (S18°48.883, E48°25.855).

E. rubriventer were observed close to camp (S18°48.737, E48°25.775). Two males were observed near camp on 09 February 2005. On 18 February 2004 three individuals were observed (S18°48.766, E48°25.989). The following day (19 February 2005) four *E. rubriventer* were observed in camp. On 28 February 2005 *E. rubriventer* were observed while following Group One *H. g. griseus* (S18°48.871, E48°25.860). The group consisted of two adult males, an adult female and a juvenile female, approximately 10m high in the trees. Two *E. rubriventer* were seen within 10m of *P. diadema* on 11 March 2005 (S18°48.840, E48°26.050). A group of *E. rubriventer* was seen close by *I. indri* on 18 April 2005 (S18°48.910, E48°26.206). Four *E. rubriventer* were seen on 15 January 2005 (S18°48.808, E48°25.906), two males mobbed observers. On 08 April 2005 *E. rubriventer* were observed during follows of *P. diadema* (S18°48.206, E48°25.111). On 11 August 2005 two *E. rubriventer* were observed close to resting *I. indri* (S18°48.854, E48°26.358).

A group of *E. f. fulvus* were seen while following *H. g. griseus* on 07 June 2005 (S18°48.868, E48°25.857). On 04 October 2005 a group of *E. fulvus* were observed crossing the road, presumably having a territory encompassing both sides.

Appendix B2: Climate at Mantadia

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
12-Nov-04	17:58	28	13	86	0
13-Nov-04	17:17	24	15	85	0
14-Nov-04	17:28	25	12	86	0
15-Nov-04	17:25	24	14	95	25
16-Nov-04	17:27	25	15	83	0
17-Nov-04	17:39	27	14	86	0
18-Nov-04	17:51	24	14	80	1
19-Nov-04	17:28	28	10	83	0
20-Nov-04	18:16	27	16	91	0
21-Nov-04	18:28	25	13	87	0
22-Nov-04	17:35	26	14	84	0
23-Nov-04	17:25	26	12	84	0
24-Nov-04	17:24	27	17	80	0
25-Nov-04	17:14	27	14	85	0
26-Nov-04	17:18	25	17	81	0.5
27-Nov-04	17:14	24	14	82	0.5
28-Nov-04	17:22	25	13	76	0
29-Nov-04	17:35	24	14	89	1.2
30-Nov-04	17:20	24	13	82	0.1
01-Dec-04	17:27	21	14	99	5
02-Dec-04	17:20	21	13	90	8
03-Dec-04	17:20	21	15	95	6.5
04-Dec-04	17:20	25	14	78	1
05-Dec-04	17:20	25	16	95	1.2
06-Dec-04	17:20	22	16	90	7.3
07-Dec-04	17:35	22	14	85	7.8
08-Dec-04	17:30	24	9	84	0
09-Dec-04	17:30	26	10	80	0
10-Dec-04	17:52	27	12	84	0
11-Dec-04	17:50	27	14	86	0
12-Dec-04	17:20	30	16	79	1.6
13-Dec-04	17:00	26	17	91	6
14-Dec-04	17:30	25	18	89	1.8
15-Dec-04	17:30	29	19	90	0
16-Dec-04	17:30	28	16	100	10
17-Dec-04	17:25	22	17	100	22.5
18-Dec-04	17:30	23	18	100	21
19-Dec-04	17:20	23	18	100	84
20-Dec-04	17:30	23	17	100	6.5
21-Dec-04	17:30	23	17	100	8.5
22-Dec-04	17:25	23	16	100	16
23-Dec-04		30	16	100	4.5
24-Dec-04		30	17	100	2.6
25-Dec-04		30	16	100	2.5
26-Dec-04		30	17	100	27
27-Dec-04		30	17	100	31
28-Dec-04		30	17	100	28
29-Dec-04		28.5	16.5	100	19
30-Dec-04		30	17	100	22
31-Dec-04		31.5	17	100	20
01-Jan-05		31	17	100	6
02-Jan-05		30	17	100	2
03-Jan-05		32	17.5	100	1
04-Jan-05		33	16	86	0
05-Jan-05	17:15	29	16	74	0

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
06-Jan-05	17:30	30	15	95	1.2
07-Jan-05	17:18	24	18	100	22
08-Jan-05	17:58	23	15	100	44
09-Jan-05	17:30	27	16	98	12
10-Jan-05	17:30	24	16	96	25
11-Jan-05	17:30	23	17	99	52
12-Jan-05	17:30	23	15	95	1
13-Jan-05	17:30	26	13	82	0
14-Jan-05	17:30	27	14	81	0
15-Jan-05	17:40	26	14	81	0
16-Jan-05	17:40	30	15	78	0
17-Jan-05		34	15	82	0
18-Jan-04	17:30	25	16	80	1
19-Jan-04	17:30	24	15	95	2
20-Jan-05	17:25	21	17	100	46.5
21-Jan-05	17:30	24	16	94	1.3
22-Jan-05	17:25	25	15	86	0.6
23-Jan-05	18:00	30	17	87	0
24-Jan-05	17:30	27	17	85	9
25-Jan-05	17:35	27	15	100	10
26-Jan-05	17:30	26	15	95	0
27-Jan-05	17:20	26	15	100	5
28-Jan-05	17:30	24	17	100	25
29-Jan-05	17:30	24	16	95	3.5
30-Jan-05	17:20	27	14	88	2
31-Jan-05	17:25	28	16	90	1.5
01-Feb-05	17:20	27	19	95	12
02-Feb-05	17:30	25	15	89	6.7
03-Feb-05	17:20	27	18	85	2.7
04-Feb-05	17:40	25	17	99	20
05-Feb-05	17:30	24	17	100	18
06-Feb-05	17:20	22	17	100	6
07-Feb-05	17:50	21	15	95	1
08-Feb-05	18:15	24	15	93	0
09-Feb-05	17:20	26	16	93	0.5
10-Feb-05	17:30	28	17	82	0.2
11-Feb-05	17:40	25	14	86	3
12-Feb-05	18:00	26	14	96	6.7
13-Feb-05	18:05	24	14	86	2
14-Feb-05	17:25	25	17	83	0.7
15-Feb-05	17:30	26	16	84	0
16-Feb-05	17:00	28	17	86	0
17-Feb-05	17:30	25	17	100	11
18-Feb-05	18:10	25	17	100	10.2
19-Feb-05	17:30	27	18	95	2.5
20-Feb-05	17:30	25	16	100	26
21-Feb-05		27	16	100	2
22-Feb-05	18:10	25	19	100	7.5
23-Feb-05		27	17	95	8
24-Feb-05	17:35	25	18	96	9.5
25-Feb-05	17:25	24	17	100	42.5
26-Feb-05	17:45	24	18	100	12.6
27-Feb-05	17:30	25	17	90	0.5
28-Feb-05	17:30	24	17	99	5.9
01-Mar-05	17:30	23	18	100	13.5
02-Mar-05	17:40	22	18	100	48
03-Mar-05	17:25	22	18	100	31
04-Mar-05	17:15	23	18	100	1.4
05-Mar-05	17:20	24	16	99	18

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
06-Mar-05	18:05	23	18	100	1.7
07-Mar-05	17:20	25	16	98	1.6
08-Mar-05	17:20	26	18	94	0.1
09-Mar-05	17:30	25	16	95	17.9
10-Mar-05	17:25	25	16	90	0.2
11-Mar-05	17:20	25	16	86	0
12-Mar-05		27	15	90	0
13-Mar-05		27	17	95	0
14-Mar-05		26	15	85	3.5
15-Mar-05		25	13	90	0
16-Mar-05		27	16	90	0
17-Mar-05		30	16	100	18
18-Mar-05	17:30	20	15	100	12
19-Mar-05	17:30	20	14	100	5
20-Mar-05	17:25	20	16	100	7.3
21-Mar-05	17:35	21	15	100	4
22-Mar-05	17:15	24	15	95	0.9
23-Mar-05	17:25	27	15	89	0
24-Mar-05	17:20	27	16	73	0
25-Mar-05	18:00	26	10	94	0
26-Mar-05	17:25	28	14	90	0
27-Mar-05	17:05	25	18	100	45
28-Mar-05	17:20	25	15	100	12.5
29-Mar-05	18:05	23	16	100	4.3
30-Mar-05	17:20	22	18	100	11
31-Mar-05	17:20	24	17	100	2.5
01-Apr-05	17:20	22	17	99	5.9
02-Apr-05	18:05	22	15	99	3.1
03-Apr-05	17:20	23	13	86	0
04-Apr-05	17:30	23	12	86	0
05-Apr-05	17:20	23	13	86	0
06-Apr-05	18:00	23	15	86	0
07-Apr-05	17:05	20	15	100	5.1
08-Apr-05	17:20	18	15	100	3.5
09-Apr-05	17:20	18	14	100	3.5
10-Apr-05	17:50	21	15	100	0
11-Apr-05	17:30	23	13	95	0
12-Apr-05	17:15	23	16	92	0
13-Apr-05	18:15	23	14	95	0
14-Apr-05	17:45	25	15	90	0
15-Apr-05	17:20	25	15	80	0
16-Apr-05	17:30	24	14	90	0
17-Apr-05	17:25	25	16	90	0
18-Apr-05	18:00	25	16	87	0
19-Apr-05	17:30	24	15	88	0
20-Apr-05	17:35	23	15	87	0
21-Apr-05	17:40	24	14	85	0
22-Apr-05	17:15	22	14	95	7.5
23-Apr-05	17:50	21	14	99	18.6
24-Apr-05	17:45	22	13	95	0
25-Apr-05	17:20	23	13	90	0
26-Apr-05	17:20	24	13	89	0
27-Apr-05	17:20	22	14	95	0.5
28-Apr-05	17:30	21	15	100	9.5
29-Apr-05		21	14	100	0
30-Apr-05		23	13	90	0
01-May-05		23	14	95	0
02-May-05		22	16	90	0
03-May-05		21	16	100	11

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
04-May-05		19	16	100	8
05-May-05		19	16	100	8
06-May-05		20	17	100	10.4
07-May-05		20	14	100	3
08-May-05		19	13	100	3
09-May-05		21	12	90	0
10-May-05		17	12	100	13
11-May-05		17	14	100	11
12-May-05		18	16	100	11
13-May-05		18	14	100	6
14-May-05		17	17	100	3
15-May-05		18	17	100	15
16-May-05		19	12	100	10
17-May-05		18	15	100	23
18-May-05	17:30	18	12	100	3.2
19-May-05	17:10	19	14	100	1.4
20-May-05	17:25	20	15	100	0.3
21-May-05		21	15	100	2
22-May-05		18	15	100	8.5
23-May-05		18	14	100	21
24-May-05		17	14	100	5
25-May-05	17:00	17	14	100	4
26-May-05	17:20	18	13	100	1
27-May-05	17:30	19	13	100	0.9
28-May-05	17:30	20	15	100	0.9
29-May-05	17:15	19	12	100	0.2
30-May-05	17:10	18	13	100	4
31-May-05	17:20	18	14	100	2
01-Jun-05	17:10	17	15	100	15
02-Jun-05		16	12	100	2
03-Jun-05		17	11	100	3.5
04-Jun-05	17:20	18	13	100	16
05-Jun-05	17:10	17	13	100	32
06-Jun-05	17:10	19	12	100	1.2
07-Jun-05	17:15	19	9	100	0.5
08-Jun-05	17:15	19	15	100	1.7
09-Jun-05	17:30	17	12	100	4.5
10-Jun-05	17:30	17	10	100	1.1
11-Jun-05	17:10	18	11	100	0
12-Jun-05	17:10	17	13	100	12
13-Jun-06	17:05	18	13	100	8
14-Jun-05	17:15	20	12	100	3.5
15-Jun-05	17:10	18	15	100	16
16-Jun-05	17:10	19	10	100	0.2
17-Jun-05	17:00	17	10	100	4.5
18-Jun-05	17:10	16	13	100	1.8
19-Jun-05	17:10	16	13	100	10
20-Jun-05	17:00	15	12	100	16
21-Jun-05	17:10	17	10	100	0.6
22-Jun-05	17:15	17	13	100	6
23-Jun-05	17:00	17	12	100	16
24-Jun-05	17:00	15	12	100	2
25-Jun-05		18	13	100	2.5
26-Jun-05		17	14	100	1.5
27-Jun-05		18	12	100	0
28-Jun-05		19	12	100	0.1
29-Jun-05		19	10	100	0
30-Jun-05		19	12	100	1
01-Jul-05		17	12	100	14

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
02-Jul-05		19	11	100	0
03-Jul-05		19	10	100	0
04-Jul-05	17:00	18	9	95	0
05-Jul-05	17:00	16	13	100	6.5
06-Jul-05	17:10	15	12	100	16
07-Jul-05	17:10	15	10	100	19
08-Jul-05	17:15	15	13	100	37
09-Jul-05	17:00	15	11	100	3.5
10-Jul-05	17:00	15	10	100	8.5
11-Jul-05	17:00	15	11	100	1.5
12-Jul-05	17:00	15	9	100	3.5
13-Jul-05	17:00	15	8	100	9
14-Jul-05	17:00	15	12	100	8.5
15-Jul-05	17:00	16	9	100	11
16-Jul-05	17:00	16	10	100	0.2
17-Jul-05	17:00	16	8	100	0
18-Jul-05	17:00	17	11	100	2
19-Jul-05	18:30	16	10	100	42.5
20-Jul-05	19:30	17	10	100	1
21-Jul-05	16:55	18	14	100	5
22-Jul-05	17:10	18	14	100	0.5
23-Jul-05	17:10	18	10	100	0
24-Jul-05	18:00	16	13	100	7
25-Jul-05	17:00	16	8	100	0
26-Jul-05	17:00	17	8	94	0
27-Jul-05		18	5	90	0
28-Jul-05	17:45	18	5	90	0
29-Jul-05	17:20	14	6	100	1.9
30-Jul-05	17:20	14	12	100	7
31-Jul-05	17:00	15	11	100	4.9
01-Aug-05		15	12	100	14
02-Aug-05	17:30	15	10	100	5.4
03-Aug-05	17:15	15	11	100	12
04-Aug-05	17:15	15	11	100	11
05-Aug-05	17:45	15	9	100	0.3
06-Aug-05	17:20	15	10	100	1.4
07-Aug-05	17:00	15	12	100	7.2
08-Aug-05	17:00	15	11	100	10.6
09-Aug-05	17:00	15	10	100	6
10-Aug-05	17:00	16	10	100	4.3
11-Aug-05	17:00	15	11	100	4
12-Aug-05	17:00	16	12	100	9.4
13-Aug-05	17:30	16	12	100	2.8
14-Aug-05	17:20	18	8	100	0.1
15-Aug-05	17:30	16	9	100	8.3
16-Aug-05	17:00	18	13	100	4
17-Aug-05	17:00	18	8	100	0
18-Aug-05	17:40	19	9	90	0
19-Aug-05	17:30	19	9	90	0
20-Aug-05	17:00	20	9	85	0
21-Aug-05		21	9	90	0
22-Aug-05		19	8	90	0
23-Aug-05		15	12	95	1.5
24-Aug-05		16	10	95	0
25-Aug-05		17	11	95	1
26-Aug-05	17:20	17	10	90	0
27-Sep-05	17:10	15	9	95	3.5
28-Aug-05	17:30	16	11	100	6
29-Aug-05	17:30	16	9	100	12.8

Date	Time	Max. temp. (°C)	Min. temp. (°C)	Humidity (%)	Rainfall (mm)
30-Aug-05	17:20	15	12	100	29
31-Aug-05	17:00	14	12	100	35
01-Sep-05	17:00	15	11	100	26
02-Sep-05	17:00	14	12	100	19
03-Sep-05	17:00	14	11	100	18.5
04-Sep-05	17:00	15	11	100	14.5
05-Sep-05	17:00	17	11	100	1.3
06-Sep-05	17:00	17	10	100	0.5
07-Sep-05	17:10	16	10	100	4
08-Sep-05		15	11	100	12
09-Sep-05	17:30	16	9	100	0.2
10-Sep-05	17:30	16	12	100	12.7
11-Sep-05	17:20	16	12	100	6.2
12-Sep-05	17:00	16	13	100	38
13-Sep-05	17:00	18	9	100	1.4
14-Sep-05	17:20	17	5	100	0
15-Sep-05	17:00	15	13	100	3.9
16-Sep-05	17:00	17	9	88	0.2
17-Sep-05	17:40	17	10	89	0
18-Sep-05	17:00	17	10	81	0.6
19-Sep-05	17:00	21	10	83	0
20-Sep-05	17:00	22	14	84	0
21-Sep-05	17:00	22	14	82	0
22-Sep-05	17:00	20	15	85	0.5
23-Sep-05	17:05	19	13	84	1.4
24-Sep-05	17:00	17	12	100	6.5
25-Sep-05	17:00	16	12	100	4.5
26-Sep-05	17:00	18	16	100	2.8
27-Sep-05	17:00	16	13	100	17
28-Sep-05	17:00	17	12	100	5
29-Sep-05	17:00	18	12	100	3
30-Sep-05	17:30	19	12	100	1
01-Oct-05	17:50	19	11	95	0
02-Oct-05	17:00	21	13	86	0
03-Oct-05	17:10	21	14	86	0
04-Oct-05	17:30	19	10	85	0
05-Oct-05	17:45	16	10	94	4.9
06-Oct-05	05:40		8		1.9

Appendix C: Supporting Information for Chapter 4

Appendix C1: Habituation

Indri indri

A group of *I. indri*, 'white-heads', were first located on 18 November 2004; an adult male and adult female, with an infant, were observed resting. The adult female moved first, following an alarm-call the male followed. They were followed for 35 minutes. Habituation continued into December 2004, when observers were able to follow *I. indri* for an hour. A sub-adult was also observed in this group.

Early December (02 and 03 December 2004) a second group of *I. indri* was located and followed, the 'black-head' study group. By mid-December (13 December 2004) they could be followed for five hours. With continued difficulties in locating the group, they were followed all day for the first time 19 January 2005. Following darting and radio-collaring of the adult and sub-adult females (20 January 2005), finding the group no longer proved so problematic. The sub-adult female was the most difficult and took the longest to habituate. Only at the end of March did she cease to alarm-call observers.

Hapalemur griseus griseus

Group One was first observed 13 November 2004 and habituation commenced. After counting seven individuals the group dispersed, after which only three or four individuals were observed together; possibly as a predator avoidance tactic. On the first day, using four observers, Group One was followed from 05:30 to 17:00. They frequently alarm-called and 'tail wagged'. 'Tail wagging' is when an individual sits on a branch flicking its tail back and forth. Group One was followed continuously the following day (12 November 2004) from 06:00 to 17:00. Alarm calls were fewer and all seven individuals were seen together. The following day (15 November 2004) the group was again followed from 06:00 to 17:00. Alarm calls were rare, and mainly originated from the adult male, even the adult female with a baby seemed unconcerned. After this data could be collected and the group followed with ease.

Appendix C2: Sightings of Additional Groups of Study Species

Indri indri

In February (20 February 2005) while following *I. indri* in the north of their territory (S18°48.789, E48°26.332) a second *I. indri* was heard calling, at 12:18, at what was estimated to be less than 50m away to the north-east. Twice in early March (02 and 09 March 2005) a group of *I. indri* were heard calling approximately 30m south of the study group, which later were at the southern extremity of their home range. A group was heard calling approximately 25m to the south during observations of *I. indri* on 23 March 2005, at the southern border of the study group's range. While following *I. indri* in July (04 July 2005) a second group of *I. indri* was heard calling nearby to the east, to the east of the 'Joseph' and 'Indri' trails. Again in July (21 July 2005) a second group of *I. indri* were heard approximately 30 to 40m away to the east of 'Joseph' hill. In August another group of *I. indri* was heard calling at 10:15, apparently on the northern most part of 'Joseph' hill.

While following *P. d. diadema* in April (18 April 2005) the study group of *I. indri* was observed and heard at 08:40 (S18°48.910, E48°26.206). Later in the day a group of 'white-head' *I. indri* (S18°48.867, E48°26.193) were observed, 28m from the edge of the study group's territory. This was the group of 'white-heads' that had initially been habituated. The same group were also observed in March 2005 (S18°48.816, E48°25.987) and April 2005 (S1848.872, E4826.098). In September 2005 they were observed on the trail at I57 (S18°48.869, E48°26.169), 140m away from the study group.

A white-headed, apparently solitary, *I. indri* was observed within the study group's territory (S18°48.901, E048°26.367). This individual alarm-called, but no *I. indri* were heard to respond. Unfortunately due to equipment failure, no calls were recorded. This call approximates the 'hoot' call of Pollock (1975, described as the alarm call given to ground predators and observers. The signal from the radio-tracking receiver suggested that the study group were not far away, although they could neither be seen nor heard. During darting (03 February 2005) a solitary white-head was also observed in the territory of the study group (S18°48.880, E48°26.350).

A group of *I. indri* was seen while collecting *P. d. diadema* GPS tags (S18°48.733, E48°26.085). A group, containing both black- and white-headed individuals, and presumed to be the same group was observed and heard territorially calling at 10:37 on 13 August 2005 while following *P. diadema* (S18°48.739, E:48°25.995).

Propithecus diadema

A second group was observed at the beginning of the study and observations continued throughout the study period. This group was seen in February (03 February 2005), when the baby was small, but independent (S18°48.903, E48°26.369). This group was again seen later in the month (13 February 2005) close to resting *I. indri* (S18°48.836, E48°26.226). It was also observed in March (02 March 2005) while following *I. indri* (S18°48.853, E48°26.247) and again in April (16 April 2005) (S18°48.858, E48°26.321).

A further group of *P. diadema* were observed on 09 March 2005 (S18°48.984, E08°26.320) south-east of the study group's territory. Later on the same day, the study group were observed the opposite side of their territory (S18°48.814, E48°25.965). In April (15 April 2005) a group of *P. diadema* were observed outside of the study group's territory (S18°48.880, E48°26.350).

In September (15 September 2005) two *P. diadema* were observed twice (S18°48.891, E48°26.357; S18°48.899, E48°26.287) while following *I. indri.*

Hapalemur griseus griseus

A guide (Alfred Rakotonodravelo) observed a group of *H. g. griseus* at the northern edge of Group Two's territory (S18°48.737, E48°25.775). They alarm-called and moved further north when disturbed by *Eulemur rubriventer.* A group of *H. g. griseus* was observed while following *P. d. diadema* (S18°48.740, E48°26.080). In February (13 February 2005) there was a group of *H. g. griseus* just north of the study group of *I. indri* (S18°48.835, E48°26.275). At the end of January (12 January 2005) and beginning of February (04 February 2005) two groups of *H. g. griseus* were observed on indri trail. The group nearest camp (S18°48.831, E48°26.037) was comprised of three individuals, the second group (S18°48.853, E48°26.247) was much larger, consisting of around seven individuals.

In February (26 February 2005) *H. g. griseus* where observed while following *P. d. diadema* (S18°48.777, E48°25.970). In early March (09 March 2005) *H. g. griseus* were head while following *I. indri* (S18°48.984, E48°26.320). In March *H. g. griseus* were heard at the edge of *I. indri* territory (S18°48.955, E48°26.220). 15 April 2005 *H. g. griseus* were seen twice, an hour apart, while searching for *P. d. diadema* (S18°48.853, E48°26.303 and S18°48.880, E48°26.350). The following day *H. g. griseus* were observed in a similar area (S18°48.861, E48°26.328). On 17 April 2005 a group of *H. g. griseus* were observed while following *P. d. diadema* (S18°48.975, E48°26.239). On 22 April 2005 a group of *H. g. griseus* was seen in the similar area (S18°48.814, E48°25.965). Again in April (24 April 2005), *H. g. griseus* were observed while following *P.* diadema (S18°48.698, E48°25.141). On 10 July 2005 a group was observed while following *P. diadema* (S18°48.800, E48°25.941). In October 2005 a group of *H. g. griseus* was observed while following *P. diadema* (S18°48.883, E48°26.188). Immediately across the miner's road, there were at least two groups, both seen in March (11 March 2005). One was also observed in earlier in March (01 March 2005).

Appendix C3: Inter-Group Encounters and Territorial Defence

Indri indri

The importance of the long calls of *I. indri* in territorial defence has been noted by Pollock (1975; 1986). The 'territorial' calls of *I. indri* were not systematically recorded during the study, those recorded are detailed here.

A territorial call was heard late in the day, at 15:08, in February (13 February 2005). Another late call was heard on 20 February when the adult female initiated a territorial call at 14:37, taken up by both the adult male and sub-adult female. In February (25 February 2005) the group called at 09:40 and then at 14:37, calls initiated by the male and adult female respectively.

On 02 March 2005 at 16:37 the adult female was apart from the rest of the group. She initiated a territorial call, after which the other group members came to her. The adult male initiated two territorial calls at 09:42 and 12:13 on 09 March 2005. The adult and sub-adult females joined in both calling sessions, but on the later session the adult male stopped calling once the females had started and he then moved towards them. Also in March (23 March 2005) the adult female initiated a territorial call at 11:57, seemingly in response to a second group calling approximately 25m away to the south.

In early April (08 April 2005) a territorial call was heard at 11:41. On 22 April 2005 the adult female initiated a territorial call at 11:51. The first day the disappearance of the baby was noted by the observer, (31 May 2005) the adult female initiated three territorial calls. The first, at 11:05 was started when she was approximately 60m away from the adult male and sub-adult female who were feeding together. She then called twice, close together in time (12:13 and 12:44). The sub-adult female and adult male joined in with both calls. In early June (09 June 2005) the territorial call was sung by the adult female and sub-adult female: the adult male did not participate. On the following day (10 June 2005) the adult female initiated a call, which was taken up by the male and sub-adult.

The adult female initiated two territorial calls on 04 July 2005, at 08:24 and 10:00. On 12 July 2005 the adult female initiated a territorial call, the adult male and sub-adult female joining in. In August the group called at 11:25 when it was raining, and the sub-adult female was the last group member to take up the call. This call lasted 1.37 minutes.

The group called while still in their nightly rest spot on 05 September 2005 at 08:12. On 15 September 2005 the group called at 0759. On 23 September 2005 the adult female initiated a call at 07:43, taken up by both the adult male and sub-adult female. Later in the day the adult male initiated a territorial call at 13:21, after which it was taken up by the adult female and sub-adult female and the male ceased to sing.

Occasionally the territorial call appeared to be initiated by the adults to locate the other group members. For the male this occurred on 05 September 2005 at 11:03 and the later call on 09 March 2005. On both occasions the male moved towards the females. In January (15 January 2005) a territorial call, from the direction of the study group, was heard at 19:40 (light reading of 10.3 LW/EV) when there was a half moon. The call was taken up by a second group.

Hapalemur griseus griseus

On occasion Group One and Group Two were in close proximity to each other with no apparent aggression, however aggressive encounters were observed. The frequent close proximity of both groups was exemplified in July (08 July 2005).

Observations began on Group One south of camp and following a period of rapid travel, observations unintentionally switched to Group Two found near camp.

On the evening of 11 April 2005 Group One and two were in the vicinity of camp, on their respective sides of the river. Neither group showed any antagonism towards the other. An encounter between the two groups was observed in early June (10 June 2005). Group One attacked Group Two, who initially retreated. Group One continued to alarm call, while Group Two remained silent. After this Group One retreated and Group Two remained in the area to sleep. This was an area in which Group One had been previously observed resting.

In July (21 July 2005) Group Two were in trees over camp, when at 1730 Group One appeared. Group One attacked Group Two and biting was observed. Group One remained in the area. Encounters were observed between groups either side of the miner's road. At the beginning of March (01 March 2005) Group One were observed in a vocal exchange with a group across the road. This was observed again on 26 July 2005. Both groups were in trees adjacent to the road loudly calling. Neither group crossed the road.

Appendix C4: Nightly Resting

Indri indri

In June, (17 June 2005) the sub-adult female and adult male were observed resting together in the morning. In August (11 August 2005) the adult and sub-adult female were resting in the same tree. That night the male rested alone at 14:00 and the following morning, at 08:55, he was still in the same position, but the adult female was with him.

The adult female and baby rested together in early March (23 March 2005). In March (31 March 2005) the adult male rested close to the baby and adult female who were together. On 08 and 26 April 2005 the baby and adult female rested together on horizontals at 16 and 25m high. On 22 April 2005 the adult female and baby rested on a large horizontal at 20m, the adult male later rested above them in the same tree.

In July (12 July 2005) the adult male and female rested in the same tree, while the sub-adult was approximately 20m away.

In September (15 September 2005) the adult and sub-adult female were found at 07:30 huddled together, the adult male resting approximately 10m away. Later in the month (23 September 2005) all three individuals were found in close proximity following their nights rest.

Conversely in February (05 February 2005) the group was dispersed over night. The adult female rested with her baby, the male and sub-adult female separate and as much as 50m away. Later in February (13 February 2005) the adult female again rested with her baby, the sub-adult female within sight, approximately 30m away. The male could not initially be seen.

Overnight rest-trees were observed to be re-used by *I. indri*. In June (10 June 2005) they utilised the same rest spot as in May (31 May 2005). Prior to resting the *I. indri* fed in the same tree and each individual rested in a similar position to before.

Appendix C5: Group Composition and Dynamics

Propithecus diadema

On 04 March 2005 three males were followed: adult and sub-adult collared males and an un-collared male. Later in March (11 March 2005) we began by following the previously collared male who was on his own. This male had a bad leg that he kept licking, suggesting he had been involved in a fight, possibly with other group members. After he disappeared five group members were found together, including the adult and sub-adult collared males and an adult female. In early April (02 April 2005) only five individuals were followed. On 10 and 24 April 2005 initially all seven individuals were observed; only five were together at the end of the day. Observations on 27 September 2005 were on an old collared male, and for the eight hours and forty minutes of observations (07:40 to 16:20) none of the other group members were observed.

Fighting was observed over feeding trees. In March (11 March 2005) the five individuals were fighting and squabbling. Fights were observed in April (10 and 24 April 2005), including biting on the neck. An adult female had a semi-closed right eye on 24 April 2005, which could have been injury or illness. On 10 July 2005 fighting appeared to result in one individual to move away from other group members.

On the day it was noticed the baby had disappeared (01 October 2005) the overall behaviour of the group was unusual. The young collared male alarm-called all day. It did not appear directed at observers, as he came close to feed; instead it appeared directed towards other group members. Fights, including biting, were observed between this male and the others, apparently over position in feeding trees. This was also a day during which the group was not very cohesive; all seven adults were observed together, although only one or *two individuals were usually seen* together.

A mother from another group was observed refusing to allow her infant to travel on her back.

Appendix D: Supporting Information for Chapter 6

Appendix D1. List of known plants consumed

Location: SR: Special Reserve Andasibe, NP: National Park Mantadia

Eaten by: Pd: *Propithecus diadema*, Ii: *Indri indri*, Hgg, *Hapalemur griseus griseus*

Family	Genera	Species	Vernacular name	Endemic	Use	Location	Habitat	Type	Eaten by
Acanthaceae	*Hypoestes*		Malamaravina beloalika		Medicinal	SR,NP	Primary, S	Herbaceous	Hgg
Acanthaceae	*Hypoestes*		Ravimbelatra		Medicinal	SR,NP	Primary, S	Herbaceous	Pd
Anacardiaceae	*Micronychia*		Tsiramiramy	Yes	Construction	SR, NP	Primary	Tree	Pd
Anacardiaceae	*Protorhus*	*ditimena*	Ditimena	Yes	Construction	SR, NP	Primary	Tree	Pd, Ii
Annonaceae	*Xylopia*	*flexuosa*	Hazoambo		Medicinal	SR, NP	Primary	Tree	Pd, Ii
Aquifoliaceae	*Ilex*	*mitis*	Hazondrano			SR, NP		Tree	Pd
Araliaceae	*Cuphocarpus*		Vantsilana	Yes				Tree	Ii
Araliaceae	*Cussonia*	*fraxinifolia*	Voantsilana	Yes	Medicinal			Tree	Pd
Arecaceae	*Dypsis*		Palm	Yes			Primary		Hgg
Aspleniaceae	*Asplenium*	*nidus*	Ampanga					Herbaceous	Pd
Asteraceae	*Apodocephala*	*angustifolia*	Beaty	Yes				Tree	Pd
Asteraceae	*Brachylaena*	*perrieri*	Merana				Primary	Tree	Pd, Ii
Asteraceae	*Vernonia*	Sirambengy		No				Tree	Pd
Bignoniaceae	*Phyllarthron*	Zahana		Yes			Primary	Tree	Pd
Clusiaceae	*Callophyllum*	*milvum*	Vintanona		Various	SR, NP	Primary	Tree	Ii
Clusiaceae	*Garcinia*	*mangourensis*	Kijy masina	Yes		SR, NP	Primary	Tree	Ii
Clusiaceae	*Garcinia*	*verrucosa*	Kijim-boalavo	Yes		SR, NP	Primary	Tree	Pd
Clusiaceae			Kijy	Yes			Primary	Tree	Pd, Ii
Combretaceae	*Terminalia*	*tetrandra*	Antafanala	Yes	Construction	SR, NP	Primary	Tree	Pd
Cunoniaceae	*Weinmannia*		Lalona	No	Various	SR, NP	Primary	Tree	Pd, Ii
Erythroxylaceae	*Erythroxylum*		Menahihy	Yes	Various		Primary	Tree	Pd, Ii

Family	Genera	Species	Vernacular name	Endemic	Use	Location	Habitat	Type	Eaten by
Erythroxylaceae	*Pleuroridgea*		Malambovony	Yes	Various		Primary	Tree	Pd
	Blotia		Fanjavala	Yes			Primary	Tree	Pd
Euphorbiaceae	*Blotia*	*mimosoides*	Fanjavala madinidravina	Yes			Primary	Tree	Pd
Euphorbiaceae	*Blotia*	*oblongifolia*	Fanjavala beravina	Yes			Primary	Tree	Pd
Euphorbiaceae	Macaranga		Mankaranana	Yes		SR, NP	Primary	Tree	Pd, Ii
Euphorbiaceae			Hazondomohina		Various		Primary		Pd, Ii
Euphorbiaceae	*Uapaca*	*densifolia*	Voapaka	Yes		SR, NP		Tree	Pd, Ii
Fabaceae	*Albizzia*	*gummifera*	Volomborona			SR, NP		Tree	Pd
Fabaceae	*Dallbergia*		Palissandre	No	Wood for art	SR, NP	Primary	Tree	
Flacourtiaceae	*Aphloia*		Voafotsy	Yes	Construction	SR, NP	Primary, S	Shrub	Hgg
Flacourtiaceae	*Ludia*		Menavahatra	Yes	Construction	SR, NP		Tree	Pd
Flacourtiaceae	*Tisonia*		Hazombato	Yes		SR, NP		Tree	Ii
Lauraceae	*Cryptocarya*		Tavolo	No	Construction	SR, NP	Primary	Tree	Pdd, Ii, Hgg
Lauraceae	*Ocotea*		Varongy	No	Construction	SR, NP	Primary	Tree	Pd, Ii
Lauraceae	*Ocotea*	*trichophleibia*	Varongy voara	No	Construction	SR, NP	Primary	Tree	Ii
Loganiaceae	*Nuxia*		Valanirana	Yes	Medicinal	SR, NP	Primary	Tree	Ii
Melanophyllaceae	*Melanophylla*		Marefolena	Yes	Construction	SR, NP	Primary	Tree	Ii
Melastomataceae	*Clidemnia*	*hirta*	Mazambody	No	Medicinal		Primary, S	Herbaceous	Hgg
Melastomataceae	*Lijndenia*		Tsimahamasatsokina				Primary	Tree	Pd, Ii
Melastomataceae	*Medinilla*	*parvifolia*	Takasina	Yes			Primary	Tree	Pd, Ii
Monimiaceae	*Tambourissa*		Ambora	Yes	Various	SR, NP	Primary	Tree	Pd, Ii
Moraceae	*Ficus*	*pachclada*	Voarabe	No				Tree	Hgg
Moraceae	*Ficus*	*pyrifolia*	Nonoka	No				Tree	Pd, Ii
Moraceae	*Stribulus*	*obovata*	Dipaty	Yes			Primary	Tree	Pd
Myrsinaceae	*Maesa*	*lanceolata*	Radoka	No	Medicinal	SR, NP		Shrub	Pd

Family	Genera	Species	Vernacular name	Endemic	Use	Location	Habitat	Type	Eaten by
Myrsinaceae	*Oncostermon*		Hazontoho	Yes		SR, NP	Primary	Tree	Pd
Myrtaceae	*Eugenia*	*emirnensis*	Robary	Yes	Medicinal	SR, NP	Primary	Tree	Pd
Myrtaceae	*Eugenia*	*sakalavarum*	Hazompasika	Yes		SR, NP	Primary	Tree	Pd
Myrtaceae			Rotra		Various	SR, NP	Primary	Tree	Pd, Ii
Pittosporaceae	*Pittosporum*		Hazombary	No	Medicinal			Tree	Pd, Ii
Poaceae	*Cathariostachys*	*madagascariensis*	Bamboo						Hgg
Poaceae	*Cathariostachys*	*pierreri*	Vine bamboo						Hgg
Poaceae	*Poecylostachys*	*festicaceus*	Vilonala					Herbaceous	Pd, Hgg
Proteaceae	*Dilobeia*	*thouarsii*	Vivaona	Yes	Various	SR, NP	Primary, S	Shrub	Pd
Rubiaceae	*Anthirea*	*borbonica*	Malemiravana					Tree	Pd, Ii
Rubiaceae	*Breonia*	*sinensis*	Molompangady	Yes			Primary	Tree	Pd
Rubiaceae	*Canthium*		Pitsikahitra					Tree	Pd
Rubiaceae	*Craterispermum*	*laurinum*	Hazomamy	Yes				Tree	Pd
Rubiaceae	*Schismatoclada*	*farahipensis*	Hazoporetika					Tree	Pd
Rubiaceae	*Tricalysia*	*albicaulis*	Tsikafekafe		Fire wood			Tree	Pd
Sapindaceae	*Allophylus*	*cobbe*	Karambito			SR, NP	Primary	Tree	Pd
Sapindaceae	*Filicium*		Elatrangidina				Primary	Tree	Pd, Ii
Sapindaceae	*Plagiocyphus*	*jumellei*	Volanary	Yes			Primary	Tree	Pd, Ii
Sapindaceae	*Tinopsis*		Ramaindafa				Primary	Tree	Pd, Ii
Sapotaceae	*Chrysophyllum*	*boivinianum*	Famelona	Yes	Various	SR, NP	Primary	Tres	Pd, Ii
Sapotaceae			Nanto	Yes	Various	SR, NP	Primary	Tree	Ii
Smilacaceae	*Smilax*	*kraussiana*	Fandrikataly	No	Medicinal			Liana	Pd
Solanaceae	*Solanum*	*auxicilatum*	Bakobako	No			Forest, secondary	Shrub	Pd
Sphaerosepalaceae	*Carallia*	*brachiata*	Farimamy	Yes			Primary	Tree	Ii
Stericuliaceae	*Dombeya*		Hafotra	Yes		SR, NP	Primary	Tree	Pd, Hgg

Appendix D2: Young leaf consumption by *I. indri*.

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Uapaca densifolia	Feb-Jul, Sep-Oct	163	72477	445	15	2687	10	3	30
Ocotea sp.	Feb-Jul, Sep-Oct	68	36583	538	20	1616	15	3	35
Tambourissa sp.	Feb-Oct	25	28104	1124	95	3923	13	15	30
Cryptocarya sp.	Feb-Jul, Sep	54	26362	488	32	2844	16	4	30
Syzygium sp.	Feb-Sep	29	19622	677	71	2693	11	3	20
Erythroxylum sp.	Mar, Sep-Oct	12	10663	889	106	3196	17.5	2	30
Sapotaceae family	Apr, Sep-Oct	6	5355	893	76	3086	19	15	25
Xylopia sp.	Feb-Mar, May-Jul	9	5316	665	53	1983	13	7	20
Tinopsis sp.	Feb-Mar, Jun-Jul	8	3936	492	78	1182	9	4	15
Clusiaceae family	Mar, May-Jul, Oct	6	2893	482	210	1381	10	7	15
Ficus pyrifolia	Feb-Mar, Jun	3	2665	888	247	1410	17	6	30
Rhodolaena altivola	Mar, Aug	3	1976	659	84	1515	14	9	17
Weinmannia sp.	Mar, Jun-Jul	4	1752	438	114	766	11	1	25
Liana	Jul, Sep	9	1539	171	60	396	11	8	20
Filicium sp.	Jul, Sep	2	1469	735	606	863	18	15	20
Protohus ditimena	Feb-Mar	5	1313	263	166	466	13	7	15
Callophyllum sp.	Feb, Apr	3	1304	435	86	867	22	15	25
Tisonia sp.	Jun, Aug	2	1181	591	305	867	12	8	15
Carallia sp.	Apr	1	1160	1160	1160	1160	30	30	30
Plagiocyphus jumellei	Mar	3	1043	348	159	599	13	10	15
Garcinia mangourensis	Sep	1	482	482	482	482	15	15	15

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Lijndenia sp.	Mar	2	480	240	192	288	4	4	4
Asteraceae family	Mar	4	458	115	50	197	9	7	10
Medinilla sp.	Jun	1	457	457	457	457	3	3	3
Euphorbicaea family	Mar, Aug	2	436	218	184	252	9.5	4	15
Nuxia sp.	Jun	1	383	383	383	383	15	15	15
Anthirea borbonica	Feb	2	368	184	169	199	8	7	8
Brachylaena perrieri	May, Jul	3	351	117	40	201	15	15	15
Cuphocarpus sp.	Oct	2	333	167	15	318	7	4	10
Macaranga sp.	Mar, Jun	2	328	164	90	238	5	2	7
Pittosporum sp.	Jun	1	295	295	295	295	32	32	32
Apodocephala angustifolia	Jun	1	211	211	211	211	15	15	15
Melanophylla sp.	Feb	1	180	180	180	180	12	12	12
Moss	Mar	1	174	174	174	174	20	20	20
Terminalia	Aug	1	119	119	119	119	10	10	10
Chrysophyllum sp.	Apr	1	94	94	94	94	32	32	32

Appendix D3 Young leaf consumption by *P. diadema.*

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Syzgium sp .	Feb-Oct	93	28728	309	30	1800	11	2	25
Unknown plant	Feb-Oct	101	25689	254	21	1313	11	1	35
Ocotea sp.	Feb-Apr, Jun-Oct	39	23529	619	26	3946	15	5	35
Liana	May-Oct	60	20288	338	23	1920	11	0	26
Sapotaceae family	Apr, Jun-Oct	27	20281	751	5	3159	12	0	25
Bakerela sp.	Mar, Sep-Oct	25	18476	739	55	4831	15	5	30
Uapaca sp.	Feb, Apr-Oct	32	15162	474	17	2048	11	5	20
Clusiaceae family	Mar-Jun, Aug-Sep	20	13778	725	13	2115	13	6	30
Cryptocarya sp.	Feb-Apr, Jun-Aug,	16	4716	295	34	1102	9	2	15
Tambourissa sp.	Apr-May, Jul-Aug	8	4287	536	87	2158	11	5	25
Flacouritaceae family	Feb-Mar, Jun	5	3170	634	94	1916	8	3	20
Ilex sp.	May-Jun, Sep-Oct	5	3150	630	402	1104	13	8	20
Xylopia sp.	Mar, May-Jul, Sep	9	2303	256	23	377	10	2	20
Macaranga sp.	Mar, Jul, Sep	3	2290	763	154	1265	10	1	20
Ficus pyrifolia	Jun	1	2104	2104	2104	2104	7	7	7
Erythroxylum sp.	Feb-Apr, Jul, Oct	6	2101	350	52	629	8	4	15
Pittosprum sp.	Jun-Aug	3	2079	693	157	968	14	10	20
Rhodolaena altivola	Feb, Aug-Sep	4	1859	465	47	978	6	3	9
Dilobeia thouarsii	May, Sep	4	1790	448	358	543	17	15	20
Protorhus sp.	Feb-Mar	3	1696	565	53	1242	10	7	15
Chrysophyllum boivinianum	Apr, Jun	4	1607	402	19	656	17	6	25

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Myrtacaea family	Mar	2	1603	802	372	1231	25	25	25
Filicium sp.	Jun	2	1519	759	205	1314	14	8	20
Cussonia sp.	Apr, Sep-Oct	3	1500	500	88	784	10	5	16
Ramitsihaka	Sep-Oct	3	1482	494	67	1269	12	5	15
Medinilla parvifolia	Feb, May-Jun	4	1479	370	132	931	15	4	30
Tinopsis sp.	Feb-Mar, May-Jun	5	1275	255	40	494	7	4	10
Allophylus sp.	Sep	1	1232	1232	1232	1232	12	12	12
Garcinia verrucosa	Jul	2	1212	606	347	865	7	6	8
Plagiocyphus jumellei	May-Jun	3	1082	361	70	888	10	5	20
Dallbergia sp.	Apr, Oct	3	1070	357	116	665	9	5	15
Canthium sp.	Mar	2	1063	532	187	876	9	9	9
Euphorbicaea family	Feb-Mar, Sep	4	1052	263	29	422	11	6	20
Terminalia sp.	Sep	1	1008	1008	1008	1008	9	9	9
Breonia sinersis	Jun	2	968	484	284	684	13	10	15
Brachylaena perrieri	Aug	1	955	955	955	955	12	12	12
Blotia sp.	May-Jun	3	926	309	111	547	8	5	10
Eugenia emirnensis	Sep	1	892	892	892	892	12	12	12
Manitranefitra	Jul	2	859	430	166	693	10	9	11
Poacilostachys festicaceus	Jul, Sep	2	726	363	66	660	3	2	3
Stribulus obovata	Sep	1	655	655	655	655	10	10	10
Craterispermum laurinum	Jun	4	594	149	28	419	11	8	16
Leptaulus sp.	Apr	2	520	260	155	365	10	10	10
Canthium sp.	Sep	1	490	490	490	490	4	4	4

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Pleuroridgea sp.	Mar	1	489	489	489	489	6	6	6
Apodocephala sp.	Sep	1	480	480	480	480	11	11	11
Weinmannia sp.	Mar, Jun	2	460	230	25	435	9	8	10
Schismatoclada farahipensis	Feb	3	437	146	61	255	7	6	8
Anthirea borbonica	Mar, Jul, Sep-Oct	3	356	119	81	148	6	3	9
Eugenia sp.	Sep	1	314	314	314	314	15	15	15
Oncostemon sp.	Apr	2	290	145	96	194	5	2	8
Voroinampanga	Aug	1	282	282	282	282	2	2	2
Tsingarivary	Sep	1	276	276	276	276	2	2	2
Potameia sp.	Sep	1	259	259	259	259	15	15	15
Micronychia tsiramiramy	Apr	1	242	242	242	242	5	5	5
Blotia oblongifolia	Apr	2	194	97	74	120	7	7	7
Hypoestes sp.	Apr	1	186	186	186	186	3	3	3
Brachylaena sp.	Apr	2	185	93	14	171	9	8	10
Blotia mimosoides	Apr	1	175	175	175	175	1	1	1
Maesa sp.	Sep	1	155	155	155	155	2	2	2
Molotrangaka	Mar	1	104	104	104	104	7	7	7
Dombeya sp.	May	1	93	93	93	93	5	5	5
Tricalysia albicaulis	Apr	1	86	86	86	86	2	2	2
Orchid	Aug	1	83	83	83	83	12	12	12
Asplenium nidus	Apr, Sep	2	75	38	34	41	4	2	5
Anjananjana	Aug	1	67	67	67	67	3	3	3
Hypoestes sp.	Apr	1	41	41	41	41	1	1	1

Appendix D4 Plant part consumption for *I. indri.*

Species	Months	Number of bouts	Total time observed	Average Bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Mature leaves									
Tambourissa sp.	Jul	2	1839	920	218	1621	19.5	19	20
Cryptocarya sp.	Jul	1	1623	1623	1623	1623	15	15	15
Stem									
Ocotea sp.	Jul	2	3671	1836	687	2984	15	15	15
Bark									
Octotea trichophleibia	Aug-Oct	9	10143	1127	245	2435	15	7	25
Petioles									
Ocotea sp.	Jul, Sep-Oct	7	6035	862	64	2984	15	7	25
Uapaca sp.	Jul, Oct	2	449	225	166	283	11.5	11	12
Fruit									
Symphonia fasciculata	Feb	4	1140	285	185	381	7	7	7
Open flowers									
Clusiaceae family	Mar-Apr	5	5460	1092	99	3467	24	20	30
Buds									
Uapaca sp.	Jul	4	1637	327	133	501	12	10	15
Liana	Aug	1	711	711	711	711	10	10	10

Appendix D5. Plant part comparison for *P. diadema*.

*** A combination of young and mature leaves.**

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Mature leaves									
Sapotaceae family	Sep	3	2092	697	143	990	23	21	25
Cryptocarya sp.	Aug	2	1910	955	704	1206	15	15	15
Ocotea sp.	Aug	2	1443	722	586	857	20	20	20
Hypoestes sp.	Aug, Sep-Oct	6	1125	188	49	404	1	0	3
Syzgium sp	Aug	1	256	256	256	256	8	8	8
Dilobeia thouarsii	Jul	1	146	146	146	146	6	6	6
Smilax kraussiana	Jul	1	138	138	138	138	2	2	2
Ficus pyrifolia	Aug	1	122	122	122	122	10	10	10
Phyllarthron sp.	Aug	1	112	112	112	112	10	10	10
Stem									
Liana	Apr	1	311	311	311	311	20	20	20
Fougeres	Aug	1	216	216	216	216	7	7	7
Unknown plant	Jul	1	146	146	146	146	7	7	7
Orchid	Apr	1	98	98	98	98	6	6	6
Dallbergia sp.	Sep	1	45	45	45	45	7	7	7
Bark									
Syzgium sp	Sep	1	428	428	428	428	10	10	10
New fruit									
Lijndenia sp.	Apr, Sep	13	11443	880	16	3477	11	5	23

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Ocotea sp.	Feb, Apr	5	3746	749	378	1137	20	20	22
Eugenia sp.	Oct	2	1808	904	679	1129	10	10	10
Unknown plant	Apr, Jul	4	1452	363	249	646	10	7	12
Clusiaceae family	Feb	1	848	848	848	848	20	20	20
Ficus pyrifolia	Aug-Sep	4	804	201	123	299	8	6	10
Euphorbicaea family	Mar	2	422	221	77	365	15	15	15
Ficus sp.	Oct	1	345	345	345	345	10	10	10
Solanum auxicilatum	Mar	1	96	96	96	96	3	3	3
Anthirea borbonica	Feb	1	60	60	60	60	10	10	10
Old fruit									
Ocotea sp.	Apr	1	1416	1416	1416	1416	0	0	0
Xylopia sp.	Jul	1	294	294	294	294	6	6	6
Open flowers									
Symphonia fasciculata	Apr, Jun, Aug	12	8278	690	103	2183	18	10	30
Eugenia sp.	Sep	1	1460	1460	1460	1460	16	16	16
Parasitic plant	Mar-Apr	4	735	184	65	278	10	6	16
Sakatairotrala	Sep	1	151	151	151	151	7	7	7
Pleuroridgea sp.	Apr	1	79	79	79	79	6	6	6
Breonia sinensis	Aug	1	60	60	60	60	5	5	5
Flower buds									
Lijndenia sp.	Sep	1	37	37	37	37	7	7	7

Appendix D6 Dietary composition of H. g. griseus Group One.

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Young Leaves									
Cathariostachys madagascariensis	Nov-Sep	497	161923	331	10	2477	7	1	20
Cephalostachyum pierreri	Apr-Jul, Sep	21	6041	288	46	245	3	1	8
Poecilostachys festucaceus	Nov-Dec, Jul, Sep	9	1196	133	10	322	0	0	1
Unkown plant	Jul	1	76	76	76	76	2	2	2
Mature and young leaves									
Dombeya sp. (hafotra ramiringitra)	Aug-Sep	18	4209	234	15	1016	2	1	3
Dombeya sp. (long hafotra ramiringitra)	Sep	2	673	337	77	596	2	0	3
Unknown plant	Aug	1	560	560	560	560	1	1	1
Mature leaves									
Orchid	Nov, Jul	2	127	64	61	66	7	6	7
Flowers and young leaves									
Orchid	Sep	1	165	165	165	165	10	10	10
Fruit									
Clidemnia hirta	Feb-Jul, Sep	35	8718	272	14	747	0	0	1
Dypsis sp.	Feb, Apr-May	8	5800	725	231	1241	12	8	13
Bongapiso	Nov-Dec	12	4697	391	48	1083	5	3	8
Liana	Dec	2	223	112	106	117	6	5	6
Stem									
Cathariostachys madagascariensis	Nov-Dec, Feb-Jul, Sep	37	7958	215	27	693	7	0	12
Cephalostachyum pierreri	Apr, Jun-Jul, Sep	10	2771	277	72	640	4	0	10

Appendix D8. Dietary composition of *H. g. griseus* Group Two.

Species	Months	Number of bouts	Total time observed	Average bout lengths	Min bout length (sec)	Max bout length (sec)	Average height (m)	Min height (m)	Max height (m)
Young leaves									
Cathariostachys madagascariensis	Feb-Mar, May-Sep	263	119208	453	13	3600	8	0	20
Poacilostachys festicaceus	Feb, Jun-Jul, Sep	7	1875	268	56	441	0	0	1
Cephalostachyum pierreri	May-Jul, Sep	7	1367	195	24	457	3	0	8
Ramiringitra	Jul	5	553	110	24	309	2	1	3
Liana	Feb, Aug	5	500	100	47	204	4	2	10
Voaroy	Aug	2	410	205	178	232	3	2	4
Aphloia sp.	Feb	1	229	229	229	229	2	2	2
Hypoestes sp.	Sep	2	150	75	5	145	1	0	1
Grass	Mar	1	146	146	146	146	0	0	0
Mature and young leaves									
Voaroy	Aug	8	2081	260	68	620	2	1	2
Dombeya sp.	Sep	4	596	149	42	417	3	1	4
Hypoestes corymbosa	Aug	1	99	99	99	99	5	5	5
Petioles									
Cryptocayra sp.	Aug	1	99	99	99	99	2	2	2
Fruit									
Clidemnia hirta	Feb-Mar, May-Jun	23	10971	477	29	3030	0	0	4
Unknown plant	Feb	4	663	166	38	433	5	4	7
Stem									
Cathariostachys madagascariensis	Feb-Mar, May-Jun, Aug	26	8551	329	41	1755	6	1	15

Appendix E: Supporting Information for Chapter 7

Appendix E1: Using GPS and Template Elevation Data to Measure Home Range.

By Dr. Todd Pataky.

E1.1. Introduction

Home range perimeter data were collected using GPS technology and the freeware: 'GPS Utility' was used to compute home range areas. The initial home ranges were order-of-magnitude smaller than published home range data for similar species. Since the published studies adopted a more direct measurement approach (tying strings to trees), it was speculated that the differences in home ranges were partly caused by GPS Utility's failure to consider elevation changes; GPS Utility uses a spherical model to compute surface area, and thus can not incorporate elevation data into its home range calculations.

The purpose of this report was to examine the extent to which elevation variation augments home ranges. Unfortunately equations describing spherical surface area could not be used because they do not apply for arbitrary elevations. We thus adopted a Cartesian tessellation approximation which produced practically identical results to the spherical model (10^{-6} % error, full scale). The method is summarized as follows: (i) Generate a mesh spanning the home range, (ii) Interpolate the elevation of each mesh node based on regional template elevation data, (iii) Integrate over the mesh to compute surface area.

We found that, for these species, considering elevation changes produced only small increases in home range, on the order of less than 1%. The evidence suggests that the current home ranges are indeed smaller than those reported in the literature.

E1.2. Methods

We first describe the spherical model that is employed by GPS Utility as basis for comparison with our Cartesian tessellation approach. We subsequently describe our meshing and elevation interpolation techniques. All analyses were implemented in MATLAB 7.3 (The MathWorks Inc., Natick, MA, USA).

(a) *Spherical model*

This method assumes that the Earth is a perfect sphere, a simplification which permits an analytical derivation of surface area. Firstly, define an arbitrary point ($\boldsymbol{q}_i$) on the surface of the sphere:

$$\boldsymbol{q}_i = \{\phi_i \quad \lambda_i\} \tag{1}$$

where i is an index and φ and λ are latitude (N/S) and longitude (E/W), respectively. The angular distance or central angle ($\Delta\alpha$) between two points $\boldsymbol{q_1}$ and $\boldsymbol{q_2}$ is then given by the Haversine formula:

$$\Delta\alpha = 2\sin^{-1}\left[\sqrt{\sin^2\left(\frac{\phi_2-\phi_1}{2}\right)+\cos\phi_1\cos\phi_2\sin^2\left(\frac{\lambda_2-\lambda_1}{2}\right)}\right] \tag{2}$$

To calculate the surface area of the spherical triangle defined by points $\boldsymbol{q_1}$, $\boldsymbol{q_2}$, and $\boldsymbol{q_3}$, we first define the spherical excess (E):

$$E = 4\tan^{-1}\left(\sqrt{\tan\left(\frac{s}{2}\right)\tan\left(\frac{s-a}{2}\right)\tan\left(\frac{s-b}{2}\right)\tan\left(\frac{s-c}{2}\right)}\right) \tag{3}$$

where a, b, and c are the lengths of the triangle's sides as given by Equation (2), and where s is given by:

$$s = \frac{a+b+c}{2} \tag{4}$$

Spherical excess is the difference between the sum of the angles of spherical and planar triangles; this definition (Equations 3-4) appears in standard mathematical tables.

The area (A) of the spherical triangle is finally given by:

$$A = R^2E \tag{5}$$

where R is the Earth's radius. We assume the GRS-80 equatorial radius of R = 6378.137 km (Geodetic Reference System 1980).

Cartesian approach

In Cartesian space, the surface area can be easily computed as follows:

A point $\boldsymbol{q_i}$ (Equation 1) is transformed to Cartesian space as:

$$\boldsymbol{p_i} = \begin{Bmatrix} R\cos\phi_i\cos\lambda_i \\ R\cos\phi_i\sin\lambda_i \\ R\sin\phi_i \end{Bmatrix} \tag{6}$$

The distance (Δd) between two points $\boldsymbol{p_1}$ and $\boldsymbol{p_2}$ is:

$$\Delta d = \sqrt{(\boldsymbol{p_2}-\boldsymbol{p_1})\cdot(\boldsymbol{p_2}-\boldsymbol{p_1})} \tag{7}$$

And surface area *A* is then given as:

$$A = \sqrt{s(s-a)(s-b)(s-c)} \qquad (8)$$

where *a*, *b*, and *c* are the edge lengths (Equation 7), and where *s* is as defined in spherical space (Equation 4).

(b) *Meshing*

Toward surface integration, the home range was meshed. Firstly, the perimeter was seeded (Figure 1b). To avoid computational difficulties associated with the trigonometric transforms (Equation 6), we employed a global seed size of 10% of the average φ and λ ranges. Secondly, an interior seed grid was layed (Figure 1c). Interior seeds not conforming to the 10% global seed size were discarded (Figure 1d). The connectivity of the remaining seeds was defined using Delaunay triangulation (Figure 1e). The final mesh was achieved by discarding those elements that had edges lying outside the original perimeter (Figure 1f).

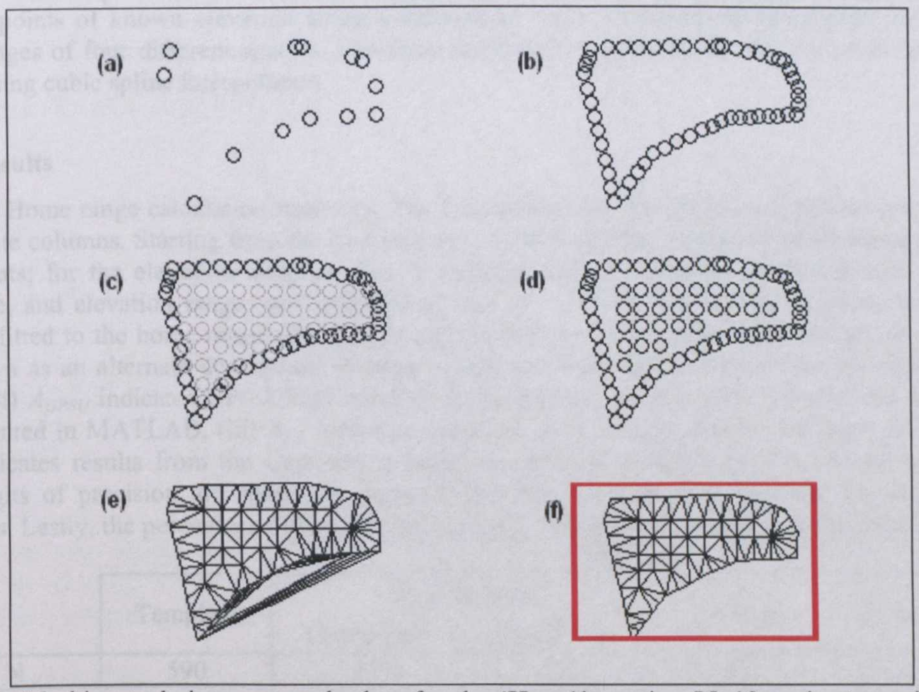

Figure 1. Meshing technique; example data for the 'Hapa1' species (N=13 perimeter points). The perimeter boundary (a) was seeded (b) using a global seed size of 10% of the average scale. Internal grid points were generated (c), and those not conforming to global seed size were discarded (d). Delaunay triangulation (e) defined connectivity, and those triangles outside the perimeter (a) were discarded, yielding the final mesh (f).

(c) *Elevation interpolation*

The elevations of the mesh nodes were not measured directly. They were interpolated from known elevations as measured on trails surrounding the home ranges (Figure 2). In total, 590 points composed the elevation template map. Cubic spline interpolation was used to determine the elevations of the mesh nodes.

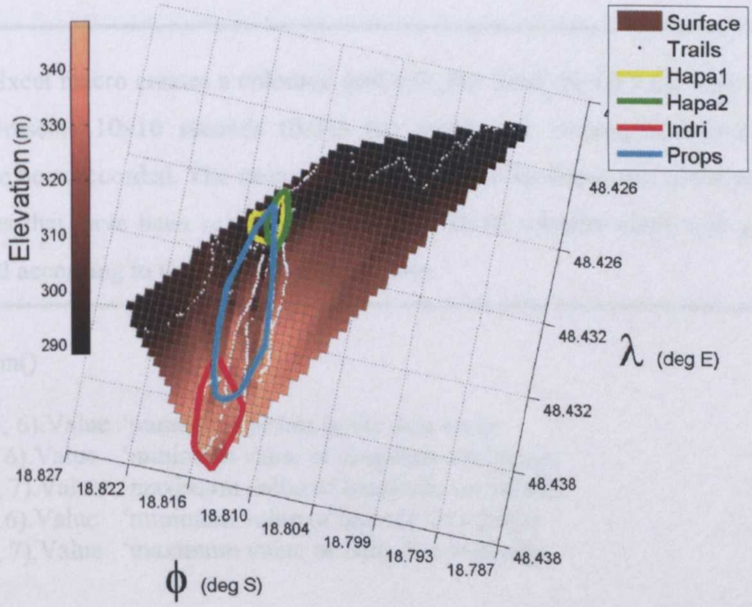

Figure 2. Bird's eye view of the template region used to define home range elevation. White dots indicate points of known elevation along a network of trails. Coloured enclosed lines indicate the home ranges of four different species. Elevation, indicated by grid colour, was computed across the region using cubic spline interpolation.

E1.3. Results

Table 1. Home range calculation summary. The four species and the elevation template are presented in separate columns. Starting from the first data row, N indicates the number of home range perimeter data points; for the elevation template data N indicates the total number of data points. Latitude, longitude, and elevation ranges are indicated by $\Delta\varphi$, $\Delta\lambda$, and Δh, respectively. Ellipses were least-squared fitted to the home range data (Fig.2) and the lengths of the major (Δx) and minor (Δy) axes are shown as an alternate description of home range size. Four area computations are subsequently shown: (i) A_{GPSU} indicates GPS Utility results, (ii) A_S indicates results from the spherical method as implemented in MATLAB, (iii) A_{CT} indicates results of our Cartesian tessellation approach, and (iv) A_{CTh} indicates results from the Cartesian tessellation approach considering also elevation changes. Four digits of precision are shown to highlight the minute differences between the various area measures. Lastly, the percentage differences between A_{CTh} and A_{CT} are presented in the final row.

		Species			
	Template	*H. g. griseus* Group One	*H. g. griseus* Group Two	*I. indri*	*P. diadema*
N	590	13	12	19	18
$\Delta\varphi$	0.0345°	0.0029°	0.0020°	0.0041°	0.0045°
$\Delta\lambda$	0.0157°	0.0021°	0.0022°	0.0041°	0.0062°
Δx (m)	4449.0	508.8	253.0	496.2	688.3
Δy (m)	1121.8	200.7	210.7	453.4	499.5
Δh (m)	61.6	10.0	11.9	27.4	45.0
A_{GPSU} (ha)	×	3.8310	3.4990	13.2400	23.9380
A_S (ha)	×	3.8399	3.5068	13.2694	23.9915
A_{CT} (ha)	×	3.8399	3.5067	13.2689	23.9915
A_{CTh} (ha)	×	3.8464	3.5167	13.3169	24.1730
A_{CTh}-A_{CT}	×	**+0.17 %**	**+0.29 %**	**+0.36 %**	**+0.76 %**

Appendix E2: Grid Cell Home Range Macro

By Mr. Paolo Caravaggi

The following Excel macro creates a coloured grid-cell plot from the GPS for each species. Each cell in the plot represents 10x10 seconds (0.033 ha) within the geographical area for which GPS coordinates have been recorded. The macro writes in the corresponding cell of the map the number of GPS coordinates that have been recorded within that 10x10 seconds range and assigns a different colour to the cell according to the number of repetitions.

```
Sub MapCreation()

Points = Cells(1, 6).Value  'number of points in the data range
minx = Cells(2, 6).Value    'minimum value of longitude coordinate
maxx = Cells(2, 7).Value    'maximum value of longitude coordinate
miny = Cells(3, 6).Value    'minimum value of latitude coordinate
maxy = Cells(3, 7).Value    'maximum value of latitude coordinate

r = 2
c = 2
gridsize = 10                    'each cell of the map represents a 10x10 seconds region
counter = 0

For h = miny To maxy Step gridsize
  r = r + 1

  For j = minx To maxx Step gridsize
  c = c + 1

    For k = 1 To Points

      If Cells(k, "c").Value >= j And Cells(k, "c").Value < (j + gridsize) And Cells(k, "d").Value >= h And Cells(k, "d").Value < h + gridsize Then
      counter = counter + 1
      End If

    Next k
    Sheets("map_HgGp2 total").Activate
    Cells(c, r).Value = counter
    Cells(c, r).Select

  If counter = 0 Then            'each cell of the map is given a colour according to the number of
                                 the repetitions in that range
  col = 2
  End If
  If counter > 0 And counter < 11 Then
  col = 36
  End If
  If counter > 10 And counter < 21 Then
  col = 35
  End If
  If counter > 20 And counter < 31 Then
  col = 37
  End If
  If counter > 30 And counter < 41 Then
```

```
   col = 39
   End If
   If counter > 40 And counter < 51 Then
   col = 4
   End If
   If counter > 50 And counter < 61 Then
   col = 45
   End If
   If counter > 60 Then
   col = 3
   End If

   With Selection.Interior
      .ColorIndex = col
      .Pattern = xlSolid
   End With
      counter = 0
   Sheets("HgGp2 total").Activate

   Next j
c = 2
Next h

Sheets("map_HgGp2 total").Activate
   Range("B2").Select
   Selection.borders(xlDiagonalDown).LineStyle = xlNone
   Selection.borders(xlDiagonalUp).LineStyle = xlNone
   Selection.borders(xlEdgeLeft).LineStyle = xlNone
   Selection.borders(xlEdgeTop).LineStyle = xlNone
   With Selection.borders(xlEdgeBottom)
      .LineStyle = xlContinuous
      .Weight = xlThin
      .ColorIndex = xlAutomatic
   End With
   Selection.borders(xlEdgeRight).LineStyle = xlNone
   Selection.borders(xlDiagonalDown).LineStyle = xlNone
   Selection.borders(xlDiagonalUp).LineStyle = xlNone
   Selection.borders(xlEdgeLeft).LineStyle = xlNone
   Selection.borders(xlEdgeTop).LineStyle = xlNone
   With Selection.borders(xlEdgeBottom)
      .LineStyle = xlContinuous
      .Weight = xlThin
      .ColorIndex = xlAutomatic
   End With
   With Selection.borders(xlEdgeRight)
      .LineStyle = xlContinuous
      .Weight = xlThin
      .ColorIndex = xlAutomatic
   End With

 Cells(1, 2).Select
 ActiveCell.FormulaR1C1 = "S18" & Chr(186) & "48." & miny
 Cells(2, 1).Select
 ActiveCell.FormulaR1C1 = "E48" & Chr(186) & "25." & minx

 End Sub
```

Appendix F. Supporting Information for Chapter 9

Appendix F1. Cross-Tabulation of Initial and Terminal Support Diameter for *Indri indri*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Initial support diamete	<5cm	Count	108	94	28	14
		Std. Res.	23.6	-3.3	-5.0	-2.5
	5.1 to 10cm	Count	84	1324	264	105
		Std. Res.	-2.7	11.9	-10.9	-6.6
	10.1 to 15cm	Count	15	286	544	124
		Std. Res.	-5.9	-10.3	15.9	1.6
	>15.1cm	Count	6	113	134	131
		Std. Res.	-3.7	-6.5	2.2	13.6

Appendix F2. Cross-Tabulation of Initial and Terminal Support Orientation for *Indri indri*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	167	121	71	102
		Std. Res.	15.1	1.1	-3.8	-6.2
	Oblique	Count	89	361	136	214
		Std. Res.	-0.6	12.5	-4.0	-6.1
	Angle	Count	60	135	387	230
		Std. Res.	-3.7	-4.1	13.8	-5.4
	Vertical	Count	86	182	216	817
		Std. Res.	-5.5	-7.2	-5.5	12.7

Appendix F3. Cross-Tabulation of Initial and Terminal Support Diameter for *Propithecus diadema*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Initial support diamete	<5cm	Count	344	226	48	31
		Std. Res.	27.6	-8.6	-6.3	-2.4
	5.1 to 10cm	Count	188	2006	307	148
		Std. Res.	-8.9	9.4	-7.6	-3.4
	10.1 to 15cm	Count	43	372	354	75
		Std. Res.	-6.6	-6.4	16.5	1.6
	>15.1cm	Count	29	163	97	79
		Std. Res.	-2.9	-4.2	3.9	9.9

Appendix F4. Cross-Tabulation of Initial and Terminal Support Orientation for *Propithecus diadema*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	115	108	43	173
		Std. Res.	13.0	3.5	-4.4	-4.4
	Oblique	Count	89	354	100	278
		Std. Res.	2.5	17.3	-4.5	-8.2
	Angle	Count	56	106	388	320
		Std. Res.	-1.9	-3.9	17.2	-7.2
	Vertical	Count	114	229	329	1708
		Std. Res.	-5.9	-9.3	-5.9	11.1

Appendix F5. Cross-Tabulation of Initial and Terminal Support Orientation for *Hapalemur griseus griseus*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<0.5cm	0.6 to 5cm	5.1 to 10cm	10.1 to 15cm
Initial support diamete	<0.5cm	Count	79	50	16	0
		Std. Res.	33.2	-4.3	-4.2	-2.2
	0.6 to 5cm	Count	49	1985	459	42
		Std. Res.	-4.0	9.6	-11.1	-4.3
	5.1 to 10cm	Count	11	502	721	55
		Std. Res.	-5.0	-10.9	16.6	2.1
	10.1 to 15cm	Count	1	57	50	34
		Std. Res.	-1.8	-3.4	1.0	13.8

Appendix F6. Cross-Tabulation of Initial and Terminal Support Orientation for *Hapalemur grisues griseus*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	430	242	92	198
		Std. Res.	15.4	0.6	-3.2	-9.8
	Oblique	Count	237	446	102	230
		Std. Res.	1.2	12.7	-2.9	-9.0
	Angle	Count	71	110	214	180
		Std. Res.	-4.8	-2.5	15.7	-3.5
	Vertical	Count	191	243	165	1138
		Std. Res.	-9.5	-8.7	-4.4	16.2

Appendix F7. Log-Linear Modelling Categories Used for *Indri indri* and *Propithecus diadema*.

Model	Categories
IP1	**Sp:** *I. indri*, *P. diadema*
	LM: leap, vertical climb, cantilever
	ISD: <5cm, >5.1cm
	ISO: 0 to 45°, 46 to 90°
	IH: <9.9m, 9.9-19.9m, >20m
IP2	**Sp:** *I. indri*, *P. diadema*
	LM: leap, vertical climb, cantilever
	IH: <9.9m, 9.9-19.9m, >20m
	TSO: 0 to 45°, 46 to 90°
	TSO: 0 to 45°, 46 to 90°
IP3	**Sp:** *I. indri*, *P. diadema*
	LM: leap, vertical climb, cantilever
	ISD: <5cm, >5.1cm
	ISO: 0 to 45°, 46 to 90°
IP4	**Sp:** *I. indri*, *P. diadema*
	LM: leap, vertical climb, cantilever
	IH: <9.9m, 9.9-19.9m, >20m
IP5	**Sp:** *I. indri*, *P. diadema*
	LM: leap, vertical climb, cantilever
	TSO: 0 to 45°, 46 to 90°
	TSO: 0 to 45°, 46 to 90°

Appendix F8. Cross-Tabulation of Species and Initial Support Diameter for Leaping, giving Actual Counts and Standardised Residuals (Std. Res.).

			Initial support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Species	*I. indri*	Count	173	1515	919	370
		Std. Res.	-6.5	-3.6	7.1	3.8
	P. diadema	Count	498	2452	816	356
		Std. Res.	5.5	3.1	-6.0	-3.2

Appendix F9. Cross-Tabulation of Species and Terminal Support Diameter for Leaping, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Species	*I. indri*	Count	128	1570	921	358
		Std. Res.	-7.5	-3.9	7.7	4.6
	P. diadema	Count	459	2565	785	313
		Std. Res.	6.4	3.3	-6.5	-3.9

Appendix F10. Cross-Tabulation of Species and Initial Support Orientation for Leaping, giving Actual Counts and Standardised Residuals (Std. Res.).

			Initial support orientation			
			Horizontal	Oblique	Angle	Vertical
Species	*I. indri*	Count	343	687	739	1208
		Std. Res.	3.7	4.5	3.4	-6.7
	P. diadema	Count	326	693	817	2286
		Std. Res.	-3.2	-3.8	-2.9	5.7

Appendix F11. Cross Tabulation of Species and Terminal Support Orientation for Leaping, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Species	*I. indri*	Count	292	698	741	1246
		Std. Res.	3.8	5.2	3.5	-6.9
	P. diadema	Count	267	672	815	2368
		Std. Res.	-3.2	-4.4	-2.9	5.9

Appendix F12. Log-Linear Modelling Categories for *Indri indri*, *Propithecus diadema* and *Hapalemur griseus griseus*.

Model	**Categories**
IPH1	**Sp:** *I. indri*, *P. diadema*, *H. g. griseus* **LM:** leap, cantilever **ISD:** <10cm, >10.1cm **ISO:** 0 to 45°, 46 to 90°
IPH2	**Sp:** *I. indri*, *P. diadema*, *H. g. griseus* **ISD:** <10cm, >10.1cm **ISO:** 0 to 45°, 46 to 90° **IH:** <9.9m, 9.9-14.9m, >15m
IPH3	**Sp:** *I. indri*, *P. diadema*, *H. g. griseus* **LM:** leap, cantilever, vertical climb **ISD:** <5cm, >5.1cm **ISO:** 0 to 45°, 46 to 90°
IPH4	**Sp:** *I. indri*, *P. diadema*, *H. g. griseus* **LM:** leap, cantilever **TSD:** <10cm, >10.1cm **TSO:** 0 to 45°, 46 to 90°

Appendix F13. Cross-Tabulation of Initial and Terminal Support Diameter for Leaping in *Indri indri*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Initial support diamete	<5cm	Count	62	81	28	14
		Std. Res.	19.1	-1.9	-3.7	-1.6
	5.1 to 10cm	Count	58	1235	254	103
		Std. Res.	-1.6	11.4	-10.8	-6.5
	10.1 to 15cm	Count	11	279	528	122
		Std. Res.	-4.6	-10.2	14.7	1.2
	>15.1cm	Count	5	112	132	129
		Std. Res.	-2.8	-6.5	1.8	12.8

Appendix F14. Cross-Tabulation of Initial and Terminal Support Orientation during Leaping in *Indri indri*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	125	104	64	88
		Std. Res.	14.0	1.6	-3.1	-5.7
	Oblique	Count	67	324	128	201
		Std. Res.	-0.7	12.1	-3.7	-5.8
	Angle	Count	52	128	372	225
		Std. Res.	-3.0	-3.9	13.0	-5.6
	Vertical	Count	74	178	213	810
		Std. Res.	-4.8	-6.9	-5.7	11.9

Appendix F15. Cross-Tabulation of Initial and Terminal Support Diameter during Leaping in *Propithecus diadema*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter			
			<5cm	5.1 to 10cm	10.1 to 15cm	>15.1cm
Initial support diamete	<5cm	Count	233	191	46	28
		Std. Res.	23.8	-6.8	-5.0	-1.6
	5.1 to 10cm	Count	158	1858	297	139
		Std. Res.	-7.0	8.5	-7.8	-3.5
	10.1 to 15cm	Count	40	362	344	71
		Std. Res.	-5.3	-6.5	15.2	1.1
	>15.1cm	Count	28	157	96	75
		Std. Res.	-1.8	-4.3	3.5	9.2

Appendix F16. Cross-Tabulation of Initial and Terminal Support Orientation during Leaping in *Propithecus diadema*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	68	75	40	143
		Std. Res.	10.2	3.0	-3.0	-3.2
	Oblique	Count	59	300	85	249
		Std. Res.	2.1	17.5	-4.4	-7.5
	Angle	Count	47	93	370	307
		Std. Res.	-0.8	-3.5	16.4	-7.5
	Vertical	Count	93	206	320	1668
		Std. Res.	-4.5	-8.7	-6.2	9.8

Appendix F17. Cross-Tabulation of Initial and Terminal Support Orientation during Leaping in *Hapalemur griseus griseus*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support orientation			
			Horizontal	Oblique	Angle	Vertical
Initial support orientation	Horizontal	Count	298	190	73	172
		Std. Res.	13.7	1.2	-2.5	-8.4
	Oblique	Count	190	378	88	212
		Std. Res.	2.1	11.9	-2.6	-8.7
	Angle	Count	55	100	190	166
		Std. Res.	-4.2	-2.0	14.8	-4.0
	Vertical	Count	160	225	149	1105
		Std. Res.	-8.4	-8.4	-4.7	14.2

Appendix F18. Cross-Tabulation of Initial and Terminal Support Diameter during Leaping in *Hapalemur griseus griseus*, giving Actual Counts and Standardised Residuals (Std. Res.).

			Terminal support diameter		
			<0.5cm	0.6 to 5cm	5.1 to 10cm
Initial support diameter	<0.5cm	Count	48	35	15
		Std. Res.	29.1	-3.4	-3.2
	0.6 to 5cm	Count	26	1627	422
		Std. Res.	-3.6	8.7	-10.8
	5.1 to 10cm	Count	9	445	702
		Std. Res.	-3.7	-10.6	15.4

Appendix G: Supporting Information for Chapter 10

Appendix G1: Morphometric Measurements of Predated *Avahi laniger*

Date found:	16 July 2005
Sex:	Male
GPS:	S: 18°48.853 E: 048°26.309

Weights recorded using a 2.5 kg Pesola scale, measurements using a fabric tape measure.

Total weight as found:	750g
Weight without skin or organs:	500g
Weight of internal organs:	200g
Weight of skin:	50g

Length of remaining small intestine:	84cm
Length of remaining large intestine:	38cm
Stomach circumference:	7cm

	With skin and fur (cm)	Without skin or fur (cm)
Length tibia and fibula	11	10.7
Length femur	10	9.7
Length foot	8.5	9
Length hallux	8.2	5.5
Length fore-limb	7.5	9
Length humerus	7.5	5.5
Length hand	5.3	*
Length thumb	3.5	*
Testicle length	3.5	1.7
Penis length	2.7	1.2
Circumference of left hand	4.4	*
Circumference of right foot	8	*
Circumference of left foot	7.9	*
Length neck to tail tip	46	45
Length neck to toe	43	43
Length tail	26.6	27.4
Length torso	22	12
Length left arm	13	20
Length right leg	20.5	20
Length left leg	20.5	20

* - missing value

Femur

Maximum proximal to distal length from the top of the greater trochanter to the most distal point on the medial femoral condyle: 10.3cm
Centre of the femoral head to the centre of the articulated knee joint: 9.4cm
Maximum anterior posterior length of the femoral condyle: 1.2cm

Tibia

From the most proximal tibial condyle to the most distal point on tibial malleolus: 9.2cm
From the most proximal tibial condyle to the taleocural joint surface: 8.8cm

Ankle and Foot

Maximum proximal to distal length: 2.2cm
The most distal point of the talus to the estimated centre of taleocural joint: 1.6cm
Maximum proximal distal length of the calcaneous: 2.2cm
Maximum left foot length, estimated from the taleocural joint centre To tip of the third metatarsul: 4.3cm
Length of proximal phalanx of DIII (third toe): 1.6cm
Length of middle phalanx of DIII: 1cm
Length of distal phalanx of DIII: 0.5cm

Humerus

Maximum length from the trochlea to the greater tuberosity: 5.6cm

Ulna

Max length: 7.4 cm
From the top of the olecranon process to the centre of the trachlear notch: 0.6cm

Spine

Max length of lumbosacral to third cervical body (most proximal point): 1.5cm
ADD c. 0.6 cm for body on atlas and ADD 2 cm for body of axis.

Pelvis

Centre of acetabulum to the most distal point of the ischium: 1.9cm
Centre of acetabulum to the most proximal point on the iliac blade: 4.2cm

Shoulder

Scapula axillary border to glenoid fossa: 3.9cm
Clavicle maximum length: 2.6cm