A Study of the Locomotor Ecology of the Indriid Primate *Propithecus verreauxi* in the Dry Deciduous Forest of Kirindy Mitea National Park, Madagascar

A thesis submitted to the University of Manchester for the degree of Doctor of Philosophy in the Faculty of Life Sciences.

2013

Simon Furnell

Contents

Word Count: 45,004

Abstract

Abstract of a thesis by Simon Furnell submitted to the University of Manchester for the degree of PhD in the Faculty of Life Sciences and entitled 'A Study of the Locomotor Ecology of the Indriid Primate *Propithecus verreauxi* in the Dry Deciduous Forest of Kirindy Mitea National Park, Madagascar'. March 2013

Primates have evolved a wide range of locomotor behaviours to enable them to negotiate a three dimensional arboreal environment. Included in the primates are the lemurs, which have gained a reputation as specialist leapers with the sifaka (*P. verreauxi*) known for incredible saltatory displays.

It is therefore necessary to have knowledge of this animals locomotor repetoire, substrate use, ranging and activity patterns in order to gain a greater understanding of sifaka ecology. The sifaka also inhabits a dry deciduous forest located in south western Madagascar which is characterized by a long dry season and short rainy season. This thesis begins with an investigation into the locomotion of *P. verreauxi* within Kirindy Mitea National Park. It was shown that leaping made up the largest proportion of the sifakas' locomotor repetoire and that vertical supports were the most utilized, supporting the idea that sifakas are vertical clingers and leapers. Seasonal changes in behaviour were also displayed with levels of traveling behaviour increasing and resting behaviour decreasing during the short rainy season. These findings added weight to the growing body of evidence that lemurs conserve energy during periods of food scarcity in order to survive during the long dry season.

These results were further supported by a ranging study, which used hand held GPS devices to measure home ranges and daily path lengths. It was discovered that the sifakas' daily path lengths are much lower than that of both Old and New World monkeys. These path lengths also vary seasonally with decreased daily ranging during the dry season. A newer method of data collection was also investigated with the use of accelerometer data loggers being used in an attempt to monitor locomotion remotely. Although a captive study displayed that different locomotor modes can be distinguished from acceleration data, a field experiment using a very similar methodology failed to yield any useable data.

The results suggest that *P. verreauxi* adapts its locomotor behaviour seasonally in order to cope with extended periods of food scarcity. helping add weight to the idea made by previous researchers that lemurs living in highly seasonal environments are adapted for conserving energy to deal with a harsh environment.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning;

Signed: Date:

Copyright Statement

1. The author of this thesis (including any appendices and/or schedules to this thesis) owns certain copyright or related rights in it (the “Copyright”) and s/he has given The University of Manchester certain rights to use such Copyright, including for administrative purposes.

2. Copies of this thesis, either in full or in extracts and whether in hard or electronic copy, may be made **only** in accordance with the Copyright, Designs and Patents Act 1988 (as amended) and regulations issued under it or, where appropriate, in accordance with licensing agreements which the University has from time to time. This page must form part of any such copies made.

3. The ownership of certain Copyright, patents, designs, trade marks and other intellectual property (the “Intellectual Property”) and any reproductions of copyright works in the thesis, for example graphs and tables (“Reproductions”), which may be described in this thesis, may not be owned by the author and may be owned by third parties. Such Intellectual Property and Reproductions cannot and must not be made available for use without the prior written permission of the owner(s) of the relevant Intellectual Property and/or Reproductions.

4. Further information on the conditions under which disclosure, publication and commercialisation of this thesis, the Copyright and any Intellectual Property and/or Reproductions described in it may take place is available in the University IP Policy (see http://www.campus.manchester.ac.uk/medialibrary/policies/intellectualproperty.pdf), in any relevant Thesis restriction declarations deposited in the University Library, The University Library’s regulations (see http://www.manchester.ac.uk/library/aboutus/regulations) and in The University’s policy on presentation of Theses

Signed: Date:

Acknowledgments

Firstly I would like to thank my supervisor, Dr Bill Sellers, for all of his guidance and scientific input and for making my PhD such an enjoyable experience. I would also like to thank all of the team from Liverpool for their input over the course of my PhD.

I would also like to thank Dr Rebecca Lewis of the University of Texas for allowing me to use her field site at Kirindy Mitea National park, Madagascar. A big thank you has to go to all of the field team in Madagascar: Vassay, Francis, Mangara, Richard, Service, Valesoo, Fidy and Dessy, for keeping me sane during extended periods in the forest. Thank you also to Madagascar National Parks and MICET for allowing my research to take place and for smoothing my transition into Madagascar with your gracious hospitality. Thanks must also go to Jamie Craig and the team of keepers at the Cottswold Wildlife Park for being so hospitable to my research needs.

I would also like to thank all of my contemporaries in my lab and the surrounding labs. Their support and friendship helped me through my PhD – Adam, Jamie, Charlotte, Peter, John, Dave, Kate, Kayleigh. Last, but by no means least I would like to thank all of the family and friends who's unwavering support of my eternal student life has been such a huge help – Mum, Dad, Lisa, Kerry, Mick, Niamhy, Blacky, Kimpo (Blacko), Billy Bugler, the Veitch, Mantis, Raj, Gush, Sammy boy, Morph, Chrissy Thomas, Wozza, De Menezes, Grease Boil, Scouse Tom, Scouse Joe, in fact all of the scousers, Les, Marie Joan and Mark.

List of Abbreviations

Abbreviation	Meaning	Page
KMNP	Kirindy Mitea National Park	5
mya	million years ago	17
VCL	vertical clinging and leaping	27
DS	diagonal sequence	36
Rh	right hindlimb	36
Rf	right forelimb	36
Lh	left hindlimb	36
Lf	left forelimb	36
LS	lateral sequence	36
GPS	global postioning system	106
MCP	minimum convex polygon	113
UTM	universal transverse mercator	113
SD	secure digital	131
VHF	very high frequency	137
MP4	media player 4	139

Chapter 1

General Introduction

Introduction

Extant primates

Living primates are a hugely diverse group, which occupy tropical and sub-tropical areas. Primates were originally defined, as placental mammals, unguiculate (do not have hooves, but claws and nails), have clavicles, three types of teeth at least at one time of life, and an opposable hallux with a flat nail (Martin 1968). A newer expanded definition has been formed from this view as it is clear that many other mammals posses most of these factors combined. The newer definition includes the facts that they are inhabitants of a tropical or subtropical ecosystem, with extremities developed for prehension and a divergent hallux for grasping, hind-limb dominated locomotion, large forward facing eyes with at least a post-orbital bar, a reduction in litter sizes and a larger brain in comparison to other mammals (Martin 1968; Fleagle 1988; Martin 1990). Therefore primates can only be defined by a combination of factors that set them apart from other mammals. The problem with this is that these features have to be general as there are no unique adaptations to define a primate, and some species do not possess most of the features listed. Extant primates fall into six natural groups defined by geographic distribution along with behavioural and morphological similarities. These groups are: the lemurs, lorises, tarsiers, New World monkeys, Old World monkeys and apes (Martin 1990). Within these groups there is a huge variation in size ranging from the smallest known primate *Microcebus berthae* (Madame Berthe's mouse lemur) weighing 30g, to 200kg weight of an adult male mountain gorilla (*Gorilla gorilla*). Locomotor patterns also show huge variety with knuckle walking, brachiation, suspensory and saltatory locomotion making up a large proportion of the primate locomotor repertoire.

Primate phylogenies were originally constructed using morphological features (Stanger-Hall 1997), however, with improved technology, molecular phylogenies are proving to be more accurate in their classification of extant primates (Delpero, Masters et al. 2001; DelPero, Pozzi et al. 2006). Morphological phylogenies depend on comparing features which are chosen, therefore these phylogenies are the only way to link extant primates to the fossil record, which continues to make it a useful method of analysis. If molecular studies and morphological studies give similar results then the features chosen in the morphological study are clearly accurate representations of relatedness and can be compared back in the fossil record. An area of huge debate that has been cleared up by molecular phylogenies is that of the position of *Tarsius* within the primates. The argument all depends on if *Tarsius* is viewed as more closely related to apes, humans, New World and Old World monkeys; or conversely, if viewed as more closely related to lemurs, lorises and galagos. There are two classification groups for primates the first is an older split which places the apes, New World Monkeys and Old World monkeys in a group known as the anthropoids. The lemurs, tarsiers, galagos and lorises are placed in a second group known as the prosimians (Fleagle 1988). Prosimians and anthropoids are divided by a set of features such as a fused mandibular symphysis against a non-fused mandibular symphysis and the presence of a tooth comb versus no tooth comb. Other features are post orbital bar, grooming claw and dentition, that differ between the two groups. The newer classification splits into two groups again, this time haplorhines and strepsirhines on the basis of split nostrils and a wet nose versus unsplit nostrils and a dry nose. Classification places the tarsiers in the haplorhine group with Old World monkeys, New World monkeys and apes. The newer strepsirhine, haplorhine split has now been validated using a molecular phylogeny (Shekelle 2005) and is now the generally accepted classification. The problem with *Tarsius* is that it has an almost intermediate morphology with haplorhines and strepsirhines and has features of both along with some completely individual features, such as its dentition. These morphological differences do not pose a problem for molecular phylogenetics, but it does pose further questions about when these traits evolved and how quickly which can only be answered if the primate fossil record is improved with new discoveries.

Madagascar is the home of the Lemuriformes, which show huge diversity and represent 11% of all primate species and 21% of all primate genera (Tattersall 2007). Lemurs are then divided into five families, the Indriidae who are renowned as specialist vertical clingers and leapers (Napier and Walker 1967). Although not a term that everybody agrees with (Anemone. R 1990), as it suggests that all species classified in this way would leap in the same way and share a similar morphology. But this is not the case as the bone morphology of indriid primates is very different from that of Galagidae and Tarsiidae. The Daubentoniidae, a family represented by one extant species which is exclusively arboreal and has claws rather than flat nails. The Lepilemuridae, which are a nocturnal species also renowned for vertical clinging and leaping. The Lemuridae, which are very general in their pattern of movement and also partially terrestrial. Lastly the Cheirogalidae, which are small arboreal quadrupeds (Fleagle 1988; Martin 1990).

The number of lemur species classified has jumped from 36 in 1982, to 83 in 2006 (Tattersall 2007) with a revised figure of 101 in 2010. The explosion in taxa has been due to the promotion of sub-species to a species level and splitting of a single species into many (Isaac, Mallet et al. 2004). In the year 2000 two species of dwarf lemur were split into seven separate species and seven new species of mouse lemur were recognised in western Madagascar (Groves 2000; Yoder, Rasoloarison et al. 2000). Whilst in 2006 fifteen new species of *Lepilemur* were described (Andriaholinirina, Fausser et al. 2006; Louis, Coles et al. 2006). In 2008 five species of *Eulemur* were promoted from subspecies level whilst one subspecies of *Varecia* and four *Propithecus* were recognised (Mittermeier, Ganzhorn et al. 2008). Some of this taxonomic explosion is due to an increase in the knowledge about lemur characteristics and population genetics. Increasing forest fragmentation due to logging has led to many previously inter-breeding populations becoming isolated, although classifying these as separate species reduces the within species diversity even further, when in fact it is highly unlikely that a speciation event has occurred at all in 24 years. An increase in species is seen by many as a useful tool for maintaining the conservation status of isolated populations of lemurs in forest fragments and could, in the long term prevent extinction events due to the protection received from species status (Yoder 2007). Other issues, such as lemurs being described as cryptic species, where differentiation cannot be discerned by the human eye, but to the animals themselves there could be differences in communication, such as olfaction, vocalisation and behaviour that set them apart as separate (Tattersall 2007), has also set lemurs apart for taxonomic inflation.

The Origin of Primates

There are three major theories that have been suggested as to why primates evolved to be how they are. The arboreal hypothesis (Rasmussen 1990), which states that a reduced dependence on olfaction, large brains, stereoscopic vision and grasping hands and feet were adaptations for locomotion in an arboreal environment. Cartmill (1987) issued an alternative hypothesis, claiming that other mammals (excluding primates), had adapted to an arboreal lifestyle without these features and that early primates were visual predators feeding on arthropods. Cartmill's theory is called the visual predation hypothesis and the crucial adaptation was the relocation of the eyes to the front of the head for visually directed hunting. Sussman (1991) suggested that fossil primates were mainly folivorous and frugivorous and in fact there were only a minority of hunters. Therefore he suggested a co-evolution theory along with the evolution of angiosperms, which had fruiting terminal branches, and the adaptations listed in the arboreal hypothesis were in fact to enable primates to reach these fruits at the end of thin branches. The angiosperm exploitation hypothesis and the arboreal hypothesis seem to link together and are very similar in their conclusions, which seem a more credible claim than the visual predation hypothesis. Together they claim that the primate adaptations seen today were evolved in reaction to the need to locomote on fine terminal supports in order to feed on the fruit and leaves available. Clearly the origin of primates and why they have evolved is an area of debate depends in part on the primate fossil record.

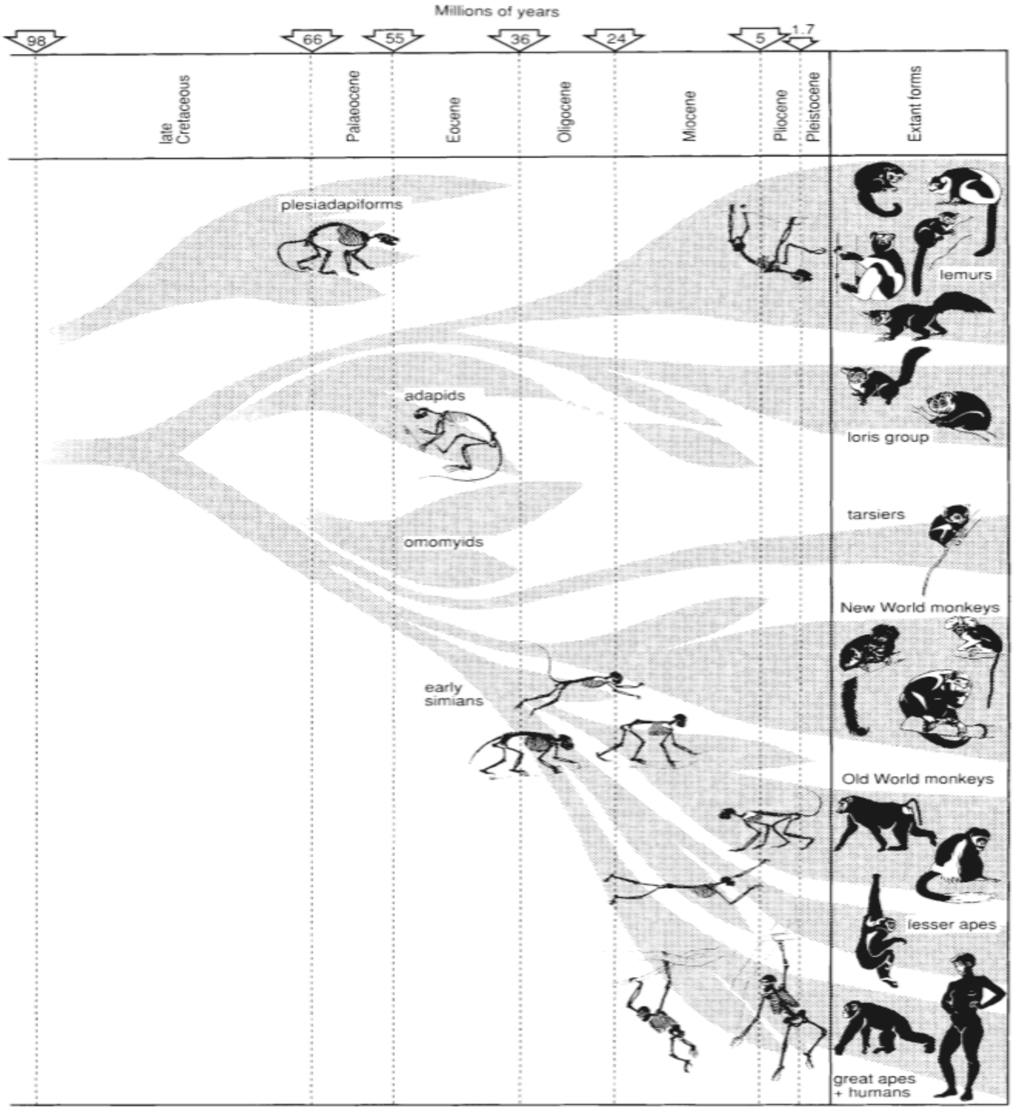


Figure 1. Timeline showing the fossil record and possible links to extant primate groups from (Martin 1993). The shaded tree shows one possible interpretation of the relationship between living primates and fossils (from relatively complete skeletons).

Mammals first appeared in the Late Triassic period just during the latter stages of the reign of the dinosaurs (Jenkins, Crompton et al. 1983). Then, large adaptive radiations of mammals took place at the beginning of the Mesozoic era, around 65 million years ago (mya). The first appearance of a group attributed to the primates evolved in the late Cretaceous or early Paleocene and are known as the plesiadapiformes (Figure 1). Pleisiadapiformes bare such a small resemblence to extant primates that some authors have chosen to place them closer to modern day colugos, suggesting that they were adapted for gliding (Martin 1993). Plesiadapiformes have a cranial structure very different from any living primate, and were thought to have died out due to competition from other mammals such as rodents (Fleagle 1988). Although most authors place the plesiadapiformes in a separate order claiming that they are not ancestral to modern primates (Cartmill 1992). *Carpolestes*, a genus of plesiadapid, has been asserted as a close relative of later primates (Bloch and Boyer 2002), due to their divergent hallux with a nail used for grasping along with other post-cranial similarities. Questions over the methods used to attain this relationship were posed (Kirk, Cartmill et al. 2003), as no cranial data had been included. Since then, Bloch and Bowyer (2007) have again compared later fossil primates and plesaidapiformes with a more inclusive set of features, and have concluded the same result, adding that a ghost lineage (yet to be discovered) led to the Eocene primates around 55 mya.

Fossil primates of a modern day aspect are documented from the beginning of the Eocene epoch (55 mya) and are labeled as euprimates, which distinguishes them from the plesiadapiformes, although some plesiadapiformes survived into the mid-Eocene (Martin, Soligo et al. 2007). The euprimates were dominated by two groups known as the adapids and the omomyids. Adapids are observed to have small eyes (signaling diurnality), large body masses (usually over 1kg) and teeth adapted for a folivorous diet. Whereas the omomyid features include large eyes (signaling nocturnality), no post-orbital closure, a small body mass (which increases on average over the Eocene period), and during the early Eocene omomyids had cheek teeth adapted for a omnivorous diet, but as the period went on there was an increasing sway towards a folivorous and frugivorous diet (Fleagle 1988).

The adapids have often been postulated as being linked to extant strepsirhines (Figure 1) due to their similar morphology with a hindlimb dominated posture, and a long tail. The *Adapis* genus has often been proposed as an ancestor of the lemuriformes (Fleagle 1988; Gibbons 2009), as the lower incisors have formed a cropping unit which looks like an intermediate form of tooth comb in extant strepsirhines. Godinot (2006) insisted that the lemuriform ancestor would be discovered among the nocturnal adapids as the lemuriformes are a nocturnal radiation. The omomyids are widely believed to be the radiation that led to the haplorhines (Figure 1) (Gebo, Dagosto et al. 2000), which is mainly due to their resemblance to the extant member of the haplorhines, *Tarsius*. There is much debate surrounding this argument as the adapids and omomyids are very similar morphologically, and the lack of postcranial fossil evidence leads to much heated debate on primate origins. There is another school of thought that states that there is a third group of undiscovered (ghost) fossil primates which diverged prior to the adapids and omomyids, which link to extant primates (Martin, Soligo et al. 2007).

The main focus of this section is to investigate the evolution of adaptations that gave rise to the specialised arboreal lifestyle shown by strepsirhines. As discussed previously (Bloch and Boyer 2002) *Carpolestes* was a plesiadapiform that had a divergent hallux with the presence of a nail, the limb length ratios suggest that it was an arboreal quadruped with no specialisations for leaping, but was an adept terminal branch feeder. There is evidence that during Paleocene plesiadapids had developed minor adaptations to enable them to live an arboreal lifestyle. The issue with this specimen depends on your view as to whether *Carpolestes* has any link to modern day primates. Also, another plesiadapid genus, *Plesiadapis*, has been described as having long laterally compressed claws, short limbs and it was suggested that it was an arboreal quadruped (Fleagle 1988). So it is a question as to which pleasiadapid, if any (Soligo and Martin 2006), gave rise to the Eocene primates and only then can the question of which genus or species it arose from be answered and the modes of locomotion deciphered.

Figure 2 Photograph of Ida (*Darwinius massilae)* from (Franzen, Gingerich et al. 2009), showing the holotype skeleton in right lateral view. Ida is a superb

fossil example of an Eocene adapid and the most complete fossil primate ever found.

An early Eocene adapid postcranial skeleton from the genus *Cantius* shows a similar morphology to modern lemuriformes, such as *Propithecus*. *Cantius* seemed suited to vertical clinging and leaping, although a limb length ratio displayed fairly long forelimbs, which suggest more usage of the forelimb in leaping and more of a dependence on the forelimb during arboreal quadrupedalism (Rose and Walker 1985). In extant mammals if a limb ratio suggests a specimen has arms as long as its legs, then it is normally predicted that this animal is not suited for leaping, whereas as animals which are hindlimb dominated (have long hindlimbs in comparison to forelimbs) tend to leap as part of their locomotor repertoire (Davenport 1935). The more famous specimen *Darwinius massilae* (also known as Ida, Figure 2), had fingernails on all forelimb hands and most feet, which demonstrates that the evolution of these traits was well established by the middle Eocene (around 47 mya). A principal component analysis of limb segment lengths with extant primates showed that *Darwinius's* chief locomotor behaviour was arboreal quarupedalism rather than leaping (Franzen, Gingerich et al. 2009). Although much hype has surrounded *Darwinius* as the missing link, the claims of the fossil being an anthropoid ancestor are unfounded; a much more plausible conclusion for this adapid, although they share some features with anthropoids, is that it should be grouped with the strepsirhines (Gibbons 2009). Due to the unknown ancestry of the strepsirhines an omomyid postcranial skeleton will be included also, *Omomyis canteri*. A middle Eocene omomyid that displays a very general morphology again suggesting an arboreal quadruped, although some specialisations to leaping were present, such as a long femur and more cylindrical femoral head (Anemone and Covert 2000).

Clearly, adaptations were present for an arboreal lifestyle in the Paleocene and Eocene. As time progresses, so do the adaptations, with more fingernails instead of claws being present from *Carpolestes*, with one fingernail on the hallux, to, *Darwinius* with fingernails on almost all digits. There is developing evidence to suggest a more specialised leaping morphology along the same time period. All of these factors depend on opinions of the fossil record. For example sub-fossil lemurs from less than 2000 years ago displayed a huge diversity in size and locomotor strategies, with the giant sloth lemurs (*Mesopropithecus*) displaying adaptations for suspensory locomotion (Karanth, Delefosse et al. 2005), which if found in the fossil record from the Eocene from a partial postcranial skeleton may never be classed as a primate. Also many errors are made due to the small samples of fossils and their poor quality, Gingerich (1980), claimed that one of the features that adapids share with haplorhines is some species show sexual dimorphism. The sexual dimorphism claim has since been refuted as the specimens Gingerich was working with have now been shown to be separate species (Rose 1994). Therefore although the primate fossil record is far from complete it infers that fingernails began to appear in the late Palaeocene, with the genus *Carpolestes* (Bloch and Boyer 2002) and continued to evolve, with the adapids and omomyids, through the Eocene period.

The Colonisation of Madagascar

The split between Africa and Madagascar was part of the earliest major rifting event in Gondwana, with eastern and western Gondwana splitting between 170-155 million years ago (Masters, de Wit et al. 2006). At that time Gondwana was a southern supercontinenet comprised of an eastern portion (Indo-Madagascar, Antartica and Australia) and a western portion (South America and Africa). Once the eastern section broke away Madagascar then split from eastern Gondwana around 88mya (Storey, Mahoney et al. 1995). Yoder et al (1996) suggest that all extant Malagasy lemurs originated from a single common ancestor, suggesting a single colonisation event. Lemurs are thought to have colonised Madagascar between 70-41 mya which is between the late Cretaceous and middle Eocene (Poux, Madsen et al. 2005). There is widespread debate surrounding the events that led to the colonisation of Madagascar by lemurs. Two major theories come to the fore; firstly, there is an island hopping theory (Martin 2000). The island hopping theory states that the sea level of the Mozambique channel between Madagascar and Africa dropped enough so that areas of land were exposed between 45 and 26 mya, which may have allowed for a series of island hopping events which eventually led to the colonisation of Madagascar. The second theory is that a single rafting event occurred from mainland Africa which allowed for the migration. Although there is strong opposition to this theory as all documented successful rafting attempts have involved reptiles (Stankiewicz, Thiart et al. 2006), who can survive for longer periods as they do not face the energy demands of maintaining a constant body temperature that mammals do. However, an argument has suggested that the Cheirogaleidae can reduce their metabolic rates by up to 90% and lower their body temperature, thereby saving around 40% of their average daily expenditure, in effect entering a state of torpor. Therefore, it is not too far-fetched to suggest that these traits were shared by ancestral lemurs, which would add more strength to the rafting hypothesis. Clearly there are two schools of thought for the colonisation events of Madagascar but there is no clear evidence in the patchy fossil record that confirms either.

Madagascar as an Island Environment

Lemurs show a lack of evolutionary convergence with anthropoid primates in many social, behavioural and physiological features. Large amounts of research have concluded that there are nine major traits where lemurs differ from anthropoid primates hugely. These nine traits are: (1) A lack of sexual dimorphism present in many anthropoid species (Godfrey, Lyon et al. 1993). (2) The presence of monogamy amongst some lemur species (Jolly 1998). (3) The presence of cathemerality amongst some lemur species (Overdorff 1988). (4) High levels of infant mortality (Sussman 1991; Wright 1995). (5) A low metabolic rate (Schmid and Ganzhorn 1996). (6) Female dominance within lemur social structures (Richard and Nicoll 1987; Radespiel and Zimmermann 2001). (7) Female – female aggression (Vick and Pereira 1989). (8) Sperm competition with male – male aggression (Pereira and Weiss 1991; Kappeler 1997). (9) The presence of a strict breeding season that is dependent on the photoperiod (Rasmussen 1985).

There are two hypotheses that have been postulated to explain why lemurs have evolved these differences from anthropoid primates. Firstly, is the evolutionary disequilibrium hypothesis which suggests that lemur traits are transitional behaviours (van Schaik and Kappeler 1996). A transition that has coincided with the arrival of humans on the island of Madagascar around 2000 years ago. When humans arrived there were mass extinctions of many species of diurnal avian and mammalian predators (Goodman 1994). The lack of diurnal predators has created new niches allowing the previously nocturnal lemurs to become more diurnal, thus leading to changes in social behavioural and physiological features. The second hypothesis is the energy conservation hypothesis (Wright 1999). The energy conservation hypothesis emphasises the role that Madagascar's climate and environment have played in selecting for lemur adaptations. The energy conservation hypothesis and its affect on lemur evolution has also been compared to that of Australian Marsupials, which suggest that both radiations were influenced by environmental factors (Smith and Ganzhorn 1996).

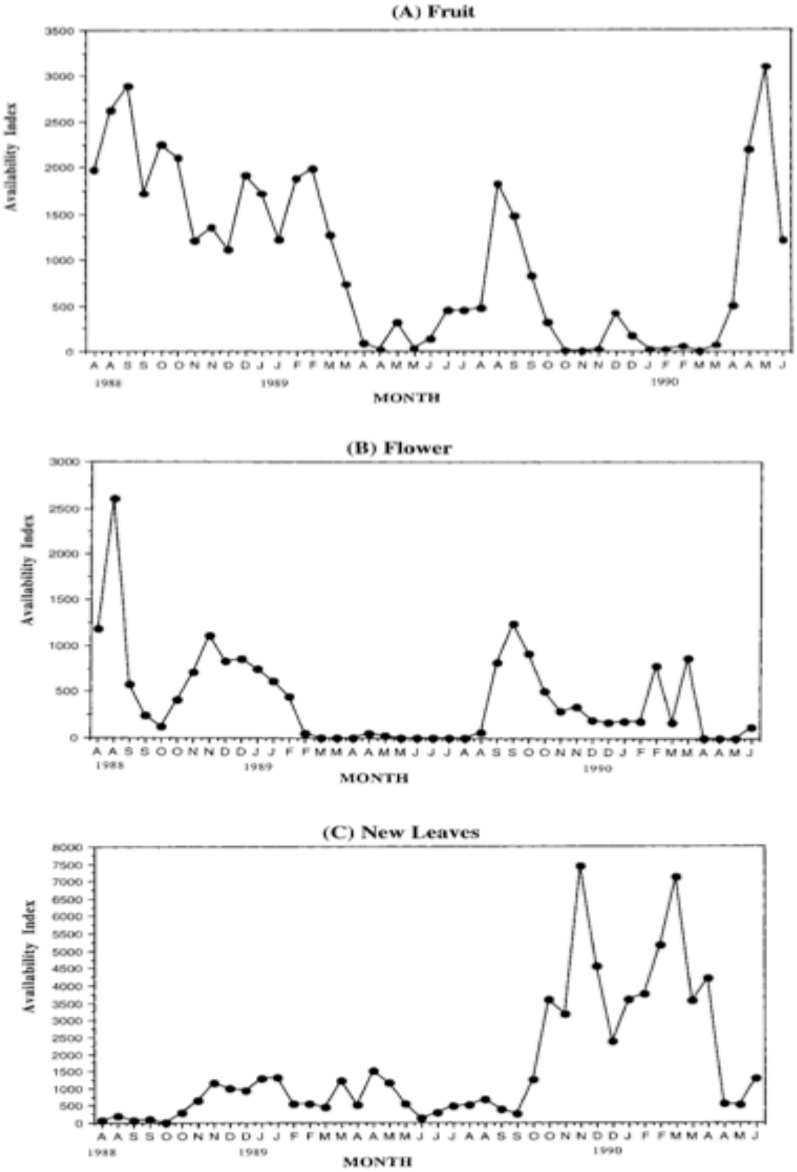


Figure 3: Food availability index for: (A) fruit, (B) flowers, (C) new leaves in ranomafana, Madagascar (Overdorff 1996), showing a marked disparity in the availability of nutrition throughout the annual cycle. The months between and including April until August show a huge decrease in the availability of fruit, flowers and new leaves.

The climactic conditions in Madagascar have been described as extremely seasonal in comparison with many more tropical habitats around the globe (Dewar and

Richard 2007). Other tropical forests in Africa, Asia and South America have trees bearing fruit constantly throughout the year (Nunes 1998). Although, there is still a tendency for lower fruit production during the driest months in these regions. Despite the seasonal variation in fruit and leaf production in Madagascar being of a more extreme nature than that of other tropical forests (Figure 3), additional factors such as cyclones and the fact that many fruiting trees also have asynchronous or alternate year fruiting cycles (Morland 1991). These factors necessitate lemurs having behavioural and physiological adaptations in order to survive periods of severe food scarcity and punctuated with short periods of abundance. Behavioural factors that are influenced by this seasonality are things such as breeding, with females only giving birth during the short period of food abundance, in order to ensure that they are able to produce adequate levels of milk in order to nurse their young (Lewis and Kappeler 2005).

The energy conservation hypothesis also has an application in terms of locomotion and ranging behaviour. It is the case that during periods of food scarcity for many predators, their response is to increase their daily ranging behaviour in order to find enough nutrition to survive (Craighead 1976). Whereas many lemur species decrease their levels of locomotion and ranging behaviour in order to cope with extended periods of food scarcity (Norscia, Carrai et al. 2006), some lemur species within the order *Cheirogaleus* even hibernate in order to survive the long dry season (Fietz and Ganzhorn 1999). One of the only exceptions to this rule is found in some *Eulemur* species, who need to visit watering holes during the height of the dry season. These watering holes can be more than three kilometres in distance, meaning that some *Eulemur* species can increase ranging behavior during the height of the dry season. Although, this is a case of inter-specific variation, as it was also found that groups whose territories were located close to the watering hole would not increase their ranging distances (Scholz and Kappeler 2004).

Primate Locomotion

Strepsirhine Modes of Locomotion

The diversity in size among the primate order necessitates their need to adopt various methods of locomotion in order to navigate around their environment e.g. knuckle walking in gorillas and bipedalism in humans (Fleagle 1988). To be able to negotiate an arboreal habitat, organisms must develop a large array of different movement types. Napier and Walker (1967) were the first to attempt to categorize the different movement patterns recruited by primates in order to do this. They defined four principal locomotor categories: vertical clinging and leaping (VCL), quadrupedalism (which includes ground running and walking, branch running and walking, and climbing), brachiation (swinging from branch to branch only using the arms) and bipedalism. Napier and Walker's classifications have come under much scrutiny (Crompton and Andau 1987; Anemone. R 1990; Preuschoft, Gunther et al. 1998), mostly attacking the phrase 'vertical vertical clinging and leaping' for being far too general. Retractors of this phrase argue that primates use different leaping strategies and have different morphologies. Tarsiers and galagos have specialised elongated tarsal bones suggesting that the foot is used for propulsion (Gebo 1987; Demes, Jungers et al. 1996) leading Demes (1996) to refer to them as 'tarsifulcrumators'. Whereas indriids and other specialised leaping lemurs are characterised by greater joint excursions at the hip and were therefore described as 'tarsirotators'. VCL was originally thought to exclusively include certain prosimian primates, but observations on new world monkeys have revealed that these species also perform leaps to and from vertical substrates (Kinzey, Rosenberger et al. 1975) although they are not classified as VCLs. Prosimian VCLs can also be further sub-divided into two categories known as specialist leapers and non-specialist leapers. The differentiation relies on the fact that specialist leapers, leap and land using only their hindlimbs (Figure 4b). Whereas non-specialist leapers, leap hindlimb first but land forelimb first (Figure 4a), or with all four limbs at the same time (Tilden 1990).

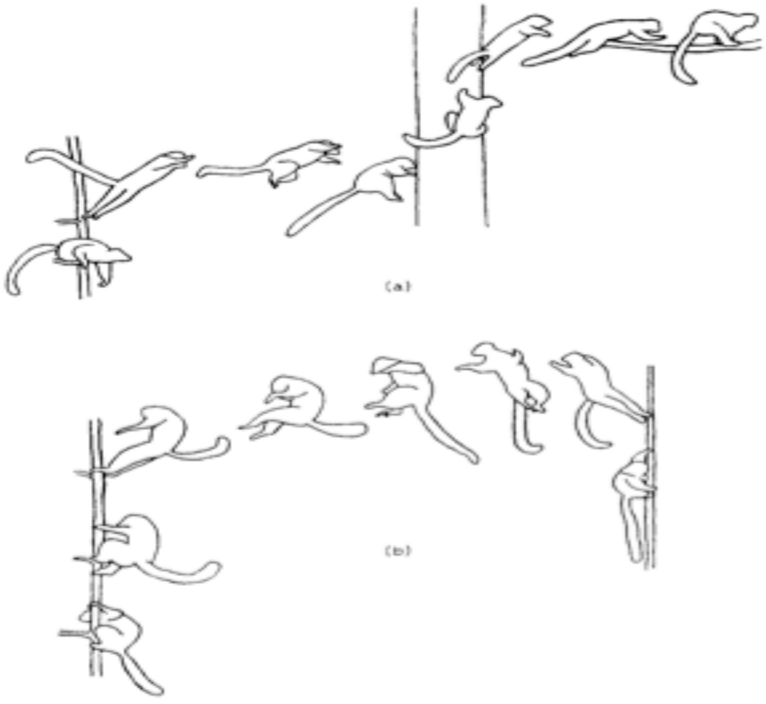
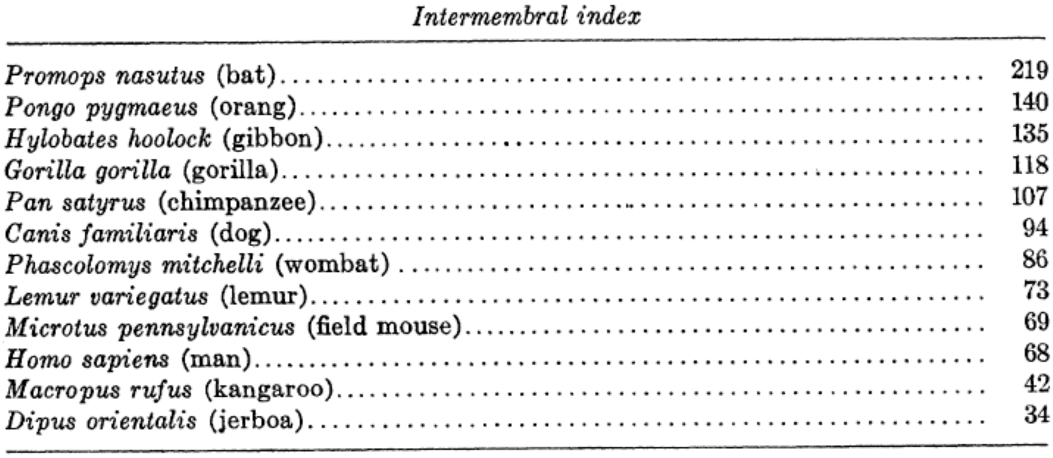


Figure 4 Comparison between a generalist leaping (a) and a specialist leaper (b) from (Tilden 1990). The generalist (a) is shown leaping from left to right, with a horizontal posture at take off and landing forelimb first. Whilst the specialist (b), is shown leaping from right to left, with a vertical posture at take off and landing hindlimb first.

Since the first primate locomotor classifications very few efforts have been made to improve upon Napier and Walker's (1967) groupings. Three types of leaping style have been defined to categorise prosimian leaping (Oxnard, Crompton et al. 1990): static leaping, where an animal jumps from standstill; running leaping, in which an animal ends a phase of movement with a jump; and ricochetal leaping, which is the linking together of several leaps in succession. A further diversification of these types of locomotion is the mechanism used to generate the power required for the leap. These mechanisms are squat leaping, where the power for the leap is attained from muscle contraction; catapult leaping, utilising a locking mechanism to allow the slow accumulation of maximum muscle tension; countermovement leaping, in which a store of elastic energy from a previous movement is attained; and vaulting leaping, where a secondary structure is used to alter the direction of a leap (Oxnard, Crompton et al. 1990; Crompton and Sellers 2007). Although these extended classifications are far more precise than prior efforts (Napier and Walker 1967), it is clearly difficult to define the type of leap and the mechanism behind it while trying to keep track of an organism in its natural habitat, therefore very few investigations mention movement classification in great detail.

Table 1 Different species and intermembral index values from (Davenport 1935) showing limb length ratios. Intermembral indices can be used as a predictor of locomotion, with smaller intermembral indeces indicating a propensity for leaping.



Intermembral index

Promops nasutus (bat)	219
Pongo pygmaeus (orang)	140
Hylobates hoolock (gibbon)	135
Gorilla gorilla (gorilla)	118
Pan satyrus (chimpanzee)	107
Canis familiaris (dog)	94
Phascolomys mitchelli (wombat)	86
Lemur variegatus (lemur)	73
Microtus pennsylvanicus (field mouse)	69
Homo sapiens (man)	68
Macropus rufus (kangaroo)	42
Dipus orientalis (jerboa)	34

A method utilised in an attempt to classify types of primate movement from morphology, were limb ratios. The most popular ratio is known as the intermembral index, which is the ratio of the forelimb length (humerus and radius) to hindlimb length (femur and tibia). Intermembral indeces are expressed as a percentage (Martin 1990). Therefore the lower the intermembral index, the longer the hindlimbs are in comparison to the forelimbs (Schultz 1936). In terms of primate locomotion a low intermembral index (Table 1) is considered to be an adaptation for propulsive hindlimb dominated leaping (Davenport 1935; Ravosa, Meyers et al. 1993; Llorens, Casinos et al. 2001). Animals whose predominant form of locomotion is brachiation have much longer forelimbs than hindlimbs. The gibbon has an intermembral index of around 135 and its predominant form of arboreal locomotion is brachiation, however, lemurs have a much lower index value, with a mean of around 73 and they exploit hindlimb dominated leaping for much of their locomotor bouts. One genus of strepsirhine renowned for its saltatory displays is *Propithecus*, correlating with the trend for a low intermembral index indicating hindlimb leaping, all species of the genus *Propithecus* have intermembral indices of between 60-67% (Ravosa, Meyers et al. 1993). A low figure that indicates legs much longer than their arms and a tendency to employ leaping much more often than other forms of locomotion. Other indices are also adopted (Llorens, Casinos et al. 2001) such as the crural index (ratio of tibia length to femur length) and the brachial index (ratio of radius length to humerus length). These indices are not as popular because they show variation in one limb rather than enabling a comparison between two sets of limbs to be made, therefore they are not as good at predicting locomotor patterns as the intermembral index.

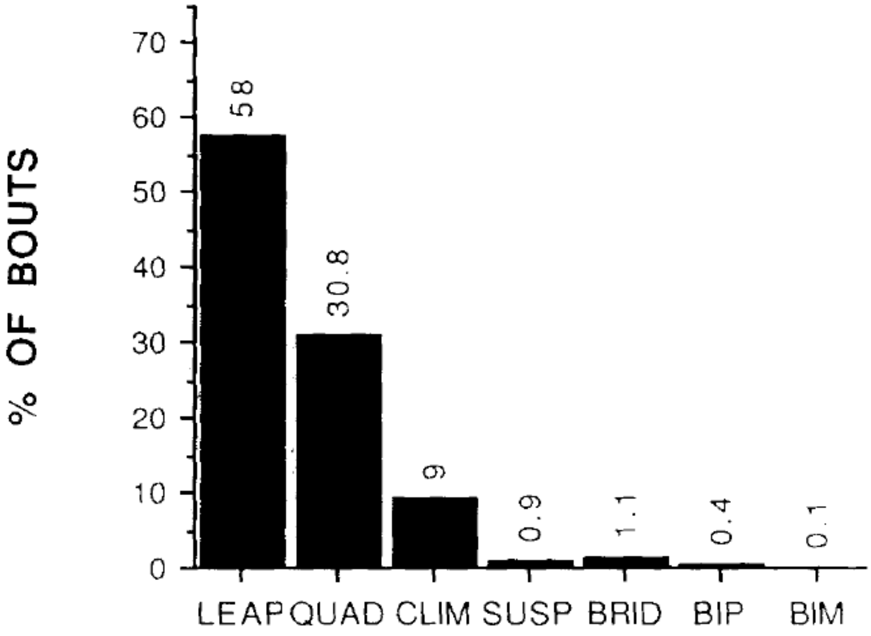


Figure 5 Locomotor frequencies of *Eulemur rubriventer*, LEAP= leaping, QUAD= quadrupedalism, CLIM= climbing, SUSP= suspensory, BRID= bridging, BIP= bipedalism and BIM= bimanual; from (Tilden 1990)

In connection with what modes of locomotion an animal is performing, another useful piece of information is how often the animal is engaging in different forms of movement. Bouting studies look at the proportion of time an animal spends executing different modes of locomotion. Lemurs show a large diversity of locomotor and postural adaptations Lemuridae, Daubentoniidae and Cheirogaleidae exhibit a range of quadrupedalism. *Lepilemur* are slow climbers and leapers. The Inriids qualify for an adaptive radiation all by themselves with high levels of VCL (Richard and Dewar 1991). Investigations looking at Lemuriformes reveal that the most frequent bouts of behaviour within the families Indriidae, Lemuridae and Lepilemuridae are leaps (Gebo 1987; Tilden 1990). The interesting finding here is that although the Indriidae are renowned as being specialist leapers, whereas the Lemuridae are known for being more general in their patterns of movement (Tattersall 1982; Fleagle 1988; Martin 1990); Tilden (1990) found that his Lemuridae subjects (Figure 5) leapt just as often as their Indriidae counterparts (Gebo 1987). But Gebo (1987), discovered within his investigation that this was not the case and that Indriidae leapt more often than the Lemuridae species. The two sets of data may not be comparable as both studies were performed in captive environments, with different enclosure sizes and support availability, which could have impacted upon the results. These investigations found that although all lemur species utilise a range of locomotor patterns (quadrupedalism, leaping, climbing and bi-pedalism), in many families the predominant locomotor pattern is leaping.

Adaptations to an arboreal environment

An arboreal lifestyle requires the development of specialist features in order to contend with the high forces of leaping and balance required for life in the trees. As previously discussed the intermembral index can indicate a preference of locomotor mode, but what adaptations accompany this? In addition, primates of different sizes are not just scaled-up or scaled-down versions of each other (Demes and Günther 1989). Primates have different adaptations for leaping, walking or brachiating. Much of the prosimian morphological data has concentrated on galagos and tarsiers in which it has been well documented that an elongated tarsus allows longer muscles to attach in the foot to generate more power which is used for propulsion (Burr, Piotrowski et al. 1982; Gebo 1987; Demes, Jungers et al. 1996). In terms of prosimians, there seems to be a large divide between the Malagasy leaping adaptations and those of the other African and Asian prosimians. The limited data on Lemuriformes species concentrates on the indriids (Demes, Jungers et al. 1996; Connour, Glander et al. 2000; Wunderlich and Schaum 2007) as they are known as specialist large-bodies leapers.

The adaptations noted so far are increased femoral length in comparison to other primates of similar size, which do not specialise in leaping (Oxnard, German et al. 1981; Connour, Glander et al. 2000). Increased length is thought to increase the efficiency and duration of take-off, enabling the animal to contract the muscle over a longer period of time and increase the impulse generated for leaps of a longer distance (Wunderlich and Schaum 2007). More generalist lemuriformes have also been noted to have an intermediate femoral length between specialist leapers and non-leaping primates (Connour, Glander et al. 2000). One of the most important factors is thought to be the surface area and size of the femoral head found in lemuriformes in comparison to galagos and tarsiers (Demes, Jungers et al. 1996; Connour, Glander et al. 2000). A larger more spherical head allows for greater joint excursions at the hip. It is thought that this hip flexion stretches tendons in the posterior hip, which in turn store elastic energy that is released when the hip extends and the centre of mass elevates into a leap (Wunderlich and Schaum 2007). Leaping is also associated with high forces, which require strong bones to absorb these forces without breaking. Therefore Indriids are also characterised by increased femoral rigidity to deal with the high forces (Demes, Jungers et al. 1996; Connour, Glander et al. 2000). Not only are the femoral bones more rigid it was discovered that within Lemuridae family there were differences talus width, with *Eulemur fulvus* (an arboreal species) possessing a broader more robust talus for leaping, than *Lemur catta* (a more terrestrial species) (Ward and Sussman 1979). Therefore it is evident that no clear set of adaptations can be attributed to Malagasy lemurs. The varying forms of locomotion utilised creates varying morphologies along with intermediate forms of these features.

Although the previous adaptations discussed explain why prosimians can leap and how they adapted to do so, the question remains as to how they can leap the distances they achieve. Galagos of 250g have been reported to jump to a height of 2.3m, which would require a force of 18 times body weight (Alexander 1985). Calculations involving the percentage of body mass involved in jumping and the maximum output of vertebrate muscle, ascertained that the power necessary for such a jump is well above the capabilities of vertebrate muscle (Aerts 1998). Primates are not the only animals who perform beyond their supposed muscle capabilities; frogs (Peplowski and Marsh 1997) and locusts (Bennet-Clark 1975) have also been discovered to leap further than they should be able. These findings have led to investigations into the possibility of power amplifiers, which enable an organism to store energy for a leap. Another name for power amplifiers is catapult mechanisms, which are thought to enable work done relatively slowly by muscles to be released much more rapidly at take-off (Alexander 1995). In the locust this catapult mechanism is thought to be an apodeme (tendon), which maintains the extensor muscle in a contracted state, when the apodeme relaxes the muscle extends with the speed and force required to power the leap (Heitler 1974; Bennet-Clark 1975). In galagos the power amplifier is thought to be the vastus muscle-tendon system (located in the upper hindlimb) where energy is stored from crouching. Strain energy is released late in the push off utilising compliant tendons to allow rapid contraction and initiating a leap (Aerts 1998). Although no data on lemuriformes' maximal leaping distance exists, they are certainly capable of long distance leaps that require huge forces but no catapult mechanism or power amplifier has yet been discovered. It would not be correct to make a direct comparison between the galago and lemur species as it has already been shown that their leaping strategies differ greatly, therefore one cannot assume their power amplification strategies to be the same.

Strepsirhine Quadrupedalism

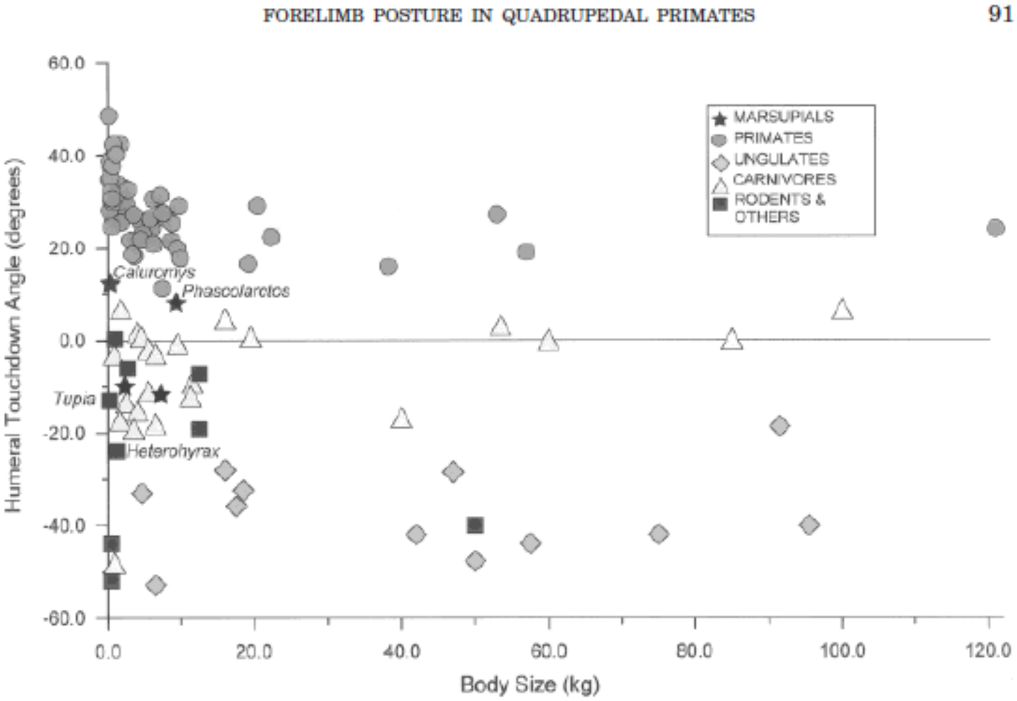


Figure 6 Mean humeral touchdown angle plotted against mean body size for a variety of mammalian genera from (Larson, Schmitt et al. 2000)

Quadrupedalism plays a large role in primate locomotion, allowing animals to climb and negotiate horizontal substrates, which do not require leaping. Primates as a whole seem to have a very different quadrupedal gait from almost all other mammals, utilizing different gait sequences, limb angles and propulsion methods. A predominantly diagonal gait sequence distinguishes all primates from other mammals, which rely on a lateral pattern. Diagonal sequence (DS) walking patterns begin with the right hindlimb (Rh) followed by the left forelimb (Lf), left hindlimb (Lh) and the right forelimb (Rf). Lateral sequence (LS) walking, adopted by all non-primate mammals follows the pattern: Rh, Rf, Lh, Lf (Vilensky and Larson 1989; Martin 1990). Although DS walking gaits are very common in primates, LS has also been observed when primates are braking, during slow or incline walking (Prost 1965). Diagonal sequence gaits have also been regularly observed on inclined branches, whereas on declined branches a higher proportion of lateral sequence gaits were recorded (Stevens 2008).

Primates also use very large limb excursions while walking quadrupedaly, this causes a more protracted limb posture compared with all other mammals, the nearest mammal with similar limb excursions is an arboreal marsupial, (Figure 6). Large limb excursions are thought to produce a more crouched posture in comparison to other mammals (Larson, Schmitt et al. 2000). Thus, possibly enabling the animal to maintain speed in the canopy, as reducing stride frequency but increasing stride length will keep speed constant (Larson, Schmitt et al. 2000). Most mammals also utilise a trot phase between walking and galloping; this is an intermediate speed, which includes an aerial phase where no limbs have any contact with the ground. In primates, there is no trot with an aerial phase; primates use what has been referred to as an “amble” (Schmitt, Cartmill et al. 2006), whereupon one limb remains in contact with the substrate while a DS gait continues. Thought to be an adaptation which allows the animal to maintain a lower centre of mass, which could reduce oscillations, in turn reducing peak forces, therefore aiding the animal to move quickly on fine terminal supports which are used for foraging (Vilensky and Larson 1989; Larson, Schmitt et al. 2000; Schmitt, Cartmill et al. 2006).

Considering these arboreal gait strategies many hypotheses have been postulated to explain them. Firstly, high frequency, high force gaits would create much significant branch sway in an arboreal habitat, so primates reduce these forces to avoid identification by predators (Larson, Schmitt et al. 2000). Although lemurs are known for leaping, which would cause a higher degree of branch sway than any form of quadrupedalism. A more plausible explanation comes from the same author (Larson, Schmitt et al. 2000), stating that high forces while walking on a compliant substrate may also create high levels of body roll, which are bad for balance during arboreal locomotion. Therefore protracted forelimbs, creating a lower centre of mass and a more crouched posture could be an adaptation for better balance on a terminal branch support. In five species of Old World catarrhines a more crouched position was noted when locomoting quadrupedally on an arboreal substrate rather than a terrestrial substrate (Schmitt 1999). Potentially, this may not be the case for strepsirhine primates, although it would be expected for primates and arboreal mammals to adopt a more compliant gait to aid balance arboreally rather than terrestrially. Although a more crouched and compliant gait is achieved at high metabolic cost (Schmitt 1999), it allows the successful negotiation of an arboreal habitat where threats from predation are limited and the quality of nutrition is good. Strepsirhine primates also do not adjust their gait sequence pattern when negotiating branches of varying diameters. The only difference noticed in the gait was that the velocity of the footfalls decreased with decreasing branch diameter (Stevens 2008), suggesting that arboreal primates sacrifice overall speed for balance on finer substrates and arboreal supports.

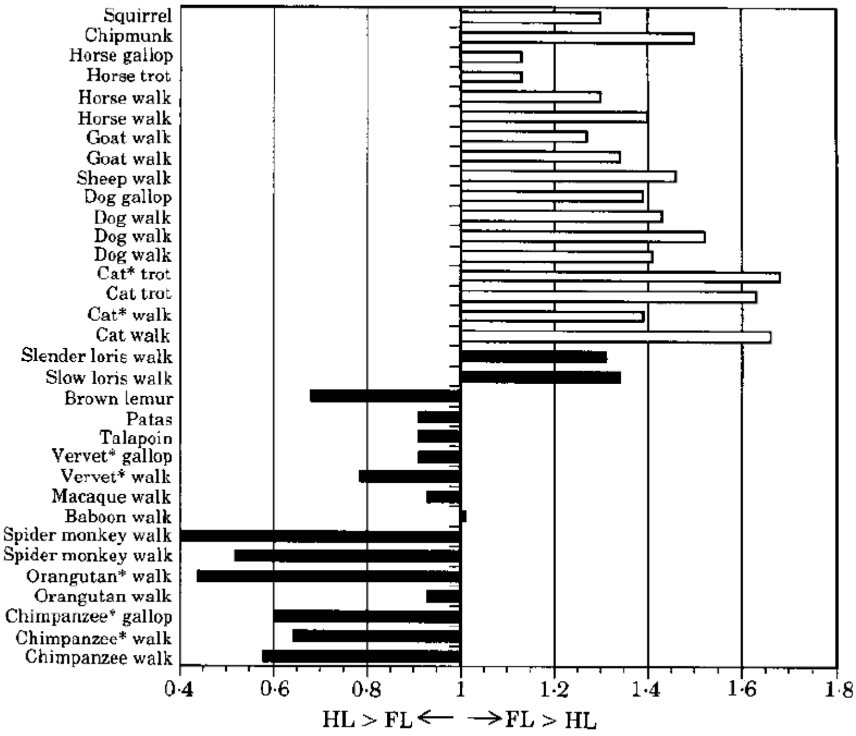


Figure 7 Ratios of forelimb (FL) over hindlimb (HL) peak vertical forces for primates (solid bars) and non-primates (open bars) from (Demes, Larson et al. 1994), showing more terrestrial animals placing higher forces on their forelimbs, whilst arboreal animals place more force on their hind limbs.

Why do primates use DS walking? The link to diagonal sequence walking is due to the fact that in primates the centre of gravity is located nearer to the hindlimbs (primates are known as hindlimb dominant), whereas in most other mammals it is located more centrally. The benefit of a DS gait is that it reduces roll and increases stability and balance features, which are crucial for an arboreal primate (Martin 1990). Another term coined is hindlimb driven (Demes, Larson et al. 1994), as primates generate most of the forces necessary to walk from their hindlimbs (Figure 7). Figure 7 shows that within the primates the amount of force placed on the hindlimbs varies, with more terrestrial species placing greater force on their forelimbs, while leapers and more arboreal species maintain greater vertical forces on their hindlimbs. The explanations given for hindlimb dominance within primates are that it reduces the stress on the forelimbs. With forelimb stress reduced, there is less of a need for strength and stability in these appendages, which leads to greater mobility in the forelimbs (Alexander 1985). More mobility has led to greater fine control of the forelimb for foraging and manipulation (Reynolds 1985; Kimura 1992; Demes, Larson et al. 1994). Although Franz et al (2005) reported that at higher velocities the differentiation of forces between the limbs decreases and forces are spread more evenly between the two sets of appendages. A reduction in hindlimb dominance is thought to be due to the higher forces associated with a faster gait (Franz, Demes et al. 2005). In a study of the more arboreal red-ruffed lemur and the more terrestrial ring-tailed lemur, forelimb forces were found to be higher in the more arboreal species, bucking the trend found in all previous research (Kimura 1992; Demes, Larson et al. 1994). Possibly explained by the fact that none of the arboreal substrates in the investigation were natural, and therefore were not compliant in any way. Lack of compliance may have led the more arboreal species to alter its gait and assume a less crouched posture when locomoting on these arboreal supports. However, a strong argument is given for these higher forelimb forces in strepsirhine primates. As lemurs do not have the fine hand control present in more dextrous New World monkeys and haplorhine species and therefore the strepsirhine hand may play less of a role in non-locomotary functions (Franz, Demes et al. 2005).

Strepsirhine Leaping

Many mammals engage in leaping behaviours in order to negotiate an arboreal habitat, although few achieve the levels of saltatory display that prosimians are renowned for. Leaping in some lemur species can account for up to 882m of every kilometer moved (Crompton and Andau 1986). Cant (1992) declares that there is no general problem solved by locomotor behavior, these saltatory displays solve a range of different problems, such as predator avoidance or locating the best food. The morphological adaptations to prosimian leaping have been discussed, but what are the behavioural tactics that prosimians adopt to aid leaping? Lemuriformes are known as jumpers who use large joint excursions at the hip to initiate a leap, but many observers have noticed preparatory counter-movements (Demes, Jungers et al. 1995; Demes, Jungers et al. 1996). These counter-movements are described as a hop or crouch before leaping, with larger indriid species opting more often to hop into this position (Demes, Jungers et al. 1996). It has been theorised that these hops are a way of storing elastic energy prior to a leap, allowing a greater power output at contraction (Demes, Jungers et al. 1996). These are just observations that have been noted and no investigations into the mechanisms behind these counter-movements have yet been undertaken, therefore there is no empirical evidence that these postural behaviours have any bearing on leaping behaviour. Forelimbs also seem to play a major role in leaping and can be used to aid in the acceleration of a leap. Increased acceleration can be achieved with a fast arm-swinging movement, similar to that of a long-jumper (Demes and Günther 1989). Linking in with the fact that larger bodied

VCL lemur species, such as the indriids, have relatively longer forelimbs (Terranova 1996) and therefore need greater acceleration in order to propel themselves during a leap. These arm-swings are also thought to aid in a reorientation of the body during flight (Dunbar 1988). The reorientation is necessary as specialist VCL lemurs begin a leap with their backs orientated towards the landing site, therefore a rotation of 180 degrees is needed for the animal to be facing the substrate it is landing on. Another behaviour observed, which aids in the rotation is applying more force with one hindlimb than the other during take-off; this action initiates the rotation (Dunbar 1988). A similar rotation is needed in leaping in galagos and tarsiers although the behaviour that initiates this rotation is very different. A tail-flick is observed to provide the same result that the arm-swing in lemurs elicits, which is a rotation of the body to allow the feet to grasp a landing area (Crompton and Andau 1986).

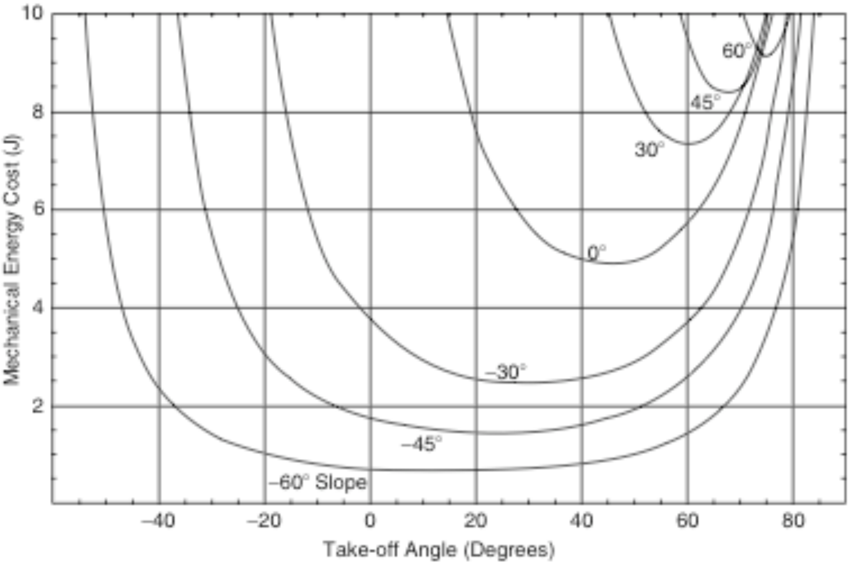


Figure 8 Energy cost of a leap by an individual of 1kg leaping 1m and the angle of the slope of the leap from (Crompton and Sellers 2007)

With leaps making up such a large proportion of locomotor behaviour, there are few data regarding the energy costs of saltatory locomotion in prosimians, which is mainly due to the fact that it is very difficult to quantify accurately. Warren and Crompton (1997) demonstrated that between 75.2 and 87.6% of energy used for locomotion was devoted to leaping in two species of nocturnal Malagasy prosimians. Although the cost of leaping is high, the cost of locomotion in terms of available energy is fairly low for some species. These factors are all dependent on the distance traveled by the animal and also the animal's body mass. Body mass has a large influence because as body mass increases so does the relative cost of locomotion (Warren and Crompton 1997). More investigations need to be performed on the energy requirements and energy budgets of Malagasy primates, such as if leaping is a more effective strategy energetically than ascending and descending trees in order to navigate through an arboreal habitat. Theoretical analyses look into the energy costs of single leaps of different angles of take-offs for an animal of 1kg leaping a distance of one 1m (Crompton and Sellers 2007). Figure 8 demonstrates the most energy efficient take-off angles when leaping 1m up or down a slope of a given angle, for example, for a leap to a substrate at the same level (0° slope) the most energy efficient take-off angle is 45°. The 45° angle has become somewhat of an optimum angle for people studying primate leaping. Clearly a 45° take-off angle will generate a leap of the greatest distance, but the arboreal environment is three dimensional and if a terminal support is higher or lower than the take-off support than a greater or lower angle may be more suitable. Crompton et al (1993), discovered that *Galago maholi* always utilise a take-off angle of 45° for leaps over large distances. Since this study many investigations tend to assume that the 45° take-off angle is the "optimum" for all leaps and that this take-off angle should always be used. Demes et al (1996), observed that indriid leapers take-off angles range from 30° - 70° although many leaps occurred around the 45° "optimum". Although a 45° take-off angle may produce maximum jumping distance, surely an "optimum" take-off angle depends on the landing height of the substrate in comparison to take-off area.

Branch compliance is also another issue where little research has taken place in terms of prosimians. In many primate species, when crossing gaps in an arboreal environment, many chose compliant substrates in order to minimise the costs of arboreal locomotion, such as gap bridging in orang-utans (Thorpe, Crompton et al. 2007). Lemur species have been shown not to take advantage of any form of elastic recoil that takes place when leaping from a branch and tend to leap before any recoil occurs, which means they are losing energy when jumping (Demes, Jungers et al. 1995). Although when landing the usage of a compliant surface is not optional, if an animal lands on a small compliant branch then it will give way under the mass of the animal therefore reducing the force of landing. Galagos on the other hand tend to leap from larger less compliant substrates such as thicker branches, in which case compliance plays no part in the takeoff (Crompton, Sellers et al. 1993).

Table 2 Substrate, diameter, and compliance preferences for a variety of indriids from (Demes, Jungers et al. 1995)

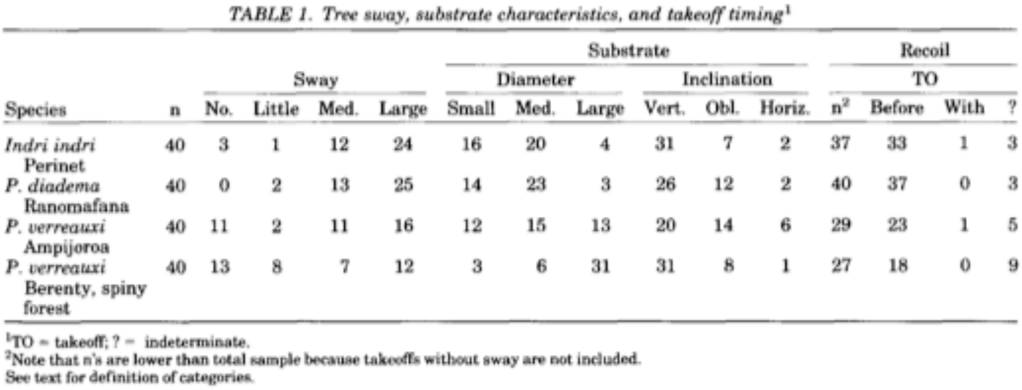


TABLE 1. Tree sway, substrate characteristics, and takeoff timing[1]

						Substrate						Recoil			
		Sway				Diameter			Inclination			TO			
Species	n	No.	Little	Med.	Large	Small	Med.	Large	Vert.	Obl.	Horiz.	n[2]	Before	With	?
Indri indri Perinet	40	3	1	12	24	16	20	4	31	7	2	37	33	1	3
P. diadema Ranomafana	40	0	2	13	25	14	23	3	26	12	2	40	37	0	3
P. verreauxi Ampijoroa	40	11	2	11	16	12	15	13	20	14	6	29	23	1	5
P. verreauxi Berenty, spiny forest	40	13	8	7	12	3	6	31	31	8	1	27	18	0	9

[1] TO = takeoff; ? = indeterminate.
[2] Note that n's are lower than total sample because takeoffs without sway are not included.
See text for definition of categories.

Much of the prosimian leaping data which has been collected relates to the forces involved with leaping. With long leaps making up a large proportion of daily locomotor bouts (Gebo 1987) and increased rigidity of the femur (discussed earlier), there are clearly large forces associated with saltatory behaviour. Early leaping force studies from Preuschoft (1985) and Gunther (1991) discovered that landing forces were higher than take-off forces. These studies were done utilising horizontal force plates, which, with prosimians being VCLs did not produce accurate data as VCLs rarely use horizontal perches as take-off or landing areas (Table 2). Demes et al

(1995) demonstrated when using vertical force poles that the reverse of this is actually the case and that take-off forces are actually higher than landing forces. The poles that Demes used were not very compliant, therefore it would be expected for the gulf between the landing and take-off forces to increase in the wild as smaller diameter tree branches will be more compliant, and large indriid species show a preference for smaller diameter substrates (Table 2). Generalists are also known to generate relatively higher leaping forces than specialist VCLs (Demes, Fleagle et al. 1999), which may be due to substrate choice or a less efficient leaping strategy. Also as the size of an animal increases the relative forces they experience in relation to leaping decrease. Factoring in larger limb lengths, which can increase acceleration time and therefore reduce the force an animal experiences (Demes, Fleagle et al. 1999). Indriids have also been observed to have skin folds beneath their arms, which appear to have an aerodynamic effect, and may reduce landing forces (Dunbar 1988), however, this hypothesis has not been directly tested and was simply an observation.

A recent improvement in technology has allowed for accelerometers to be attached to specimens in the wild. Byrnes et al (2008), showed that in colugos, peak landing forces were much lower than strepsirhine primates. These lower forces seem to be due to the colugo's ability to utilise the aerodynamic forces, which reduce pre-landing impact force. Achieved by angling their gliding skin flaps upwards just prior to landing, which reduces the animal's velocity greatly. A technique such as this could increase understanding of prosimian locomotion greatly, as it can allow constant monitoring of an animal's behaviour without the need for camera equipment or an observer. Also data can be recorded many times a second and human error will not occur during data collection (Sellers and Crompton 2004; Byrnes, Lim et al. 2008).

Target Species

The data collection for this thesis was centered around the study of the locomotion of *P. verreauxi* Kirindy Mitea Reserve in Western Madagascar. *P. verreauxi* was studied during a twelve-month period of field work in Madagascar.

Figure 9 *P. verreauxi* at Kirindy Mitea National Park showing a female sifaka at rest wearing an identification collar as part of a research program of another group of researchers.

The sifaka (*P. verreauxi*) (Figure 9) usually form groups of between two and twelve individuals, with a mean group size of between five and six (Richard 1985), but this may not be the case in Western Madagascar. Unusually among mammals, female dominance occurs within all sifaka groups (Kubzdela, Richard et al. 1992), and in almost all lemur species, female dominance is the norm (Tattersall 1982). Sifakas are renowned as specialist leapers and are also known for their lack of quadrupedalism in a terrestrial environment, choosing instead to hop bipedally. Most of their feeding occurs high in the canopy, hence, they are known as arboreal folivores, with a diet consisting mainly of leaves, seeds, fruits and flowers (Hemingway 1994). Although they are relatively large lemurs, they still have predators which include raptors, crocodiles, vivverids and large ground boas (Gursky, Nekaris et al. 2007).

Study Site Background and issues facing research

Madagascar is well known as a biodiversity hotspot, and due to the high level of endemism and deforestation, is a high priority for conservation organisations. Levels of endemism have been estimated for land vertebrates at 84% (Goodman and Benstead 2005), whilst for vascular trees and shrubs, endemism levels rise to 96% (Schatz, Lowry et al. 1996). Human impact has been largely to blame for deforestation and figures of 90% are often quoted as the level of original forest that has been cleared. The 90% figure is often debated, but what is sure is that since 1953 (when surveying of the forests began), 40% of the remaining woodland has now been lost due to deforestation (Harper, Steininger et al. 2007).

Anthropogenic deforestation in Madagascar is mostly caused by slash and burn activity, which promotes the growth of grasses upon which cattle can be grazed.

Harvesting of high value tree species such as rosewood or pallisandre leads to a more selective form of deforestation, driven by demand from the West. Lastly, large areas of forest are felled in order to produce charcoal, which almost all rural Malagasy use to cook with. Although these high rates of deforestation are alarming, it has been shown that elevating the status of a forest to a protected national park tends to significantly lower the rates of habitat loss in comparison to unprotected areas (Gorenflo, Corson et al. 2011).

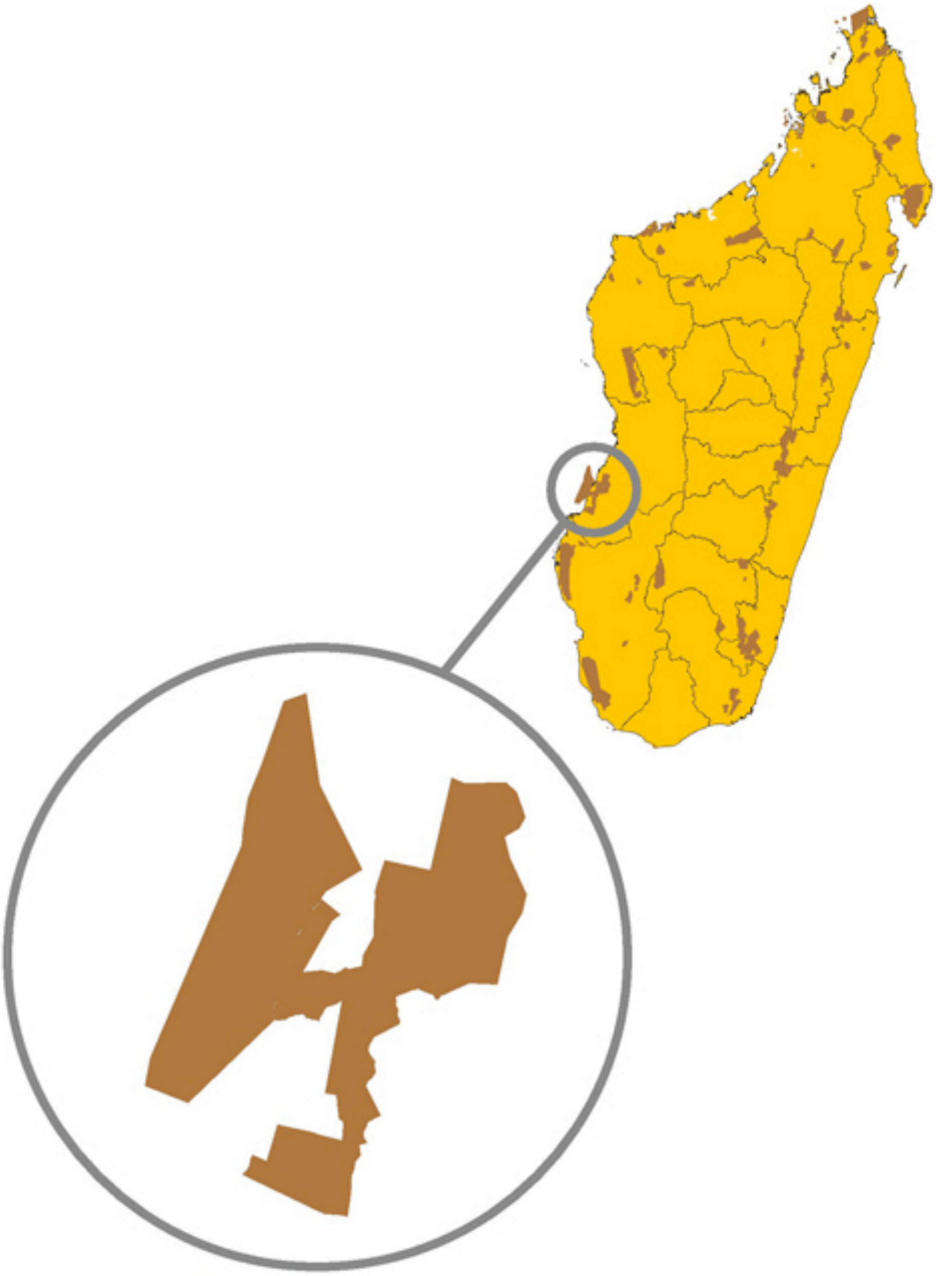


Figure 10 Map of Madagascar showing the location of Kirindy Mitea National Park (map image taken from http://www.parcs-madagascar.com/fiche-aire-protegee_en.php?Ap=19#).

Kirindy Mitea National Park is one of the largest remaining tracts of dry-deciduous forest in Madagascar. It is located in the South-Western region of Menabe, around 70km South of the coastal town of Morondava (Figure 10). As of 2006 the forested area covered 101,031ha (Whitehurst, Sexton et al. 2009), although not all of this area is fully protected by National Park status, and a buffer zone, where local people are permitted to go surrounds the protected core. Rates of forestation have increased in the protected zone since its inception, whilst forestation levels have decreased within the buffer zone during the same time period (Whitehurst, Sexton et al. 2009). Leading to an alteration in the park boundaries, increasing the size of the protected area; but effects of this increase are yet to be published. The other factor that can influence levels of forestation within a protected area are cyclones. Cyclone Fanele made landfall on the coast of Madagascar in 2009 and passed over Kirindy Mitea National Park. A mortality rate of 8.8% for trees was measured after the event, with over 95% of trees experiencing some sort of damage (Lewis and Bannar-Martin 2011).

Dr Rebecca Lewis (Assistant Professor, The University of Texas at Austin) originally founded the research station at Kirindy Mitea National Park, in 2005. The site employs four local people on a permanent basis: a camp manager, two cooks who also serve as security and work on a two week shift pattern, and a research assistant who collects data for the continuing research of Dr Rebecca Lewis. The research area is around 1km from the camp, and is a 1km^2 area of forest divided into a grid system. Trails run every 25 metres North-South and East-West, North-South trails are numbered, whilst trails running East-West are labelled with letters. A numbering system allows one to navigate in and out of the forest very easily and also gives you every opportunity to follow your target species for a full day without losing the group.

Kirindy Mitea National Park, unlike many of the more popular research stations in Madagascar, is currently very under-developed. The lack of a road to the research camp, means that during the rainy season it is necessary to get a boat to the nearest coastal village (Belo-sur-Mer) followed by a 35km walk into the forest. When moving large amounts of equipment into the forest it is possible to hire carts pulled by oxen. During the dry season, the low river levels make the journey passable with a 4x4, although this journey can often involve an overnight stay if mechanical repairs on the vehicle are needed. Once at the research station, accommodation is in tents and there is no mobile telephone connection or Internet. All electricity is provided by two 125-watt solar panels, which are connected to a car battery. Battery power provides enough power to charge lap top batteries and allow data entry of observations from the day's follows. The biggest limitation of the research station is the lack of water. As there are no rivers in the forest and the subterranean water stores are too deep for a well, all water is delivered and stored in the camp on a weekly basis. Oxen deliver 250 liters of water per week from the local village of Antsira, which has to be shared among the staff in the camp at that time.

Thesis Aims and Objectives

This thesis aims to investigate how sifakas and especially *P. verreauxi* locomote in a forest environment and what strategies they use to survive a highly seasonal environment. To achieve this it has four objectives:

1) To investigate what modes of locomotion sifakas use to navigate around the forest environment.

2) To investigate home range size, daily path lengths and activity patterns of *P. verreauxi* in Kirindy Mitea National Park.
3) To investigate the role, if any, that seasonality has on locomotion, ranging and activity.
4) To use the novel method of accelerometry to investigate remote monitoring of locomotion.

To achieve these objectives I carried out three different studies. These studies were carried out in a field season in Kirindy Mitea National Park and also a study of captive lemurs in the Cottswolds Wildlife Park. These are described in the following three chapters of this thesis.

Chapter 2

The Locomotor Ecology of *Propithecus verreauxi* in the Kirindy Mitea National Park

Introduction

Locomotion provides the means for animals to interact with their environment, and is the mechanism for much essential behaviour, such as feeding, locating a mate and predator avoidance. Making the study and understanding of how animals locomote and interact with their environment essential to understanding the ecology of a given species. Strepsirrhine primates, which show such a broad repertoire of locomotor modes, although they are generally recognised as vertical clingers and leapers (Napier and Walker 1967). Of the twenty two genera of strepsirrhines primates, only four are categorised as non-leaping (Crompton, Sellers et al. 2007). The indriid family in particular, are known to achieve huge distances when performing spectacular saltatory displays (Blanchard 2007).

Locomotor studies of wild strepsirrhines have tended to concentrate on the smaller-bodied nocturnal species, such as the galagos and tarsiers (Alexander 1995; Crompton 1983; Crompton 1980; Crompton and Andau 1986; Crompton and Andau 1987; Crompton et al. 2010; Nash 1998; Warren and Crompton 1997a; Warren and Crompton 1997b,). Whilst many of the initial studies of locomotion in large-bodied strepsirrhines were performed in a captive environment (Gebo 1987; Tilden 1990). More recently, an increasing body of data is now being collected in the wild concerning the locomotor habits of large bodied indriids (Blanchard 2007; Demes et al. 1999; Demes et al. 1996). Captive data has so far shown large discrepancies with the limited amount of wild data present in the literature for large-bodied leaping strepsirrhines (Gebo 1987; Dagosto 1989). Contrasts between studies of the same species in the wild and in captivity, may relate in part to the inevitable impoverishment of the captive environment in comparison to the natural environment (Crompton 1980). Bias such as this demonstrate the need for an increase in locomotor studies of wild diurnal strepsirrhines in order to better understand their locomotor habits and habitat usage.

Wild locomotor studies of strepsirrhine primates can also yield very variable results, which can, and have been accredited to differences in data-collection protocols (Crompton et al. 2010). Altman, (1974), was the first to describe a set of sampling methods, and defined two major sampling techniques, scan sampling and focal sampling. Focal sampling relies on an individual collecting data from the same subject for the duration of the sampling period. Scan sampling, on the other hand, allows the observer to collect data from an entire group of individuals over the study period. Disparity in data collections such as the aforementioned, can often lead to sets of results being incomparable. Other factors which can affect the comparability of data are that some studies only collect data on a very small set of locomotor categories (Dagosto 1995), usually when testing very specific hypotheses; whereas others increase the number of categories when investigating a broader set of questions (Blanchard 2007; Warren and Crompton 1997b). These methodological contrasts can often lead to sets of results being incomparable. These discrepancies have led to the need for the creation of a standard protocol, to allow more accurate cross-species inferences to be made.

Napier and Walker (1967) were among the first to attempt to categorise the different movement patterns recruited by primates. They defined four principal locomotor categories: vertical clinging and leaping (into which fall 18 of the 22 strepsirrhine genera), quadrupedalism, brachiation and bipedalism. *P. verreauxi* unquestionably falls into the first of the four categories. It is a medium-sized diurnal indriid (considerably larger than *Avahi*, but considerably smaller than *Indri* or *P. diadema*) inhabiting the Southern and Western dry deciduous forests and spiny forests of Madagascar. While other mammals, such as sciurids, may engage in frequent leaping to negotiate the discontinuities of arboreal habitats, strepsirrhines achieve both the greatest absolute leap lengths and the greatest lengths and height gains in relation to body size (see eg. (Gunther, Ishida et al. 1991)). While strepsirrhines may cover as much as (or more than) 882m of every kilometer travelled by leaping (Crompton 1983), leaping is actually a relatively slow method of movement compared to running (Gunther, Ishida et al. 1991), and so other reasons than speed need to be adduced to explain the choice of this mode of locomotion. Just as Cant (1992) observed that no single general problem is solved by locomotor behavior, leaping may serve different ends in different species. Body size may again be a factor; for smaller strepsirrhines the main advantage of leaping may be predator avoidance or predation, and basic mechanics suggests that for larger strepsirrhines energy may, on balance, be saved by a leap, despite its high costs, if height change can thereby be avoided (Crompton, Sellers et al. 2007; Blanchard and Crompton 2011). Morphological specialisations for leaping may also prove to differ according to size; larger strepsirrhine leapers tend to use elongated femora to accelerate their centre of mass, whereas smaller ones tend to use an elongated calcaneus and navicular (see eg. (Connour et al. 2000; Demes et al. 1996), but such body size distinctions cannot be necessarily assumed to cross-cut differences of phylogenetic origin.

Within the 'vertical clinging and leaping' category of Napier and Walker (1967) leapers are distinguished with different levels of specialisation (Crompton, Sellers et al. 1993) and by behavioural style (Oxnard and Crompton 1990). These further classified styles are: static leaping, where an animal jumps from standstill; running leaping, in which an animal ends a phase of movement with a jump; and ricochetal leaping, which is the linking together of several leaps in succession. Alexander (1995) refines this behavioural distinction by distinguishing leaps according to the mechanism used to generate the power required for the leap. These mechanisms are squat leaping, where the power for the leap is attained from muscle contraction; catapult leaping, which utilises a locking mechanism to allow the slow accumulation of muscle tension; countermovement leaping, in which a store of elastic energy from a previous movement is attained; and vaulting leaping, where a secondary structure is used to alter the direction of a leap. However, although these extended classifications are more precise than earlier groupings, they are difficult to record in a field environment other than by videography, and so their relative frequencies remain relatively unexplored.

Seasonal variation in locomotion has been reported for bushbabies *Galago moholi*, *Otolemur crassicaudatus* (Crompton 1983) and on Madagascar for *Lepilemur* (c. 750 g) (Nash 1998). These were carried out under more marked conditions of seasonality than would commonly be expected of rainforest environments, where most studies of seasonal variation of locomotion in large bodied strepsirrhines have been carried out (Dagosto 1995; Dagosto and Yamashita 1998). Kirindy Mitea National Park is a deciduous forest, displaying marked seasonality, defined by a long dry season when resources are scarce. A locomotor study of this sort will determine if *P.verreauxi* adapts its locomotor repertoire to cope with such extreme conditions. Seasonal variation, in affecting rainfall, temperature and day length thus exerts an effect on the abundance and distribution of food resources (Crompton 1983; Nash 1998) and exerts greater effects on large-bodied animals (Dirzo, Young et al. 2011; Stoner and Timm 2011). Seasonal dormancy is likely not an option for indriids, as it is for cheirogaleids, in Madagascan seasonally dry tropical forests such as the Kirindy Mitea National Park. Hence study of how locomotion is affected by seasonal shifts in temperature, rainfall, food availability and hours of daylight is essential in understanding why large primates in particular use certain locomotor modes, how often they use them and in which contexts.

Methods

Data collection occurred between the months of May 2010 and January 2011 in Kirindy Mitea National Park (henceforth KMNP) located in western Madagascar (S20°47.9177’, E044°10.0771’). The study area, established by Rebecca Lewis, lies within one of the largest continuous tracts of remaining dry deciduous forest in Madagascar, covering 101,031ha (Whitehurst, Sexton et al. 2009). There is a markedly dichotomous seasonality characterised by a hot rainy season between the months of December and March and a cooler dry season between April and November (Lewis and Kappeler 2005; Rasoazanabary 2006). Access to the site is possible by car from Morondava during the dry season, but during the rainy season it is necessary to take a boat to Belo sur Mer. It is access to fresh water which is the greatest constraint on work, electricity being generated at the site using solar panels.

The research area consists of a 1km^2 grid system, with trails every 25m from East to West and North to South. Eight groups of sifaka (*P. verreauxi,*) were habituated within the grid system by Lewis in 2005 and continue to be regularly radio tagged and followed by Lewis and co-workers. The structure of these groups at the time of study is given in Table 3.

Table 3 *P.verreauxi* group composition at KMNP

Group Number	Number of Females	Number of Males	Number of Adolescent/Uncaptured
1	2	3	1
2	3	2	0
3	2	2	0
4	6	2	0
5	2	1	0
6	2	2	0
7	1	1	1
8	1	1	4

Two groups of sifaka (*P. verreauxi*) were studied in KMNP over an eight-month period: one containing five individuals, the other seven. Groups 3 and 4 were chosen because their entire home range fell within the grid system. These groups were also well habituated and were followed on a regular basis by the full time staff present at Kirindy Mitea National Park, this prevented the data being biased normally associated with poorly habituated study animals. Dominant females within the group were darted and fitted with brass radio collars (model number TW3SM, Biotrack, Dorset, UK). They were chosen as the least likely candidates to emigrate from the group (Lewis pers. comm.). SIKA radio-tracking receivers (150–153.99MHz) combined with Yagi flexible element antennas (Biotrack, Dorset, UK) were used to locate groups. The day's chosen group was followed continuously from initial contact until locomotion ceased and all individuals had begun to rest. Each group was followed for two days in succession and on the third day the data were collated and transcribed. Both groups were followed for a minimum of two days each per month. A total of 41 days were sampled and 9,192 locomotor bouts were recorded for the two groups: 4,795 bouts for group 3 and 4,397 bouts for group 4.

Many different sampling methods have been described (Altmann 1974) and sampling strategy can have an effect on the results produced. Focal sampling, where an individual subject is followed, is often used, but produces small amounts of data. Scan or *ad libitum* sampling has been shown to produce similar results to focal sampling, but yields much larger quantities of data (Fragaszy, Boinski et al. 1992). Continuous scan sampling methods were therefore employed, where any bouts of locomotion from any individual within the group that are observed are recorded. As defined, e.g. in Blanchard and Crompton (2011), a bout is any occurrence of locomotion in a given mode which has an obvious beginning or an end, or can be separated by a clear delay from others. When recording a single bout, the following pieces of information were recorded following Crompton's (1983) standard protocol as modified by Blanchard and Crompton (2011): date, time, locomotor mode, initial support diameter, initial support orientation, terminal support diameter, terminal support orientation, initial height, terminal height and activity. Distance travelled in any mode, initial and terminal heights and orientation were estimated by eye. To ensure collected diameters, heights, orientations and distances were as accurate as possible, initial practice sessions were carried out in which estimations were made and measurements of distances; heights, diameters and orientations taken of the same occurrence and the two were compared. Date and time were recorded so that seasonal differences in locomotion could be investigated. Data were collected in a freeform manner using normal notebooks in the dry season and "Rite in the Rain" all-weather journals during the rainy season. Freeform data collection can also be referred to as typical field notes (Altmann 1974), where the researcher collects as much data as possible from a group of animals. It is currently the most suitable method of sampling for the quantitative analysis of behaviour: allowing comparisons to be made between different classes of behaviour, and also, between groups and seasons.

Locomotor mode was broken down into ten categories modified from Blanchard and Crompton (2011):

- Leaping – a saltatory movement in which the hindlimbs are used to propel the animal into the air which allows it to cross a gap.
- Vertical climbing – locomotion upwards or downwards on a vertical or strongly inclined support, utilising both forelimbs and hindlimbs.
- Quadrupedal walking – locomotion above a horizontal, or oblique support or on the ground using all four limbs in a diagonal sequence gait.
- Quadrupedal running – as quadrupedal walking but involves a galloping gait.
- Bipedal walking – locomotion utilising only the hindlimbs to bear body weight along a horizontal or oblique support.
- Bipedal running – as bipedal walking but involving an aerial phase.
- Hopping - both bipedal hopping along a horizontal or oblique support where only the hindlimbs are involved in take-off and landing, and also hopping where the hindlimbs are involved in the take-off phase but all four limbs contribute to the landing phase (normally observed on vertical or angled terminal support.

- Two limb suspension – movement beneath a horizontal or oblique support using only the forelimbs.
- Four limb suspension – moving beneath a horizontal or oblique support using all four limbs.
- Foliage Crossing – including cantilevering where a pair of limbs are used to grasp an initial support, whilst reaching across a gap to grasp the terminal support utilising the other pair of limbs, as well as other free-form, non-aerial phase methods of crossing discontinuities in the substrate.

Support diameters were categorised as tiny (less than 0.5cm), small (0.6 – 5cm), medium (5.1 – 10cm), large (10.1 – 15cm) and enormous (15.1cm and above). Support orientations as: horizontal (0 - 10˚), oblique (11 - 45˚), angled (46 - 80˚) and vertical (81 - 90˚). The activity data were broken down into bouts of locomotion that resulted in: rest (a period of inactivity), feed (including actual feeding and any foraging behaviour), travel (any bout of locomotion that resulted in another bout of locomotion) and other (which included behaviours such as grooming and mating) (following (Blanchard and Crompton 2011)). Activity data were collected for every bout of locomotion performed, i.e. what activity did the subject perform after each bout of locomotion. Not be confused with an overall activity budget, and is used to quantify what activities *P.verreauxi* locomotes to perform. Due to the large amount of information collected per bout of locomotion, a coded form of data collection was employed (Figure 11). Therefore increasing the rate of data collection, as it made recording the data a much quicker process.

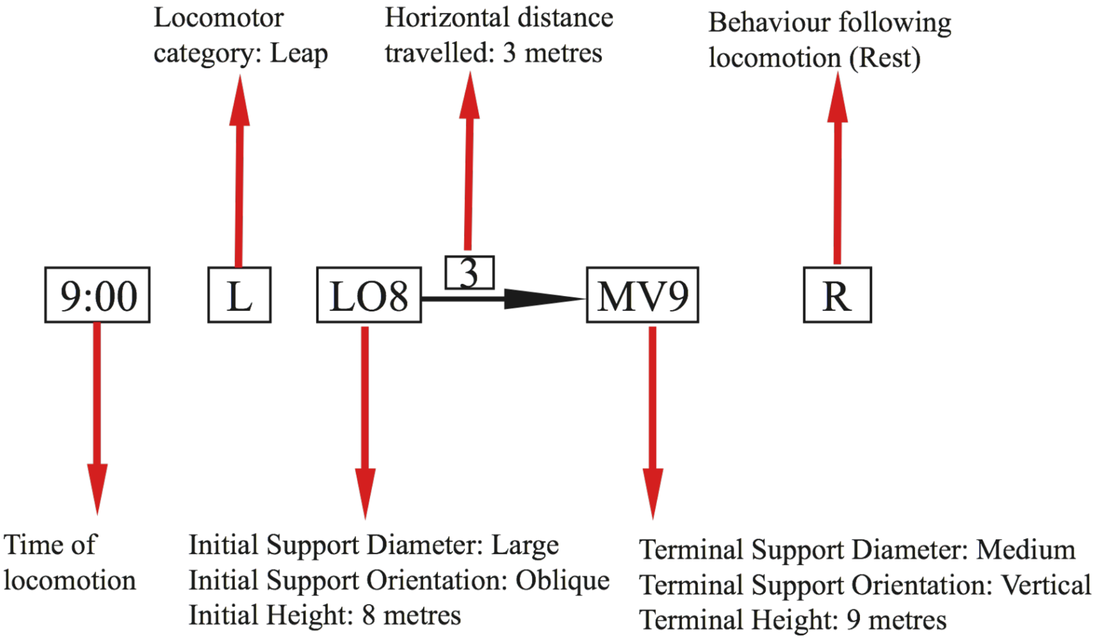


Figure 11 An example line of the coded data collection method demonstrating how ten pieces of information can be gathered in the shortest period of time.

All field notes were transcribed into excel whilst in Madagascar and all data analysis was performed in SPSS 19 for Mac. Associations between non-parametric, categorical data groups were tested using Pearson Chi-Square (χ^2). The non-parametric Mann-Whitney test (U) was used to test differences in median heights between different variables. Significance values reported here are all two-tailed. Effective distance travelled was calculated in order to estimate the distance travelled per kilometer by each mode of locomotion described above. It would have been biased to have used only the horizontal distance travelled, as this figure does not take into account the height changes an animal may make in a three dimensional environment. Therefore horizontal distance travelled and height change (initial height of observation minus terminal height of observation) for every bout were used to calculate effective distance travelled with Pythagoras theorum.

To allow an examination of possible seasonal effects, dates from 24 May to 18 October 2010 where grouped as the ‘dry’ season and dates from 16 November 2010 to 27 January 2011 grouped as the ‘rainy’ season. Separating out all behavioural observations by group membership tested any within species group wise differences. Testing differences between sex, age and individuals was impossible due to a lack of sexual dimorphism shown by *P.verreauxi* or any distinguishing features that would allow rapid individual indentification. The results presented here are separated into three distinct sections. The first section deals with the data as a whole, not using any grouping variables to divide the data. Secondly, group membership is used as a grouping variable to investigate any within species variation. Lastly, seasonality is examined in order to quantify the impact this has on locomotion.

Results

Overall Results

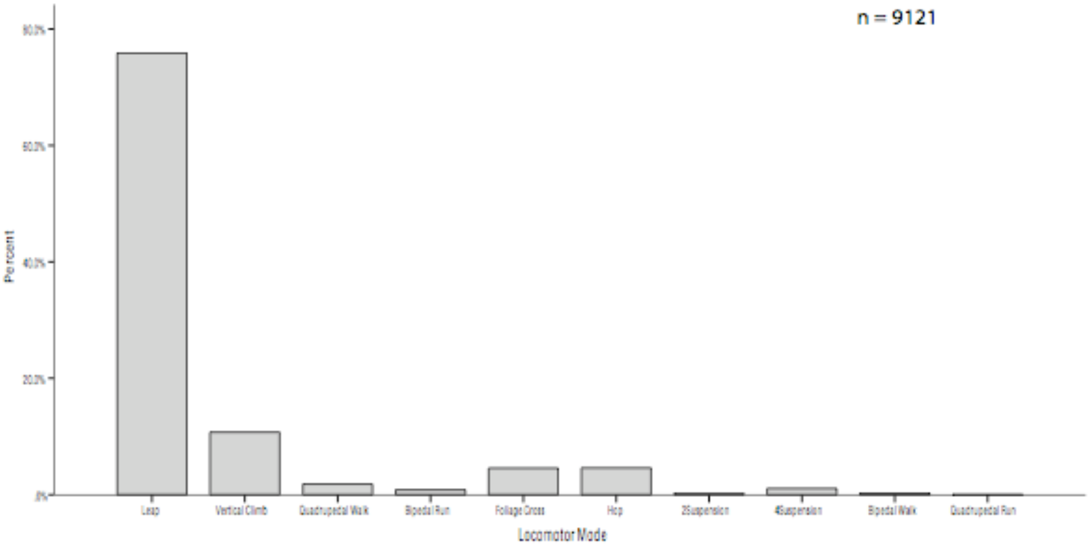


Figure 12 Frequency percentages of locomotor bouts for both groups over the entire study period, showing *P.verreauxi* uses leaping as a mode of locomotion in 76% of all locomotor bouts.

Clearly the most prevalent mode of locomotion utilised was leaping which accounted for 76% of all locomotor bouts (Figure 12), much more than the frequencies of all of the other locomotor categories combined. The next three most commonly observed modes of locomotion were vertical climbing (11%), hopping and cantilevering (both 5%)(Figure 12). All other modes of locomotion (2suspension, 4suspension, quadrupedal walking, quadrupedal running, bipedal walking and bipedal running) combined only accounted for the remaining 3% of locomotor bouts. Of these less commonly observed forms of locomotion, the least popular by far was quadrupedal running, with only one recorded bout out of a total of 9,192 observations. Also noted, all observed bouts of bipedal running (78 in total) were terrestrial.

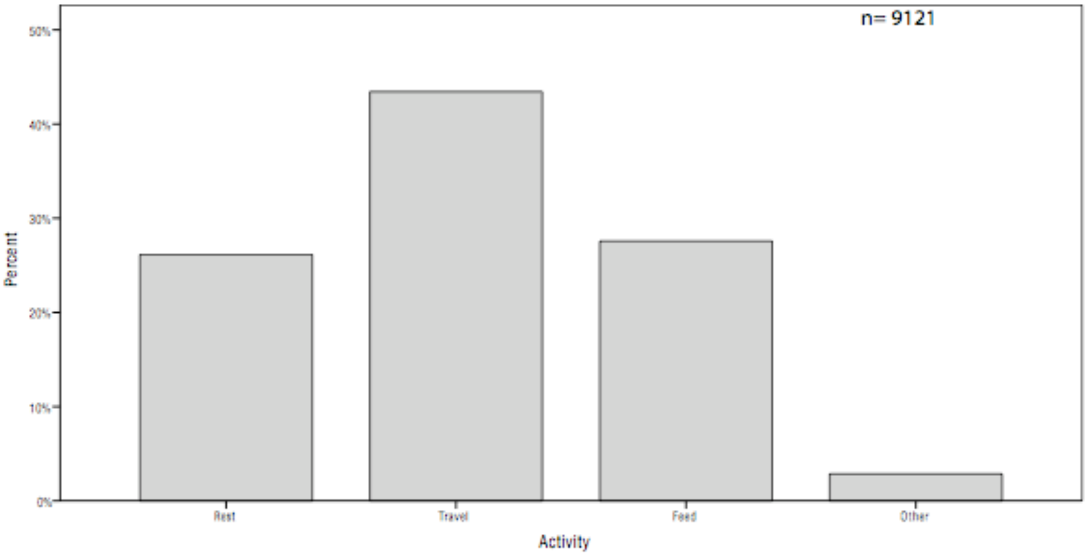


Figure 13 Frequency percentages for activity following locomotion for both groups over the entire study period, showing that 43% of all locomotor bouts resulted in travel behaviour.

Travelling was the most commonly observed activity for both groups over the entire study period and accounted for 43% of all locomotor bouts (Figure 13). The categories of resting and feeding were the next most prevalent activities accounting for 26% and 28% of activities respectively. The ‘other’ category, which included behaviours such as grooming, only contributed to 3% (Figure 13).

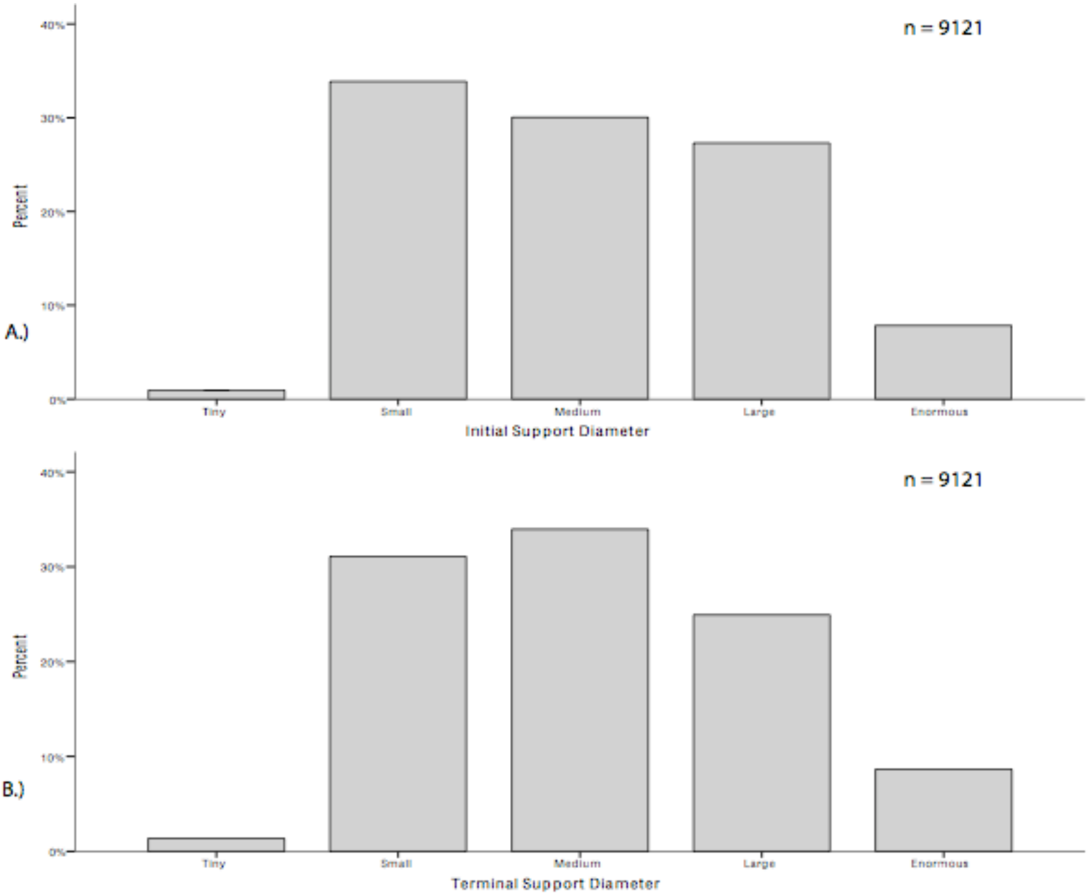


Figure 14 Initial (A) and Terminal (B) Support Diameter frequencies for both groups over the entire study period showing a preference by *P.verreauxi* for the supports in the mid-range categories of small, medium and large.

From the data collected there is a clear preference for supports within the mid-range categories for diameter. Proving the case for both initial and terminal supports. Small, medium and large supports accounted for 91% of all of the initial supports utilised by the sifaka during the 11-month study. The same calculation for terminal support diameter displays that 90% of all terminal supports used were in the small, medium or large categories (Figure 14). When considering if there is any difference between support diameter selection between initial and terminal supports, there is a significant difference between initial and terminal support diameter choice (χ^2 = 53.362, p = 0.000). There is a slight preference for small supports as the initial support, but this preference shifts to a slight preference for slightly larger, medium sized supports when considering terminal support usage.

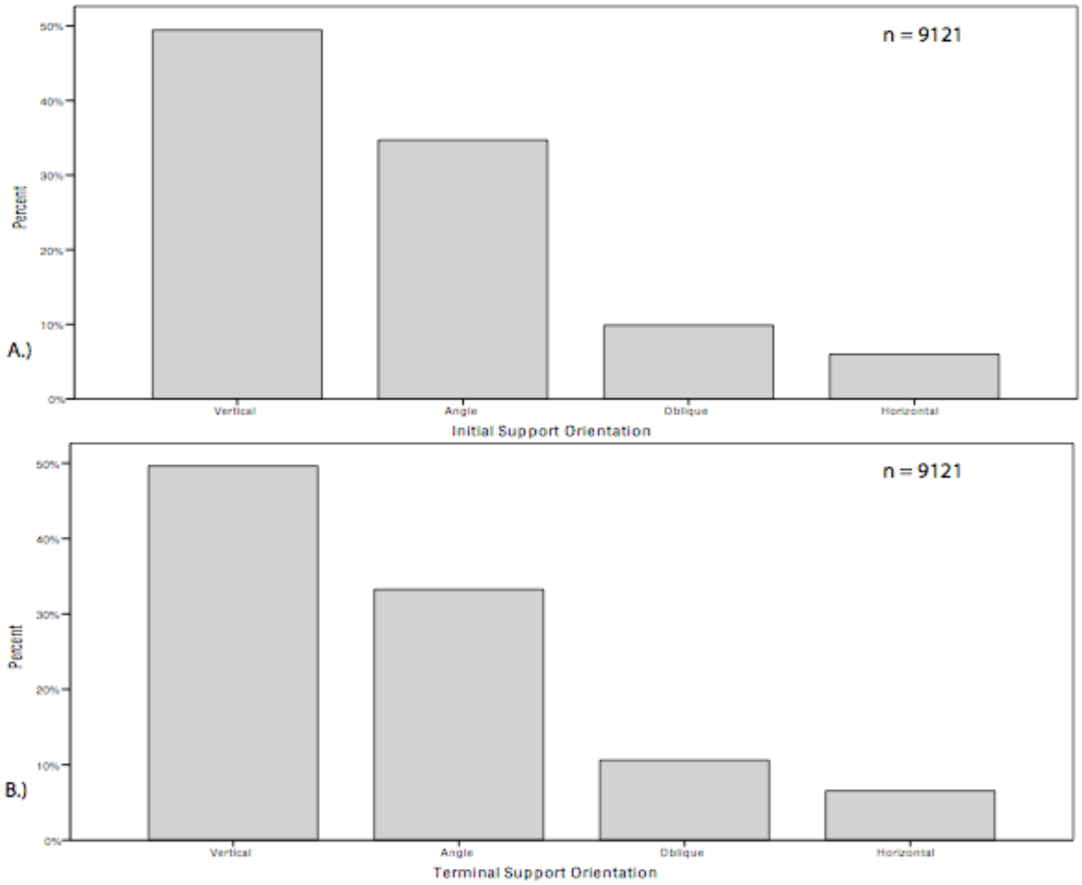


Figure 15 Initial (A) and terminal (B) support orientation frequencies for both groups over the entire study period with *P.verreauxi* showing a preference for supports in the vertical and angled categories.

When investigating support orientation preferences in *P.verreauxi* it is very clear that they favour more upright supports (vertical and angled categories) when locomoting (Figure 15). Vertical and angled supports account for 84% of all initial supports used for both groups over the entire study period, with 49% of initial supports used being vertical in orientation. In contrast to support diameter, the terminal support diameter choices very much mirror that of initial support diameter choices, with 83% of all supports utilised being made up of vertical or angled supports and 50% of those being vertical in orientation. The result of a chi-square analysis showed that any difference between initial and terminal support orientation choices were purely down to chance ($\chi^2 = 7.634$, $p = 0.054$).

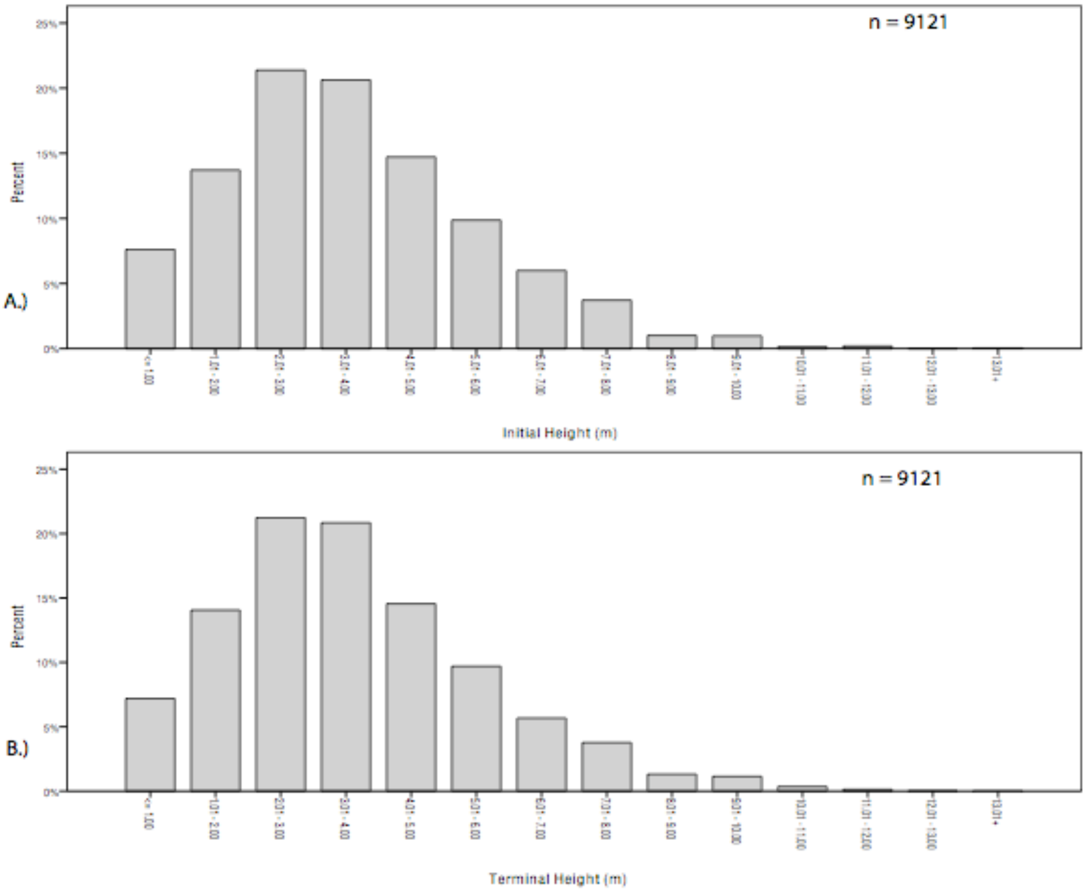


Figure 16 Frequency percentages of observed heights for both initial (A) and terminal (B) supports for both groups over the entire study period, with the mean initial and terminal heights observed being four metres.

The mean initial height recorded for both groups over the entire study period was four metres and the mean terminal height observed was four metres. The maximum height both groups were observed at was 14 metres and the minimum height they were recorded locomoting at was ground level (Figure 16). The vast majority of locomotion occurred between ground level and eight metres in height (Figure 16), and this is the case for both initial and terminal heights. The majority of locomotor bouts that took place above this range did so when entering or leaving a resting tree at the beginning or end of the activity period.

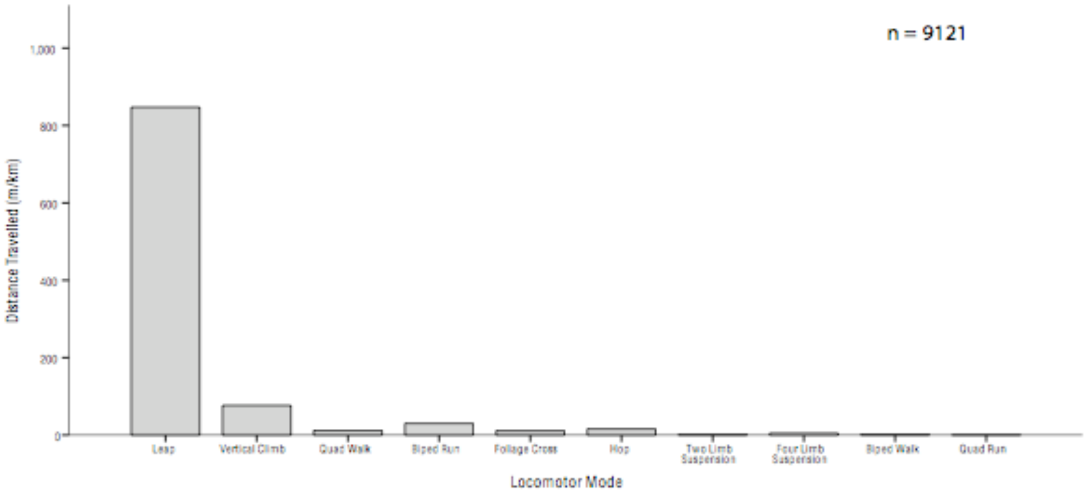


Figure 17 Distance travelled in metres per kilometer for each mode of locomotion, for both groups, over the entire study period showing that the majority of distance travelled per kilometre was done use using leaping as a means of locomotion.

Leaping again clearly accounted for the largest amount of distance travelled per kilometre, with 847m/km of travel using this mode of locomotion (Figure 17). Vertical climbing accounted for 77m/km and was the second highest contributor to distance travelled, but still accounted for a vast amount less than leaping. The less preferred means of locomotion which accounted for very small amounts of distance covered (<5m/km) were two limb suspension (1m/km), four limb suspension (5m/km), bipedal walking (1m/km) and quadrupedal running (0.2m/km)(Figure 17).

Intergroup Results

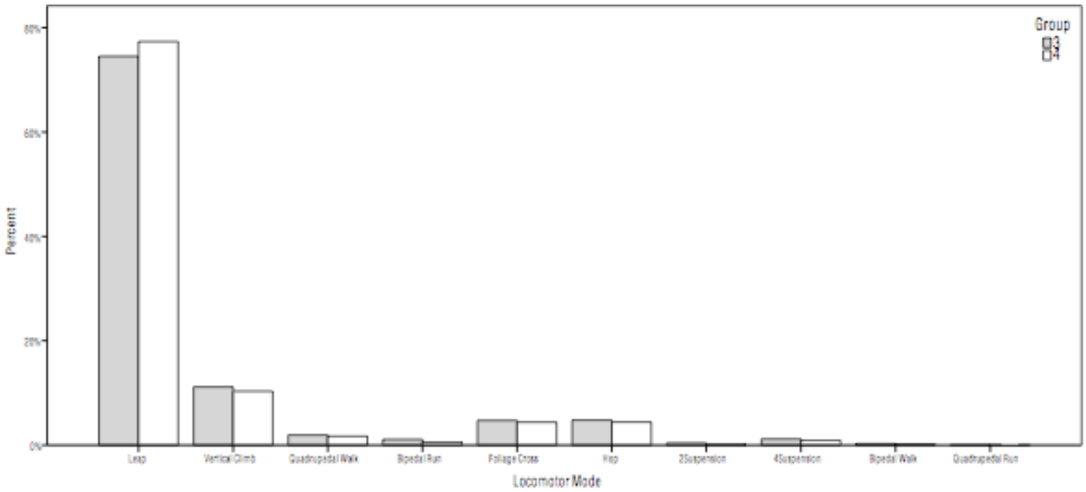


Figure 18 Frequency percentages for locomotor mode separated by group showing both groups move predominately using leaping as a mode of locomotion (group 3, n = 4795 and group 4, n = 4397).

When considering if there are any differences in locomotion between the two study groups (Figure 18), leaping is still far and away the most popular mode (accounting for 75% for group 3 and 77% for group 4). The small decrease in leaping frequency for group 3 means that in all of the nine other categories group 3 has a larger frequency than group 4. The results of a Pearson chi-square (χ^2 = 23.388, p = .008) show that there is a small but significant difference between the ways that the two groups studied locomote.

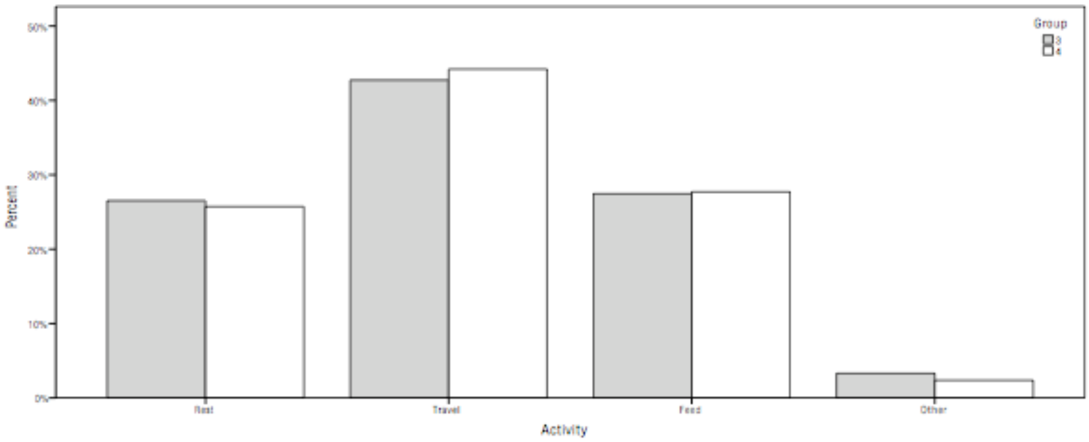


Figure 19 Frequency percentages for the activities following locomotion separated by group showing that both groups mainly locomote as a means of travel (group 3, n = 4795 and group 4, n = 4397).

When looking at any differences observed in activity between the groups (Figure 19) there appears to be very little changes in activity patterns between the two groups, but a Pearson chi square test calculated a small but significant difference between activity in the two groups (χ^2 = 8.738, p = 0.033). There is a slight increase in travelling frequency in group four (44%) compared to group three (43%). Whereas frequencies of resting and other were higher in group three (27% and 3% respectively) than group four (26% and 2% respectively).

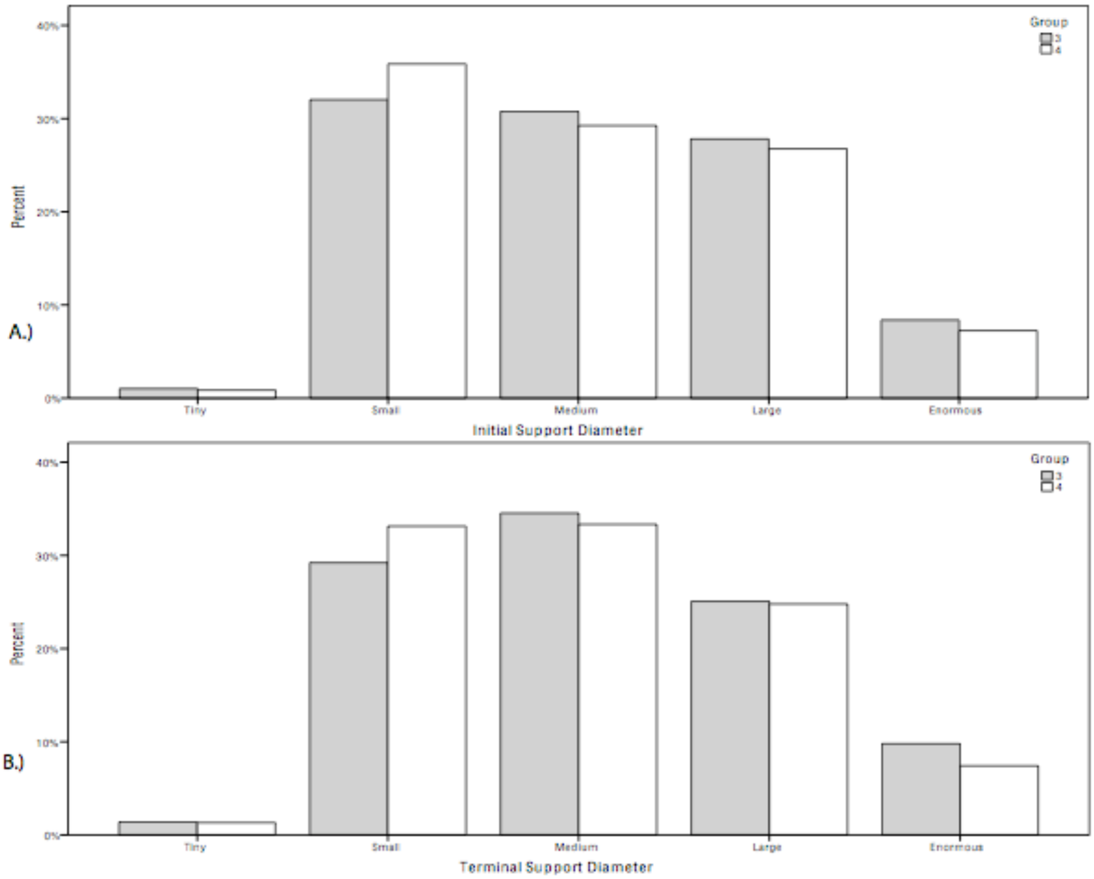


Figure 20 Initial (A) and terminal (B) support diameter frequencies separated by group showing both groups locomote predominately utilising the mid-range diameter categories of small, medium and large (group 3, n = 4795 and group 4, n = 4397).

Looking into any variation between the two groups in regard to support diameter, there are small but significant differences between the groups in both initial and terminal support diameter choices (Figure 20). A Pearson chi-squared value of 16.918 and an asymptotic significance of 0.002 shows a significant difference between the two groups with regard to initial support diameter. Group three utilised small supports 32% of the time, whereas group four showed a slight increase in the same category, using small initial supports in 36% of locomotor bouts. Enormous support use in initial support diameter conversely displayed that members of group three more regularly locomoted using enormous supports (8% of bouts) than members of group four (7% of bouts). When terminal support diameter is considered, much the same pattern arises, with small but significant differences between the two groups ($\chi^2 = 27.322$, $p = 0.000$). Again group four's usage of small terminal supports shows a slight increase on that of group three (33% versus 29%). Similarly enormous support usage is higher in group three (10%) than in group four (7%).

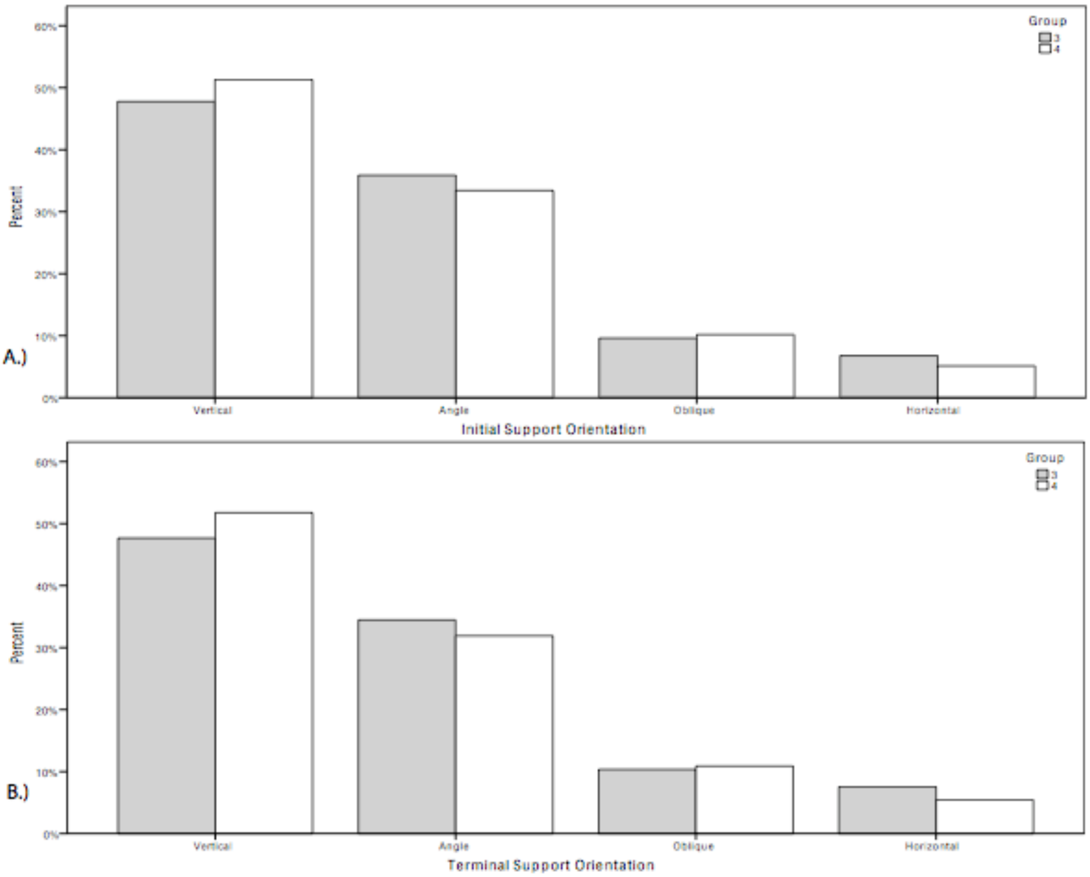


Figure 21 Initial (A) and terminal (B) support orientation frequencies separated by group showing both groups preferred to locomote using more upright supports (group 3, n = 4795 and group 4, n = 4397).

When look at inter-group choices regarding support orientation, there are some small but significant differences (χ^2 = 21.185, p = 0.000) in initial support orientations. These differences are demonstrated by a higher level of angled and horizontal initial support orientation usage in group three (36% and 7% respectively) compared to group four (33% and 5% respectively)(Figure 21). Whereas, the converse situation is true for vertical and oblique support usage. Group four utilised vertical (group four = 51% versus group three = 48%) and oblique supports (group four = 10% versus group three = 10%) more often than group three (Figure 21). A very similar pattern is observed with terminal support orientation usage. Vertical and angled supports combined account for the overwhelming majority of supports used (82% in group three and 84% in group four)(Figure 21). Although a small but significant difference in support orientation was discovered using a chi-square test (χ^2 = 28.190, p = 0.000). Again, with group three showing higher levels of angled and horizontal support orientation usage. While group four had higher levels of vertical and oblique support usage (Figure 21).

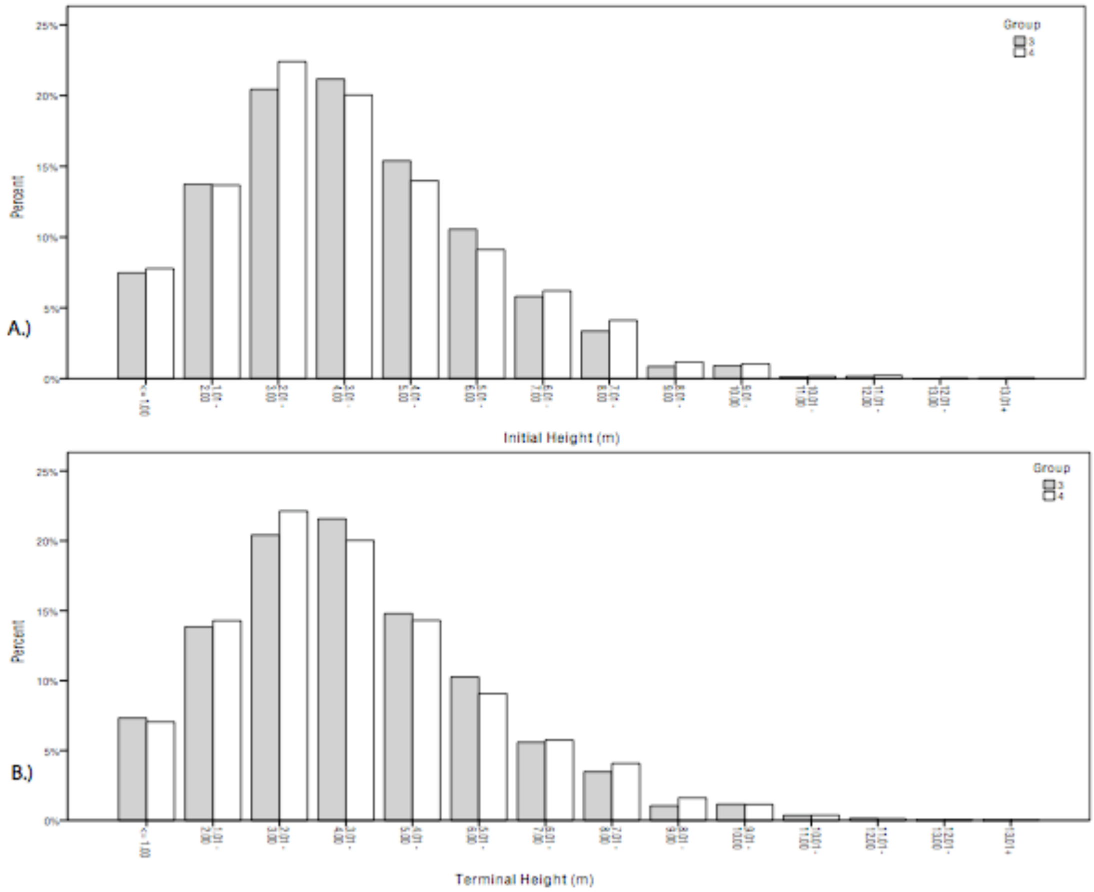


Figure 22 Frequency percentages of initial (A) and terminal (B) height based on group membership showing that both groups used similar heights to locomote within the canopy (group 3, n = 4795 and group 4, n = 4397).

The vast majority of all locomotion took place between ground level and a height of eight metres. Of the initial supports used, 97% were between ground level and eight metres for both group three and four. Whilst terminal height usage occurred between the same distribution of heights 97% of the time for group three, and 96% of the time for group four. No significant difference was found between the two groups in relation to initial height (Mann-Whitney U = 10474893.5; P= 0.595) and there was only a small difference in mean initial height (group three = 4.02m and group four = 4.04m)(Figure 22). When terminal height was investigated, again, no significant differences were found between the two groups (Mann-Whitney U= 10523653; P=

0.885) and again, only a small difference of 0.02m was found between mean terminal height (group three = 4.02m and group four = 4.04m).

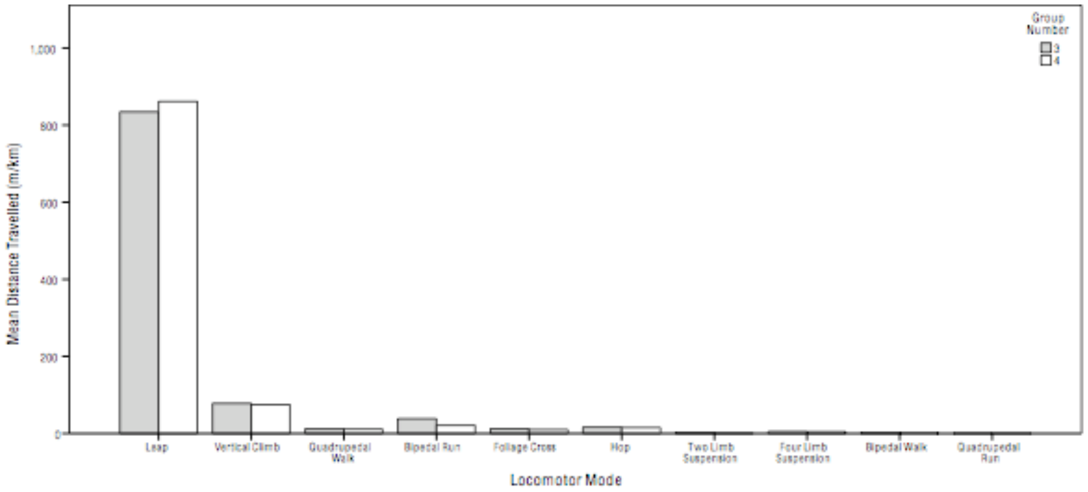


Figure 23 Distance Travelled in metres per kilometer for each mode of locomotion, separated by group. Shwong that both groups use leaping to travel the majority of the distance per kilometre travelled (group 3, n = 4795 and group 4, n = 4397).

When looking at how group membership affected the distances travelled by each mode of locomotion, leaping was clearly the preferred mode of locomotion and accounted for 834 m/km and 861 m/km for group 3 and 4 respectively (Figure 23). Vertical climbing accounted for 78 m/km for group 3 and 75m/km for group 4, making this the mode of locomotion that accounts for the second largest distance covered per kilometer. The least favoured modes of locomotion in terms of distance travelled were: Quadrupedal running (0.3m/km for group 3 and 0.0m/km for group 4), two limb suspension (2m/km for group 3 and 1m/km for group 4), and bipedal walking (2m/km for group 3 and 1m/km for group 4) (Figure 23).

Seasonal Results

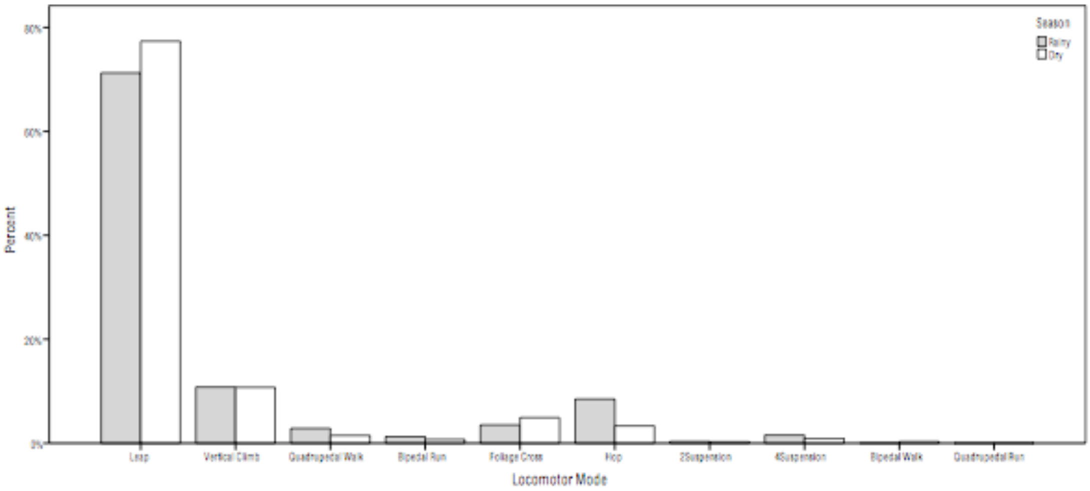


Figure 24 Frequency percentages for locomotor mode separated by season showing the changes in locomotor frequencies during the rainy and dry seasons (dry season, n = 6941 and rainy season, n = 2251).

Figure 24 shows the differences in locomotion when seasonality is explored, comparing locomotion in rainy and dry seasons. Once again leaping is clearly the preferred mode, but there is a decrease in leaping frequency during the rainy season (77% during the dry season versus 71% during the rainy season). Another mode that displays a decrease in frequency during the rainy season is the cantilever (5% during the dry season versus 4% during the rainy season). Hopping shows the reverse effect, more than doubling in frequency during the rainy season from 3% during the dry season increasing to 8% during the rainy season. The other regularly utilised mode is vertical climbing which only shows a very modest increase during the rainy season (11% during the dry season versus 10% during the rainy season). The results of a Pearson chi-square show a significant difference in locomotor modes between the seasons (χ^2 = 149.795, p = 0.000).

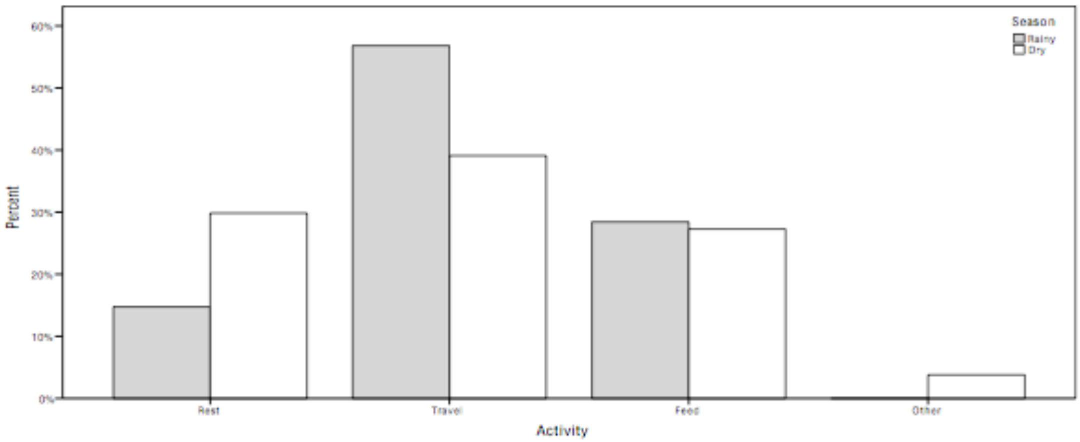


Figure 25 Frequency percentages for the activity performed following locomotion separated by season showing the differences in activity during the dry and rainy seasons (dry season, n = 6941 and rainy season, n = 2251).

Much larger differences were found when activity was separated into seasons. When a chi-square test was performed to see if there were any differences in activity between the rainy and dry seasons, a Pearson chi-square value of 356.634 with an asymptotic significance of 0.000, showing significant differences in activity when seasonality is explored. From Figure 25 it is clear that the main difference in activity between seasons in a sharp increase in the amount of bouts, which resulted in travel during the rainy season (57% during the rainy season, compared to 39% during the dry season). Whereas in the dry season locomotor bouts more regularly resulted in rest activity (30%) than during the rainy season (15%). Feeding activity resulted in much less dramatic changes, with slightly increased feeding frequencies in the rainy season (28%) which only dropped by 1% during the dry season.

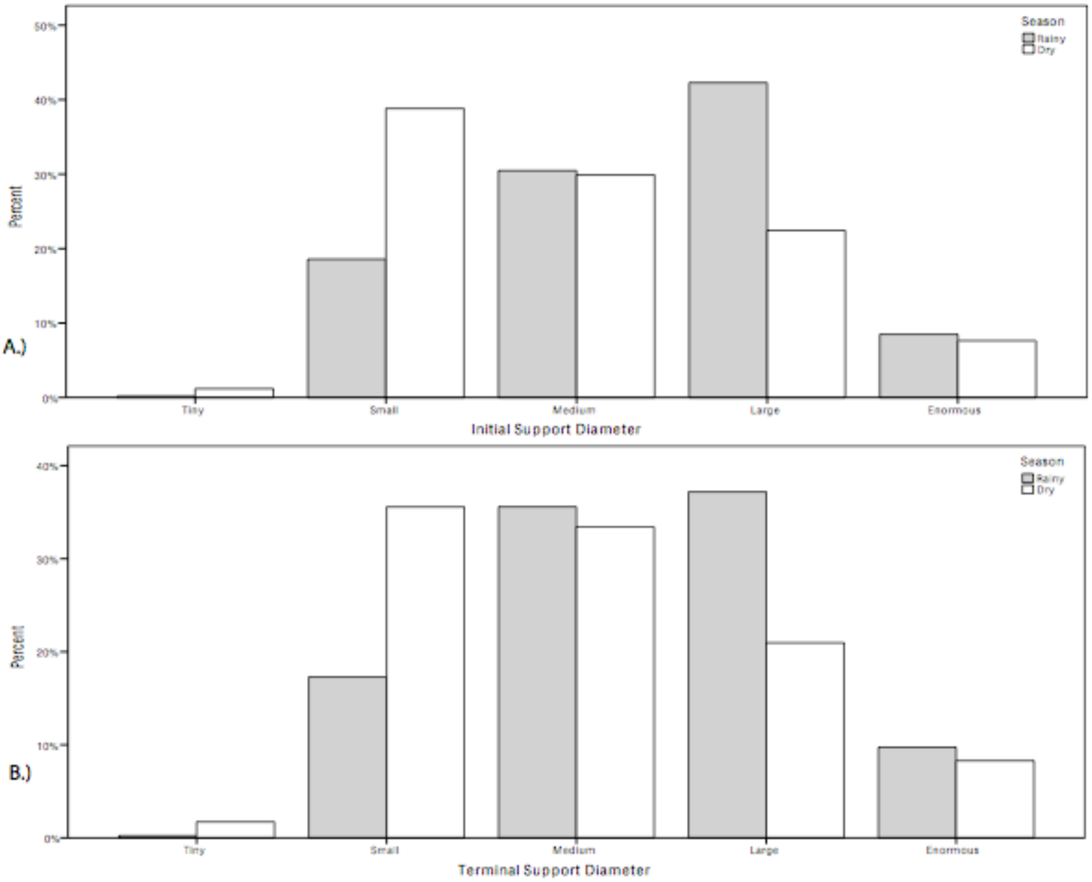


Figure 26 Initial (A) and terminal (B) support diameter frequencies separated by season showing support diameter frequencies for *P.verreauxi* during the dry and rainy seasons (dry season, n = 6941 and rainy season, n = 2251).

The differences within initial and terminal support diameter categories are much more pronounced when they are separated into seasonal categories. A clear increase in preference for larger supports in the rainy season (excluding the enormous category) and smaller supports in the dry season (again, excluding the extreme, tiny category) is demonstrated (Figure 26). A chi-square test demonstrated a significant difference between the seasons with regard to initial support diameter (χ^2 = 471.508 p = 0.000). During the try season the percentage frequency of small initial support diameter was 39%, compared to the rainy season frequency of 19%. With regard to large initial supports, the converse is true, with a frequency of 22% in the dry season, compared with 42% during the rainy season. Again, a similar trend is seen in the terminal support diameter categories, with a preference for smaller supports during the dry season (excluding the extreme tiny category) and larger supports during the rainy season (excluding the enormous category). A Pearson chi-square test gave a value of 369.947 with an asymptotic significance of 0.000, displaying that any differences between the seasons in terminal support diameter are not due to chance. Small diameter terminal supports were used to locomote 36% of the time during the dry season, compared to 17% of the time during the rainy season. In contrast, large terminal supports were used 21% of the time during the dry season, in contrast to 37% of the time during the rainy season.

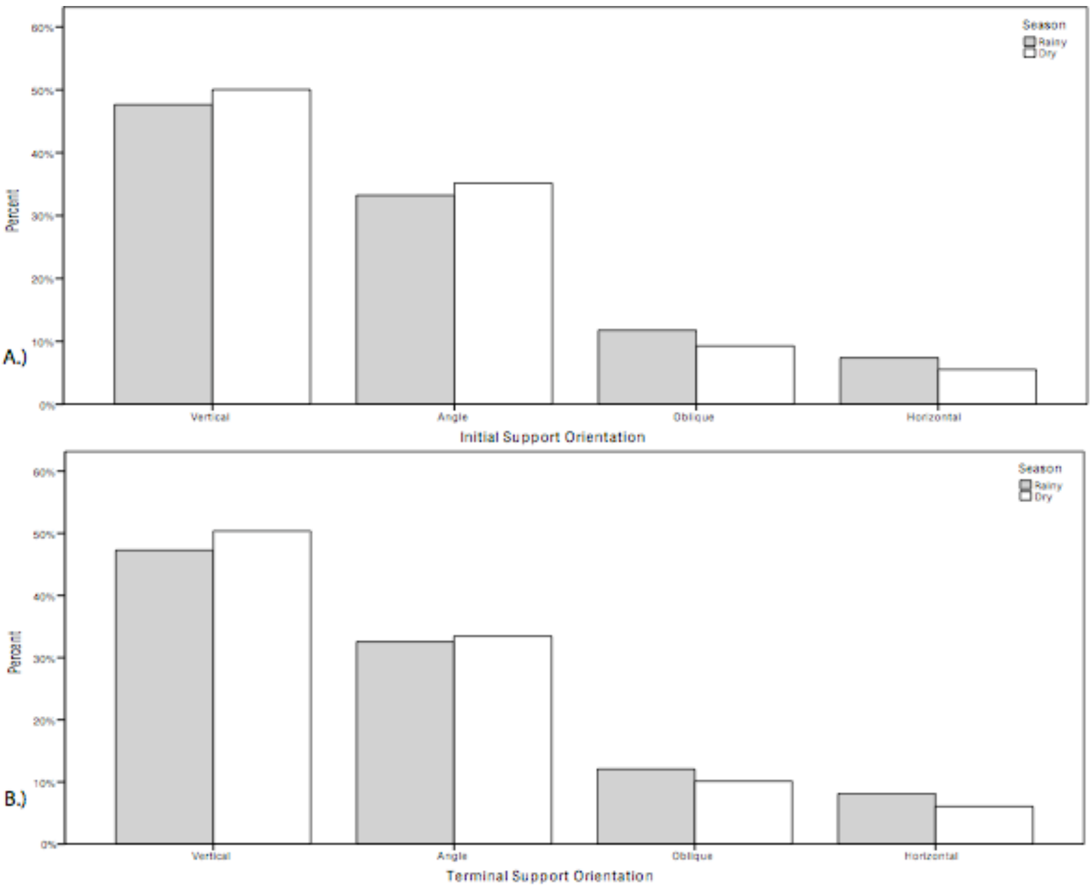


Figure 27 Initial (A) and terminal (B) support orientation frequencies separated by season showing a preference in the more upright support categories (vertical and angled) in both the rainy and dry seasons (dry season, n = 6941 and rainy season, n = 2251).

A slightly different pattern occurs when seasonal changes are taken into account. There are again small but significant differences between the seasons in the way that *P.verreauxi* chooses initial support orientations ($\chi^2 = 24.472$, p = 0.000). During the dry season slightly higher levels of vertical and angled initial support orientations are used (85% vertical and angled during the dry season, versus 81% during the rainy season). While the converse is true of oblique and horizontal initial supports, which are used more regularly during the rainy season than they are in the dry season (19%

oblique and horizontal during the rainy season, versus 15% during the dry season)(Figure 27). The exact same pattern is also displayed in terminal support orientation when season is used as a variable. Vertical and angled terminal supports are favoured during the dry season (84% vertical and angled during the dry, versus 79% during the rainy season). Whilst the oblique and horizontal supports are used more regularly during the rainy season (20% oblique and horizontal during the rainy season, versus 16% during the dry season).

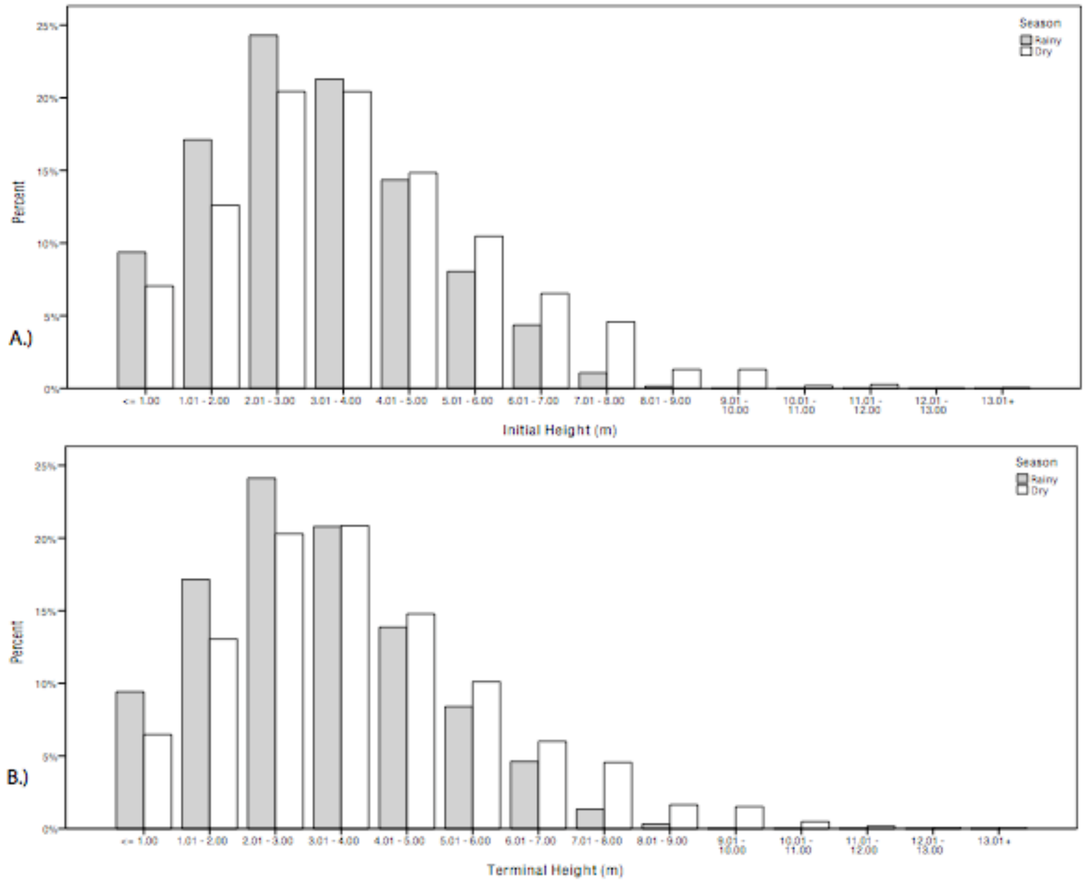


Figure 28 Frequencies of initial (A) and terminal (B) height observations based on season showing the frequency of observations of height in the rainy and dry seasons (dry season, n = 6941 and rainy season, n = 2251).

When seasonal changes were considered with regard to initial and terminal heights, much greater changes were seen between the dry and rainy seasons. The results of a Mann-Whitney U test (Mann-Whitney U = 6485215.5; P = 0.000) showed a significant difference between initial height in the rainy and dry seasons. With lower initial heights (<4m) being utilised more often in the rainy season than the dry season. Whereas, *P.verreauxi* was observed at higher initial heights (>4m) more often in the dry season, than then rainy season (Figure 28). A very similar pattern was observed with the terminal height observations, with a significant difference between the two seasons (Mann-Whitney U = 6481449.5; P = 0.000). Similarly to the initial height, *P.verreauxi* was observed more often at a low terminal height (4m), during the rainy season; but was observed more often at a higher terminal height (>4m), during the dry season (Figure 28).

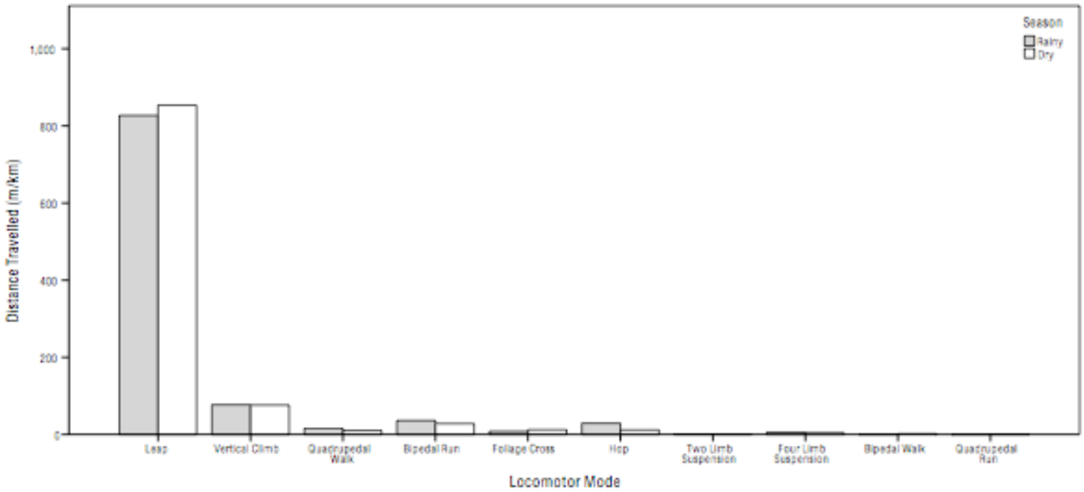


Figure 29 Distance travelled in metres per kilometre for each mode of locomotion, separated by season, showing that in both dry and rainy seasons, lemurs travel the majority of every kilometre by leaping (dry season, n = 6941 and rainy season, n = 2251).

During both the dry and rainy seasons, leaping behaviour made up the largest proportion of the distance travelled per kilometre (827m/km for the rainy season and 854m/km for the dry). Again, the second most popular mode of locomotion, in terms of distance travelled, was vertical climbing which accounted for 77m/km during the dry season, and 76m/km during the rainy season (Figure 29). The least favoured modes of locomotion in terms of distance travelled, in both seasons were: quadrupedal running (0m/km during the rainy season and 0.2m/km during the dry season, two limb suspension (1m/km during the rainy season and 1m/km during the dry season), and bipedal walking (0m/km during the rainy season and 2m/km during the dry season) (Figure 29).

Discussion

Key Findings

- Leaping is clearly the predominant mode of locomotion regardless of group membership or season. It accounts for the larges distance covered per kilometer under all of the variables studied.
- Support orientation choice follows a similar pattern with more upright supports of the angled and vertical categories being utilized most regularly, regardless of group or season. Suggesting that *P. verreauxi* is accurately described as a vertical clinger and leaper.
- Mid-range supports between 0.6 – 15cm in diameter were used overwhelmingly for locomotion by *P. verreauxi*, with a similar pattern of usage for all variables. Although, when seasonality was explored, there was a

clear preference for using the larger supports to locomote during the dry season.

Overall Discussion

Leaping is clearly the predominant mode of locomotion for *P.verreauxi* and the species is regularly referred to as a specialist vertical clinger and leaper (Napier and Walker 1967), although more specialised definitions of leaping have now been proposed (Oxnard and Crompton 1990). Saltatory displays account for 75.9% of all locomotor bouts and although directly comparable data is quite rare, some previous studies do exist. Dagosto (1995) found a leaping frequency of 89% in *P.diadema*, which exceeds the leaping frequency of *P.verreauxi* by a large amount. The leaping frequency of *Eulemur fulvus rufus* in the same study, which is known more as a locomotor generalist (Demes, Fleagle et al. 1999), was a more comparable figure. Discrepancies in results could be caused by Dagosto only using four locomotor categories, as opposed to the ten used in this study. Captive data (Gebo 1987) gives the only direct comparison with the same species and the leaping frequency of 46% is a lot lower than was found in the wild. A similar captive study (Tilden 1990) conducted at the same research facility gave a leaping frequency of 58% for *Eulemur rubriventer*, which is again considered a generalist in terms of locomotion. It must be concluded that the above studies mentioned have a methodology that is too different from our own and are therefore the results are not comparable.

Blanchard (2007) performed a study with very similar methodology, which gave much more comparable results with members of the Indriidae family. She found that

P.diadema had a leaping frequency of 75% and the larger *I.indri* used leaping to locomote 81% of the time. These results compare very favourably with *P.verreauxi* in this study that leapt 75.9% of the time. *A.occidentalis*, a smaller member of the Indriidae family was found to leap 69.7% of the time (Warren and Crompton 1997). With this pattern it seems that the larger members of the Indriidae family leap more often than the smaller members. Increased size does not normally lead to higher rates of saltation, and in South American species (not of the same family) an increase in body size leads to a decrease in the amount of leaping behaviour (Fleagle and Mittermeier 1980). Other strepsirrhine genera follow a similar pattern of decreasing leap frequencies as size increases, with the larger *G.crassicaudatus* having a leap frequency of 22.4%, whereas the smaller *G.senegalensis* utilises leaping 54.1% of the time (Crompton 1983). Another primate known for its salutatory displays is *T.bancanus*, which has a similar adult weight to *G.senegalensis* and has a leaping frequency of 66.1% (Crompton and Andau 1986), all of these frequencies, aside from that of *I.indri,* are lower than that found for *P.verreauxi*, this shows that *P.verreauxi* relies heavily on leaping as a means of locomotion.

Activity patterns in *P.verreauxi* over the entire study period showed that travel accounted for most of the activity (43.4%), whereas resting and feeding had very similar frequencies (26.1% and 27.6% respectively). Travelling only accounted for 21% of *P.diadema* activity and 13% of *I.indri* activity (Blanchard 2007). Creating a fairly large discrepancy for members of the same family and may be explained by the fact that our study was performed in a highly seasonal dry forest where food was often scarce, whereas a rainforest shows far less seasonality and changes in food availability are far less dramatic, therefore reducing the need for long periods of travel to feeding sites. More comparable levels of travel come from more omnivorous species with *G.crassicaudatus* travelling with a frequency of 52.1% (Crompton 1983) and the New World monkey *L.lagothricha* which had a travelling frequency of 31.9% (Cant, Youlatos et al. 2001). A similar coastal forest environment leading to similar strategies regarding energy budgets may explain the similarities between travel rates with G.crassicaudatus. Rates of resting are very similar between *P.diadema* (27%), *I.indri* (33%) and *P.verreauxi* (26.1%), which is very high in comparison to *G.senegalensis* (4.5%) and *G.crassicaudatus* (9.4%)(Crompton 1983). High levels of resting may be due to the constraints of the relative cost of locomotion placed on folivores leading them to need longer resting periods (Warren and Crompton 1998).

With *P.verreauxi* being referred to as a vertical clinger and leaper on a regular basis, it is no surprise that such high frequencies of vertical and angled support use were discovered. In comparison to other indriid species, Blanchard (2007) found 56.45% overall vertical support usage in *P.diadema* and 41.25% in *I.indri*, while Warren (1997) had a vertical support frequency of 42.8% in *A.occidentalis*. The value of 49.62% found in this study for vertical support use compares very well with these figures and shows that within the indriid family vertical supports are used for almost half of all locomotor bouts. Although for angled support use, *P.verreauxi* had a frequency of 33.24% which was much higher than *P.diadema* (19.8%) and more comparable with other genera within the indriid family with *A.occidentalis* having a frequency of 29.4% and *I.indri* utilising angled supports with a frequency of 24.6% (Blanchard 2007; Warren and Crompton 1997b). Differences within genera maybe caused solely by differences in habitat and a smaller proportion of angled supports being available to *P.diadema* in a rainforest environment. Dagosto (1995), discovered seasonal differences in support orientation, displaying a decrease in vertical support use and an increase in oblique support use during the wet season. These seasonal changes were not detected for *P.verreauxi*, and may be due to forest structure differences between rainforest and deciduous forest. The other reason could be caused by differences in sampling methods, in this study continuous scan sampling methods were employed, whereas Dagosto (1995) utilised focal sampling at two minute intervals. Again, large discrepancies between the results of the two data sets have emerged and data relating to support orientation, are incomparable. The dependence on upright supports is symptomatic of the indriid family whereas other more generalist lemur species, in terms of locomotion, have been discovered to locomote using more oblique and horizontal supports. Britt (2000) found that *V.v.variegata* locomoted using oblique and horizontal supports 86.5% of the time. A stark contrast to the indriids, but may be caused by *V.v.variegata* being a more frugivorous species that spends more time locomoting on terminal branches while foraging.

Support diameter in leaping primates is a well researched area of biomechanics. Leaping is a high impact and high energy form of locomotion and Cromton (1993) discovered that large bodied leapers use larger supports as they are less compliant and therefore less energy is lost during the take-off phase of the leap. Demes (1999) found that locomotor generalists tend to generate greater take-off and landing forces in comparison to specialist leapers, such as those in the indriid family. A reduction in forces is thought to be due to an increased intermembral index of specialist vertical clingers and leapers (Davenport 1935), allowing the long hind limbs to absorb forces over a greater period of time during take-off and landing. Within this data set, *P.verreauxi* showed a high degree of preference for small medium and large supports in both initial and terminal supports with these three categories making up 91.22% and 89.98% of support diameter usage respectively. Blanchard (2007) found very similar frequencies for initial and terminal support diameter in other indriids, *P.diadema* had an initial support diameter frequency of 91.4% and a terminal frequency of 92.4% for the three middle categories combined. *I.indri* again showed high frequencies for supports between 0.6 and 15cm in diameter, displaying an initial support diameter frequency of 88% and a terminal support diameter frequency of 88.3%. Although within these data sets there was a high level of preference for medium sized supports, whereas this data set shows a fairly even distribution for preference of the three mid-range categories for support diameter.

Mean heights of observation for *P.verreauxi* were shown to be much lower than in other indriid species. Blanchard (2007) discovered a mean height for *P.diadema* of 10.55m and for *I.indri* of 12.62m, which in comparison for my initial and terminal heights of observation of 4.03m and 4.04m respectively is substantially higher. Britt (2000) found that *V.v.variegatai* spent 75.2% of its time between 10m and 25m within the canopy, which again is much higher than the figures for *P.verreauxi*. These large differences in height preference may be caused by the forest structure. All three of the species compared above are rainforest dwellers and although average tree heights in two rainforest environments of 9.6m and 10.4m (Grassi 2006) are very similar to those in the dry forest of 10.63m (Chouteau 2006), rainforests are observed to have trees which are upwards of 30m in height (Dagosto and Yamashita 1998); a height that was never even nearly achieved within a dry forest environment.

Increases in the height of the tallest trees within the rainforests could lead to a higher average observation height in rainforest species.

Groupwise Discussion

Leaping is still very much the predominant mode of locomotion for *P.verreauxi* and both groups display such high frequencies of saltatory behaviour, that they still fit Napier and Walker's (1967) vertical clinger and leaper classification very well. The locomotor frequencies for *P.verreauxi* are still comparable to other similar studies (Blanchard 2007; Warren and Crompton 1997b), even when separated into their distinct social groups. Leaping frequencies only differed by 2.8% between the two groups over the entire study period, and this was the largest difference in frequency of any of the locomotor categories. Comparisons with any captive data (Gebo 1987; Tilden 1990), must again be avoided due to the differences in methodology rendering the results incomparable. Although a significant difference was found in the frequency of bouts between the two groups, this was a small difference, and the overall pattern of locomotion of both groups was very similar.

The idea of locomotor plasticity within species is something that has not been researched heavily, and the majority of studies, which include studies of the same species at different sites have concluded that very little within species variation in locomotion occurs (Garber and Pruetz 1995; Hunt 1992). Normally, one would expect that different studies using different methodologies would give results that are dissimilar or incomparable. There is one case involving *Ateles geoffroyi*, using distinct methodologies, where Cant (Cant 1986), in a dry forest, and Fontaine

(Fontaine 1990) in a lowland rainforest, found very similar results for locomotor frequencies. These results were very similar, even though the forest architecture at the two sites was very different and the methodologies were also distinct from each other. These findings suggest that locomotion is not plastic, and that locomotion may be bound by anatomical constraints, which prevent individuals of the same species adapting their locomotor repertoire to varying forest architecture. The only comparable indriid study was performed on *P.diadema* (Dagosto and Yamashita 1998), which took place in a rainforest environment, with a much taller canopy and very different forest architecture. As previously discussed, the results are incomparable due to the differing number of categories, but, what is certain is that the dependence on leaping as a means of locomotion is present in both species at different sites with very different forest structure. Between the two groups of *P.verreauxi* studied at Kirindy Mitea National Park, it cannot be claimed that the sites varied in any way, both groups home ranges were located next to each other and there was even some overlapping territory. Therefore it would be expected that the two groups locomote in a similar manner, this similarity also allows more general inferences to be made about the behaviour of the species as a whole in Kirindy Mitea National Park as neither group locomoted substantially differently from the other.

Rates of activity were also do not seem to vary intraspecifically, with the pattern of activity mirroring the frequencies seen for the overall analysis. Travel dominates the activity of both groups, whilst feeding and resting show very similar frequencies. Intraspecific activity patterns also seem to display very little plasticity when studied between groups of primates in a similar environment. Maruashi (Maruhashi 1981) found very little variation in the activity patterns between groups and individuals of

Macaca fuscata yakui. Fashing (Fashing 2001) also found very little group wise variation in activity for *Colobus guereza*, which also compared very favorably with the activity budgets for the same species at two different sites (Oates 1977). Within the *Propithecus* genus, very little intraspecfic variation has been recorded in relation to activity budgets. Hemingway (1999) also found no differences between groups in relation to time budgets in *Propithecus diadema edwardsi*, but did find some variation in feeding activity between the sexes. During times of lactation, there were no differences in the frequencies of feeding, but the quality of food consumed differed between the sexes, with females eating higher quality food. One case does show intraspecific variation, the woolly spider monkey was studied at two different sites by Milton (1984) and Strier (1987). At one study site the wooly spider monkeys spent more time resting and feeding, whereas, at the other, more time was devoted to travelling. The majority of data in this field point towards very little intraspecific variation in activity budgets with regard to primates. But the lack of data in this area necessitates the need to compare very broad studies involving new world monkeys, old world monkeys and strepsirrhines. Until more data is collected involving activity budgets and intraspecific variation this will still be a poorly understood subject.

Intraspecific variation in support use is something that has not been studied in great detail with regard to primates. Due to the lack of data in this area, gender differences were compared in order to give reference to some sort of intraspecific variation. With some of the most extreme examples of sexual dimorphism being among the great apes, even when the locomotor repetoires of bonobos and chimpanzees were investigated, based on gender, patterns of positional behavior are almost identical

(Doran 1993). Further suggesting that support use may also be fairly stable between the genders; therefore there may be very little intraspecific variation in support usage in both orientation and diameter. Whilst in smaller Old World monkeys there is also a lack of evidence for gender differences, the red colobus showed very little variation in support usage when gender was investigated (Gebo and Chapman 1995). These results support the findings in this investigation, although there were significant differences between the support usage in both initial and terminal support diameter and orientation, these were small differences, proved to be significant due to the large volume of data. The overall patterns of support diameter for both groups showed a preference for supports between 0.6 and 15cm in diameter. Whilst in regard to orientation preferences, both groups of *P.verreauxi* utilised vertical and angled supports, rather than the more horizontal supports.

The only within species data that shows any sort of intraspecific variation comes when a group is separated into infants and adults. Crompton (Crompton 1983) showed in two species of *Galago* that support use and locomotion can vary with regards to age (infant or adult). The infants in this study were found to use smaller supports more often than the adults, this change is attributed to the size differences between adults and infants, with infants having smaller grasping feet and hands preferring smaller substrates. Unfortunately, this study was not able to compare adults and infants, as data collection began at the start of the gestation period and ended whilst all infants were still traveling on their mothers' backs. Although this is the closest, directly comparable study, due to the similar data collection methodology, another study showed that the same species of *Galago* showed no gender differences with regard to substrate usage and locomotion (Harcourt and Nash

1986). Suggesting that although there may be some difference in substrate usage between adult and infant sterpsirrhine primates, adult support usage seems to be fairly uniform.

Height observations have yielded some contrasting results on an interspecific level with regard to stepsirrhine primates on the island of Madagascar. Dagosto (Dagosto 1995), found no significant difference between height above ground measures for three sympatric species of lemur in the same location. Suggesting that at this field site, that the presence of food may occur in specific strata of the forest canopy and this will increase interspecific competition between the given species. Sussman (Sussman 1977) on the other hand found that in a dry forest environment, separate species use very different strata of the forest. *L.catta* spent over 58% of the daytime outside of the conopy, whereas *E.fulvus rufus* was very rarely seen terrestrially. Promoting the idea that forest architecture may well have a large effect on the position that a given animal may find itself within a three dimensional forest environment.

P.verreauxi in this study, showed no significant difference intraspecifically in the initial height of observation and only a small difference was recorded for terminal height of observation. The only other study which compared any sort of intrapecific variation in observation height in the same geographic location, did so with regards to age (Crompton 1983). Crompton's study shows that in *G.senegalensis*, infants were observed at lower heights within the canopy than the adults. The data presented here cannot compare with Crompton's findings, as during the period of this study, we arrived during the start of the gestation period and work ceased whilst all infants still traveled on their mothers' backs. Other intraspecific studies have concentrated on animals inhabiting different locations with varying forest architecture. Moustached tamarin monkeys were found to locomote at different heights in the canopy at different sites, but although they were using different heights, it was found that this species still used the high canopy in both areas and it was the differing average tree height which caused the differences (Garber and Pruetz 1995). Demonstrating that when a forest has similar architecture, such as Kirindy Mitea National Park a given species will tend to be found at similar heights within the canopy.

It is clear that from the results gained, *P.verreauxi* favours leaping greatly to cover the majority of its distance traveled. The measure of effective distance traveled is not a widely utilised technique when it comes to analysing locomotor data, therefore there is not a huge amount of data for a comparison. There is also no comparable intraspecific data regarding effective distance traveled. The lack of intraspecific variation with regard to categorical locomotor frequencies would suggest that the effective distance traveled by each mode of locomotion would also be constant intraspecifically, which would agree with the results which were presented here. Among strepsirrhine primates, this finding is not unusual, *Lepilemur*, known as a specialist leaper also displayed a high effective distance traveled by leaping (Warren and Crompton 1997) and also a high leaping frequency. The same pattern is also displayed with *Tarsius*, previously described as a prosimian and also known as a specialist leaper (Crompton and Andau 1986). Within the indriid group, which has been more widely studied, a similar dependence on leaping also leads to a high effective distance traveled by leaping, this pattern is seen in *I.indri*, *P.diadema* and *A.langier* (Warren and Crompton 1997; Blanchard 2007). High levels of leaping and a high effective distance traveled using this mode of locomotion may be due to anatomical constraints on the animal. Fleagle and Anapol (Fleagle and Anapol 1992) showed that primate leapers are unusual among mammals for having a relatively short ischium, this anatomical feature, may prevent these animals from displaying other forms of locomotion, such as quadrupedalism on a more regular basis. Therefore the lack of intraspecific variation shown in *P.verreauxi* may be due to anatomical constraints and seems to be a feature of most specialist leapers.

Seasonal Discussion

Seasonality plays a large role in the activity patterns of *P.verreauxi*, with rest periods decreasing by 15.1% and travel rates increasing by 17.7% during the rainy period. With the extreme seasonal changes that take place in southwestern Madagascar (Ganzhorn 2002), some changes in activity patterns were to be expected. Hanya (2004) showed that during times of food scarcity that Japanese macaques reduced the amount of time they spent travelling, but also the amount of time spent feeding. The amount of time spent feeding during our study remained fairly constant irrelevant of season during the entire study period, with a 1.1% increase seen during the rainy season. Vasey (2005) found a very similar pattern studying *V.rubra*, with lemurs moving less during times of food scarcity, although not spending a significantly larger amount of time feeding. An increase in travel may be due to the rainy season producing more young, nutritious leaves for the sifakas to feed upon (Hemingway 1998). Whereas during the dry period, the only leaves available are mature less nutritious leaves so *P.verreauxi* increases the frequency of rest periods to conserve energy. Erkert (2004), demonstrated a bimodal activity pattern in *P.verreauxi* during the dry season which may explain the similar results found for an increase in resting frequency in our data.

The largest change in support orientation frequency came when seasonality was compared, with a significant change to larger supports (excluding the enormous category) during the wet season. A previous study by Youlatos (1998) investigating red howler monkeys showed that during the dry season larger supports were used more often. It was postulated that this change was due to food availability and fruiting and that during the wet season, red howlers feed on fruits using terminal branches to locomote. The converse situation is found in this study, with *P.verreauxi* locomoting using larger diameter supports during the wet season. With sifakas being obligate folivores with no major seasonal shift in diet (Yamashita 2002), diet can therefore not be a major contributing factor for an increase in large diameter supports. One thing that could cause this shift in support diameter size is the properties of the wood that make up the trees in the forest. Crompton (1993) discovered that specialist leapers prefer larger less compliant supports so that less energy is lost during take-off. With southwestern Madagascar showing such a high degree of seasonality the moisture content in the wood of the supports would be very low during the dry season. Low moisture content, according to Young's modulus would reduce the elasticity of the support and make it less compliant (Cannell and Morgan 1987). Whereas in the rainy season an increase in humidity and moisture content would increase the elasticity of the support making it more compliant. Leading to *P.verreauxi* using larger supports in the rainy season because the smaller supports would be more compliant and mean locomoting using these supports would be more costly.

A decrease in the average height of observation during the rainy season was also recorded. Height reduction could be caused by the dietry needs of *P.verreauxi*. Sifakas are folivores and have shown a large dietry preference for young leaves (Irwin 2008) and young leaves will begin to grow at the beginning of the rainy season. Much of the new growth can be observed at lower heights, Chouteau (2006) displayed a decrease in visibility at a height of 1.5m during the rainy season in a dry deciduous forest from 6.22m to 5.03m, much of this is down to new leaves sprouting. New growth may cause *P.verreauxi* to alter its feeding height and therefore lower the average height of observation during the rainy season.

Chapter 3

A study of *Propithecus verreauxi* ranging behavior and activity rhythms in the dry deciduous forest of Kirindy Mitea National Park

Introduction

P.verreauxi is a large-bodied strepsirrhine primate that inhabits the dry deciduous forests of southwestern Madagascar. It has an adult body weight of around 3.8 kilograms (Milton and May 1976) and is one of the larger members of the indriid family. The indriid family is one of the most widespread of the Malagasy lemurs and contains the largest of the lemurs *Indri indri* and also some large bodied nocturnal folivores of the genus *Avahi*. What is unusual about this family of lemurs is that although they are large bodied in comparison to other strepsirrhine primates and are also obligate folivores; they maintain a very high energy leaping strategy as their predominate form of locomotion. Whilst the majority of other saltatory primates have a large proportion of their diet dedicated to frugivory or insectivory. Research into *P.verreauxi* has tended to concentrate on the more unusual aspects of their ecology, such as their locomotion (Dagosto 1995; Demes, Jungers et al. 1995; Demes, Jungers et al. 1996; Demes, Fleagle et al. 1999) and female dominated social structures (Kappeler, Trillmich et al. 2004; Lewis 2006). The behaviour and ecology of any given species is affected by a whole raft of variables such as food availability, climate and predation, to name but a few. Therefore, in order to understand the ecology of a given species, general information such as home range, day range and activity rhythms must be documented over an extended period of time.

Almost all of the previous research performed in dry-deciduous forests on *P.verreauxi* has been performed in the Kirindy Forest (CFPF) which is around 70km north of the Kirindy Mitea National Park (Erkert and Kappeler 2004; Kappeler, Trillmich et al. 2004; Lewis and Kappeler 2005). Very little research of any ecology has been performed in the Kirindy Mitea National Park, mainly due to its very remote location and the logistical difficulties of creating a long-term research station in the area. But the importance of gaining even a basic knowledge of the forest ecology cannot be underestimated, as it is the largest remaining continuous tract of dry deciduous forest in Madagascar (Whitehurst, Sexton et al. 2009; Lewis and Bannar-Martin 2011).

Previous research has suggested that there are two major contributing factors which can influence home range size in primates: body size and diet (Milton and May 1976; Harvey and Cluttonbrock 1981). These theories have recommended that the larger the body mass of a primate, it increases that individuals metabolic needs, which, in turn, necessitates the need for a larger home range in which to forage. Due to the dispersed nature and masting events of certain fruiting trees and plants, frugivores have also been shown to require a larger home range than folivores in order to satisfy their metabolic requirements. Although these factors play a large role in explaining variation in interspecific home range size, there is also a body of evidence which demonstrates variability in home range size on an intraspecific level. One other factor that has been shown to affect home range size in Malagasy primates is deforestation. Madagascar's forest cover has been reduced in area by around 40% since the 1950s (Harper, Steininger et al. 2007), this has reduced core areas of forest dramatically and led to an increase in the number of forest fragments. Forest disturbance has created an increase in population density within forests with a knock on effect of reducing the home range sizes of many of the primate species. Glessner and Britt (2005) compared the home range sizes of *Indri indri* in forests which had experienced varying degrees of habitat disturbance, concluding that as levels of deforestation increased, so, home range size decreased.

Seasonality can also play a big role in affecting not only behaviour, but also physical attributes such as body mass. Within the indriid family, body mass has been found to correlate positively with the annual rainfall, but also negatively with the length of a given dry season (Lehman, Mayor et al. 2005). When regarding intraspecific changes within an annual cycle, *P.verreauxi* has been exhibited to display significantly lower body mass and fat levels during the long dry season, which is linked to long periods of food scarcity (Lewis and Kappeler 2005). Behaviours such as activity rhythm, day range and home range size can also vary within a population due to environmental factors such as temperature and rainfall. *P.verreauxi* in a seasonal forest environment has been shown to display a diurnal activity pattern, which is mainly bimodal until the onset of the breeding season (January – March) when the duration of activity increases and the pattern becomes unimodal (Erkert and Kappeler 2004).

Seasonality has a huge impact on the behaviour of any given species in a forest. The degree of variation in the behaviour would be expected to be more pronounced in a forest that displays a more extreme seasonal dichotomy. Rainforest environments have been shown to express a more subtle seasonality and a more stable environment in comparison to dry deciduous forests, such as Kirindy Mitea, which has a more clearly defined dry and rainy season pattern (Murphy and Lugo 1986). The long dry season occurs between April and October, whilst the shorter rainy season, defined by higher average temperatures and more rainfall, occurs between November and March

(Sorg 1996). Dry seasons in all forest and savannah environments are synonymous with periods of food scarcity, and there are three main theories relating to how animals cope with food scarcity. The first theory seems to relate more to carnivores who seem to range further and for longer in order to locate prey in order to fulfill their metabolic needs (Orsdol, Hanby et al. 1985). Strategies such as this have also been displayed in chimpanzees, although this was more a case of higher ranking individuals with in a troop gaining access to better feeding positions and lower ranking individuals having to range further in order to forage (Murray, Eberly et al. 2006). Another strategy, which seems to be more suited to folivorous primates, such as *P.verreauxi*, is to travel less in an attempt to conserve energy during periods of food scarcity (Irwin 2006). The final theory, mainly employed by more generalist feeders, is dietry adaptation during periods of food scarcity, this has been observed in squirrell monkeys which maintain their home range and daily ranging behaviour throughout the year, but adapt their diet to include different foods dependent on the season (Stone 2007).

Although a regularly studied family of primates, there are still some poorly understood areas of ecology in regard to the indriids. Much of the data collection regarding species within the *Propithecus* genus has centred around rainforest environments (Irwin, Gould et al. 2007), which may be due to the remoteness of the remaining dry deciduous forests. Much of the more current research has, quite importantly, concentrated on species which are more threatened, mainly due to habitat destruction. Leading to many of the current studies investigating the effects of forest fragmentation on the home range, day range and activity rhythms of the rarer species within the genus, such as *Propithecus diadema* and *Propithecus* *diadema perrieri* (Lehman and Mayor 2004; Irwin 2008). A similar pattern has arisen in regard to activity rhythms in Malagasy primates. The concept of cathemerality was discovered in *Eulemur fulvus fulvus* in 1974 (Tattersall 2006), whereby an animal will spread out periods of activity equally over a twenty four hour period, rather than the more commonly observed crepuscular (active during dawn and dusk) rhythm. Since this point much of the literature has concentrated on attempting to identify the proximate factors which effect such an activity rhythm (Curtis and Rasmussen 2002; Colquhoun 2006). Whereas the volume of literature looking at activity rhythms in *Propithecus* species (widely accepted to be strictly diurnal) has been somewhat limited and the importance of day length, temperature and rainfall on activity rhythms, has been very sparsely studied (Erkert and Kappeler 2004).

Methodologies when investigating factors such as home range, day range and activity rhythms have progressed significantly with the advent of new technologies such as GPS, accelerometers and lightweight radio racking equipment. There are two basic ways to measure animal movement, the Langrangian approach where a single organism is measured everywhere it goes. As opposed to the Eulerian approach, where a specific area is monitored and all organisms that enter this area are monitored (Kays, Tilak et al.). Eulairian approaches include using equipment such as camera traps which are more often than not used for estimating species richness or population density in a given area (Tobler, Carrillo-Percastegui et al. 2008). Camera trapping is also being utilised more often in dense rainforest environments where sightings of individuals can be rare. The other benefit of this method is that it is completely non-invasive and does not require the animal to be captured or tagged, resulting in no stress whatsoever to the animal. Langrangian approaches include radio telemetry techniques, which necessitate the use of signal towers, placed at strategic points to gain a location on an animal using triangulation from bearings. Techniques such as this, are more often than not, either used when studying large mammals with vast home ranges (De Villiers and Kok 1997), or birds (Mellen, Meslow et al. 1992), which are almost impossible to track any other way. More recently, GPS collars which work wirelessly are now available and record the coordinates of a given animal at pre-determined intervals (Mills, Patterson et al. 2006). A more popular method among primatologists is to habituate a given troop of primates to a researchers presence and follow this group throughout the day. Flagging tape is then used to mark the point where the troop are located at given intervals and the coordinates are recorded using a hand-held GPS receiver (Crompton and Andau 1987; Blanchard 2007).

Activity studies pose a much more limited set of available methodologies when performed in a field environment. Laboratory methods tend to utilise small mammal models such as mice, rats and hamsters. The enclosures that these subjects are housed in contain infrared sensors and when a beam is tripped the animal is classified as being active. Studies that use a methodology such as this can also control the environment that the animal lives in to look at the effects of different variables, such as photo period, which can be controlled (Weinert, Weinert et al. 2001). Another technique which has been used to study circadian rhythms in captive primates (Gander and Moore-Ede 1983), is the use of a mercury switch. These switches work using the orientation of the switch, which in turn moves the mercury and dependent on the orientation, can allow, or interrupt the flow of electricity in an electrical circuit. A change in the signal from the switch can then be used to define if an animal is active or not. With regard to field methods for monitoring the activity rhythm of a given species in the wild, there has been a more recent trend toward using data loggers which contain accelerometers to gain information on activity patterns. Data loggers have proven to be particularly popular in the ongoing investigation into cathemerality amongst Malagasy primates (Kappeler and Erkert 2003; Erkert and Kappeler 2004).

In order to monitor the home range of *P.verreauxi* in this study, the more traditional method of full day follows, marking locations of the group at given intervals and retrieving GPS points at a later date from a hand held unit was utilised. Triangulation methods are difficult to employ in such a remote area, as they need large amounts of equipment to construct towers and there have been issues with the accuracy of the locations that they produce. GPS collars were also rejected as a viable method for home range data collection. At the time of the field season, the development of GPS collars was still in its infancy and as with most new technology, the units were quite large and very expensive. GPS collars were mainly being used at that time, to study much larger mammals, such as large carnivorous cats. The usage of camera traps was also rejected due to the arboreal habits of the primate we were studying. Terrestrial animals locomote in a two dimensional environment, whereas arboreal creatures locomote in three dimensions. A three dimensional environment drastically decreases the likelihood of capturing an animal in the trap, unless you drastically increase the number of cameras placed in a given area. The follow and tag method employed also gives direct comparability with many other primate home range studies which employ almost exactly the same methods.

Monitoring activity patterns in a field environment poses some obstacles to overcome which would not be present in a laboratory environment. Using an infrared laser technique would be impossible in a field environment due to the animal not being in an enclosed space, which can be carefully monitored. Field methods successfully used in the past, including mercury switches and accelerometers were also not a viable option for this project. Although accelerometers were available during the field season, these had been programmed to log data at a rate of 50Hz. Clearly this is an incredibly high sampling rate for circadian studies and due to the size of the battery being limited (due to a 10% limit on weight carrying by the animal) meant that sampling time would have been a maximum of 36 hours until it needed to be replaced. Necessitating capturing an animal once every day and a half to replace the battery, which would have been far to stressful for the animal concerned. A similar issue would be caused by the use of a mercury switch, due to the remoteness of the field station and the lack of a trained darter in the forest, capture periods were limited to three in the time research was taking place. Due to all of the factors to consider, a much more simple methodology was decided upon. Full day follows were implemented and the time of first movement was recorded, along with the start and finish of any significant rest periods, then the time of rest in the evening was recorded.

This chapter aims to answer a number of questions regarding the behavioural ecology of *P.verreauxi*. Many previous studies have taken place in rainforest environments, or have been restricted by the size of a forest or fragmented forests. This study aims to look at how *P.verreauxi* behaves in terms of its home range size, home range usage and daily path lengths in one of the largest remaining tract of dry deciduous forest in Madagascar. It was also investigate if there is any intraspecific variation present in Kirindy Mitea National Park by studying more than one group of *P.verreauxi*. Seasonality and the effect of climatic variables will also be studied to see if these factors have any influence on the behaviour of this species in terms of home range, daily path length and activity patterns.

Materials and Methods

P.verreauxi was studied at the Ankoasifaka site in the Kirindy Mitea National Park, Madagascar. All data was collected between the months of May 2010 and December 2010. The Kirindy Mitea National Park is located roughly 70km south of the coastal town of Morondava and is accessible by 4x4 during the dry season (April to November), but can only be accessed by boat during the rainy season (December to March). The study site consists of a 1km^2 grid system, with trails running from north to south and east to west every 25 metres. Due to the effects of cyclone Fanele in February 2009, the shrub layer within the forest has become so dense due to delimbing (Lewis and Bannar-Martin 2011) as to prevent the possibility of working off of the trail system quickly enough to enable full day follows. Nine groups of *P.verreauxi* have all, or some part of their home range within the grid system present at Ankoasifaka. Two groups of *P.verreauxi* were chosen as their entire home ranges fell within the boundaries of the grid system, making full day follows possible at any time and not just as and when the groups ventured into the grid system.

To enable follows of the groups to occur, the dominant females of two groups of habituated *P.verreauxi* were darted with telazol (dosage of 20mg/kg) using the telinject darting system (http://www.telinject.com/). The darting was performed by an experienced local darter who administered the darts using a blowpipe. The sedated animals were then fitted with brass radio collars (model number TW3SM from Biotrack, Dorset, UK). Darted animals were left to recover in pillow cases left in a shady area to prevent the individual escaping when it had not fully recovered from the anesthetic. Rectal thermometers were used to ensure core temperatures were within an accepted range, if temperatures exceeded this range then animals were cooled using water. Once the animal had recovered from the anesthetic, they were released from the point of capture and followed until they had located the rest of their group members.

Thirty-four full day follows were performed between two groups of *P.verreauxi* over a seven-month period. Groups were located prior to the onset of activity using Yagi flexible element antennas combined with a Sika radio-tracking receiver (150 – 153.99MHz) (Biotrack, Dorset, UK). Follows were continued for the full activity period of the group of animals until they came to rest in the evening. During full day follows, a five-minute tagging regime was employed where upon the group would be followed and every five minutes a tag would be placed on the nearest part of the grid piste if the group had moved during the five minute period. If the group had not moved during this period then a new tag would not be required and another five-minute period would begin. Tags were made from lengths of forestry flagging tape that were numbered using a permanent marker and tied to trees to mark the spot where the group were sighted. The following day the tags were collected in number order and the location way pointed using a handheld GPS receiver (Garmin eTrex Vista, part number: 010-00630-00). During follows the times of first activity and final activity were noted along with the duration and times of any rest periods that took place during the course of a follow. Weather conditions were also monitored every day for the entire study period. Rainfall data was collected at the same time every evening using a conical rainfall gauge, whilst maximum and minimum temperature data was collected using an analog max/min thermometer. Sunrise and sunset data was obtained for the region from the National Schools Observatory (http://www.schoolsobservatory.org.uk/) website (Figure 30).

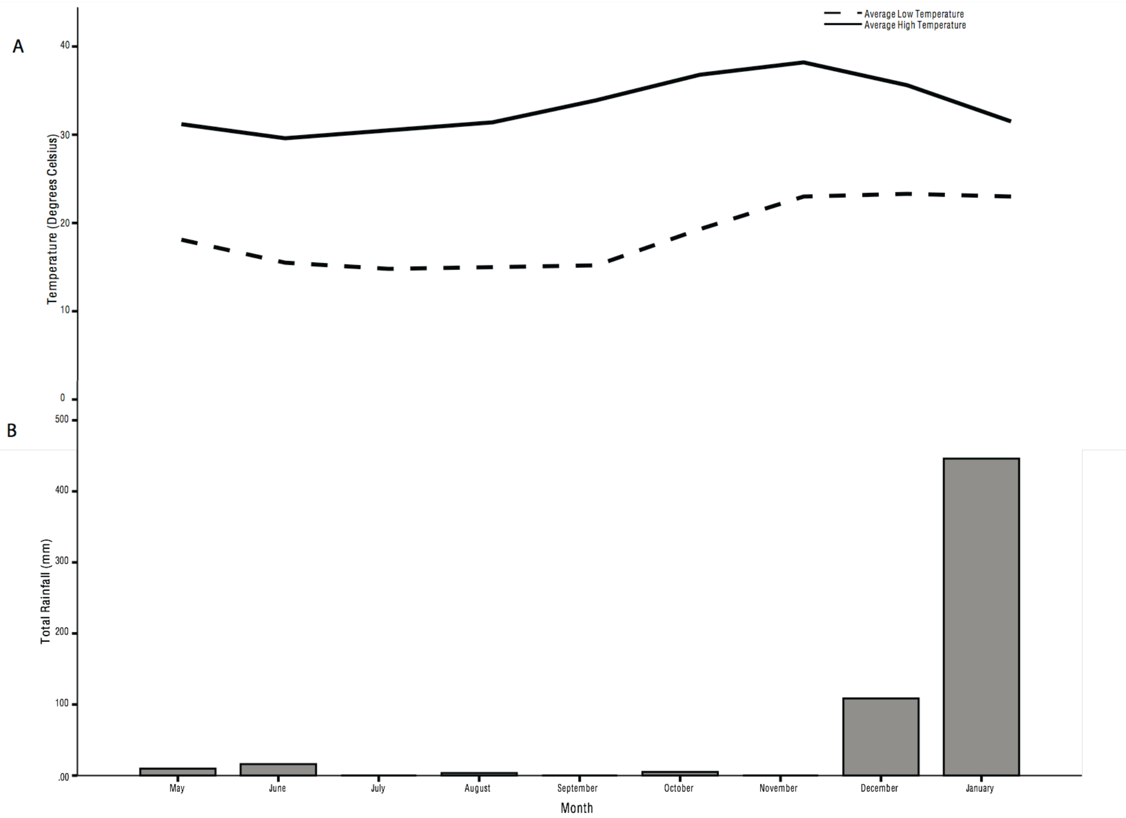


Figure 30 Climatic variables during the course of the study period. A. Average monthly temperature for the study period B. Average monthly rainfall for the study period.

Data Analysis

All GPS data was collected using the WGS84 projection and waypoints were collected using the degree minutes format. Waypoints were then converted into UTMs (Universal Transverse Mercator) using GPS Utility software and minimum convex polygons (MCP) were created using the Hawth's tools toolbox in ArcMap version 9.2. The data were also split into daily follows and the area utilised per day was plotted as an MCP and compared back to the overall home range for the given group.

Day range distances were also calculated using the well-known distance formula, which calculates the distance between two arbitrary points (Equation 1). The formula calculates the distance between (x_1, y_1) and (x_2, y_2) in metres when the data is in the UTM format.

Equation 1

$$d = \sqrt{(x_2 \quad x_1)^2 + (y_2 \quad y_1)^2}$$

Results

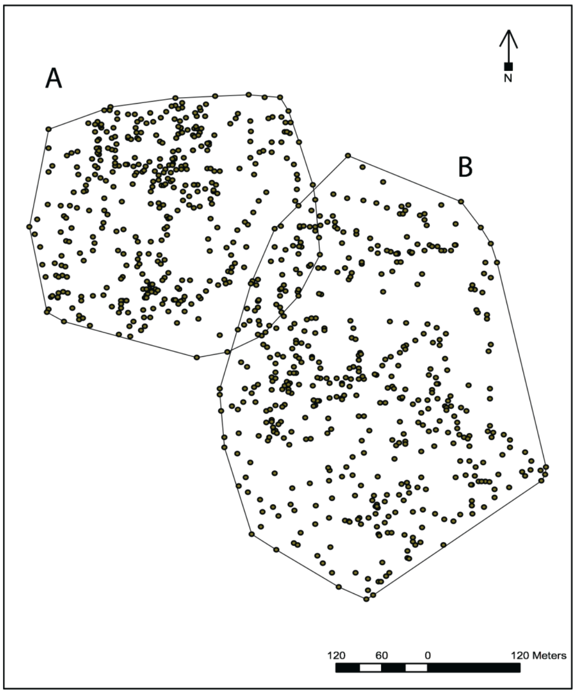


Figure 31 Minimum convex polygons displaying the home ranges of the two groups of *P.verreauxi*, A = group 3 and B = group 4, showing the groups entire home ranges over the entire study period and all waypoints collected during this period.

The mean home range size for *P.verreauxi* in the Kirindy Mitea National Park is 15.69 ha. The home range size between the two groups did differ with group three having the smaller home range of 11.97 ha, only 62% of the size of group four's home range, which was 19.41 ha. It is also clear that there is a small area of overlap between the ranges of the two groups (Figure 31). The overlap has an area of 1.18 ha, which equates to 6.1% of the entire home range of group four and 9.9% of the total home range of group three.

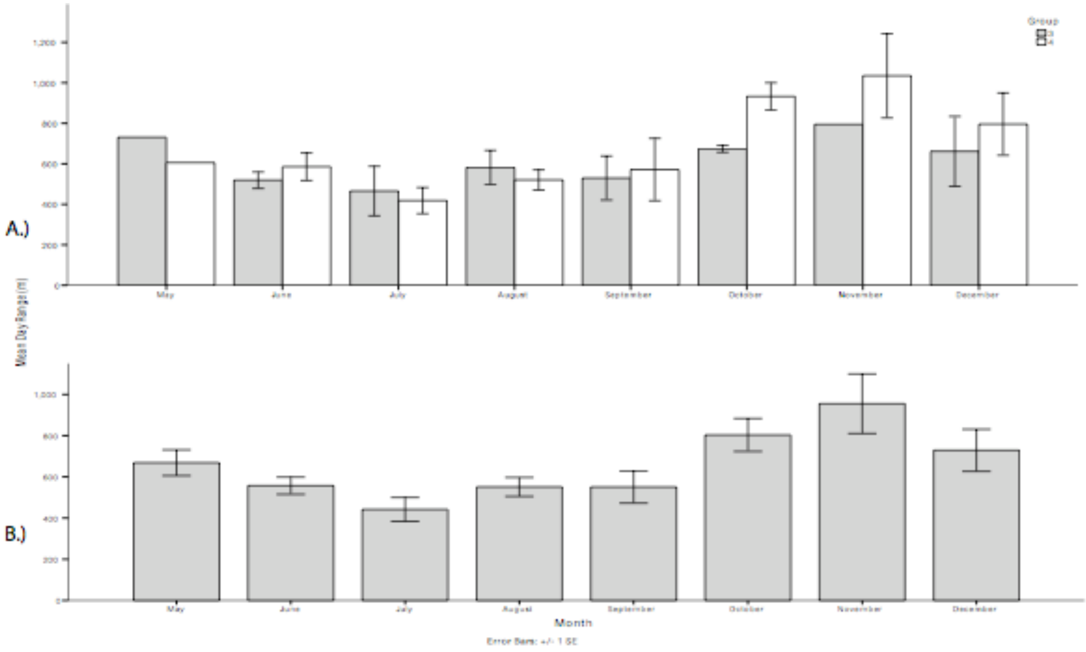


Figure 32 Mean overall day ranges and day ranges for both groups (B), in meters and separated by group (A): for the months of May until December 2010. Showing a gradual increase in day range which coincides with the start of the rainy season.

Mean daily ranging behaviour differed hugely during the eight-month study period. The lowest day-range during this period was 343 meters (July 2010) and the highest ranging period was 1243 meters (November2010). There is a positive correlation between the average monthly home ranges (Figure 32) and day length. A scatter plot of these two variables produces a line of best fit with the formula: Day range = -643.913 + (108.122X). A relationship that proved to be significant (t (32) = 4.001, $p < 0.0001$, $R^2 = 0.333$), although an R^2 value of 0.333 suggests that there is a large amount of variation around the regression line. As the dry season continues from May until June the mean day range decreases; but from August until September there is a slight increase in mean day range (551m). During the late dry season (October and November) there is a drastic increase in the mean day range (879m).

When investigating if there were any differences between the groups with regard to day range it is clear that during the late dry season that group 4 had a larger average day range (Figure 32). Group 4 had a mean day range of 985m during the late dry season (October and November), whilst group 3 had an average daily range of 745m during the same period. Mean day range decreased for both groups during the start of the rainy season (Figure 32). A Mann-Whitney U-test found that any difference in day range between the groups was down to chance (U = 124, two tailed p = 0.506).

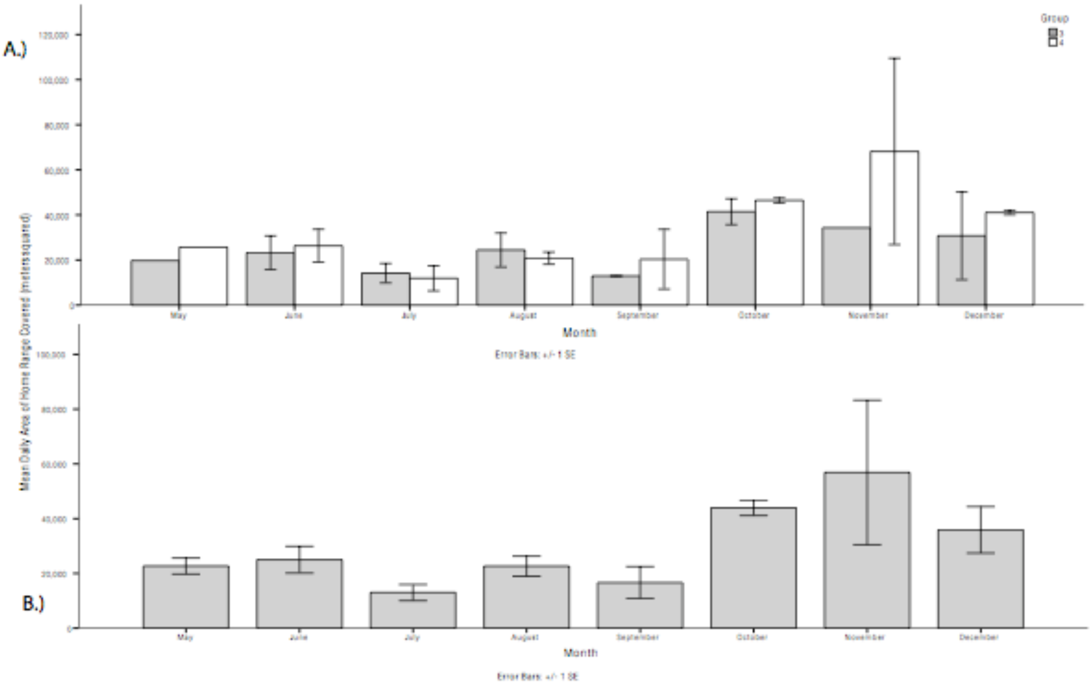


Figure 33 Mean monthly area of home range covered combined for both groups (B), and separated into group variables (A). Showing an increase in area of home range covered during the rainy season.

During the onset and the midmost dry season (May – September), the mean area of home range covered per day was fairly low and constant. The mean percentage of home range covered, for both groups, during this period was 13.4%. The lowest mean percentage of home range covered for both groups, was 9%, which equates to 12,996m^2 (Figure 33). At the end of the dry season (November and December) the daily area of home range covered increases dramatically to a mean of 50,392m^2 (31% of the home range). The start of the rainy season (December), sees this figure drops to 35,900m^2 (23% of the home range)(Figure 33).

Differences between the groups were much more noticeable during the months of November and December. Group 4 covered a mean daily area of 33,868m^2 more then group four, but this only accounted for an extra 6% of the home range covered. This is due to the increased size of group 4's territory, which in 38% larger than group 3's. In December, group 4's mean daily area covered was 10,363m^2 larger than group 3's, but due to the difference in home range size, this accounted for 5% less of the mean daily home range covered. Although any differences between the mean area of home range covered was shown to be down to chance (U = 121.000, two-tailed p = 0.443).

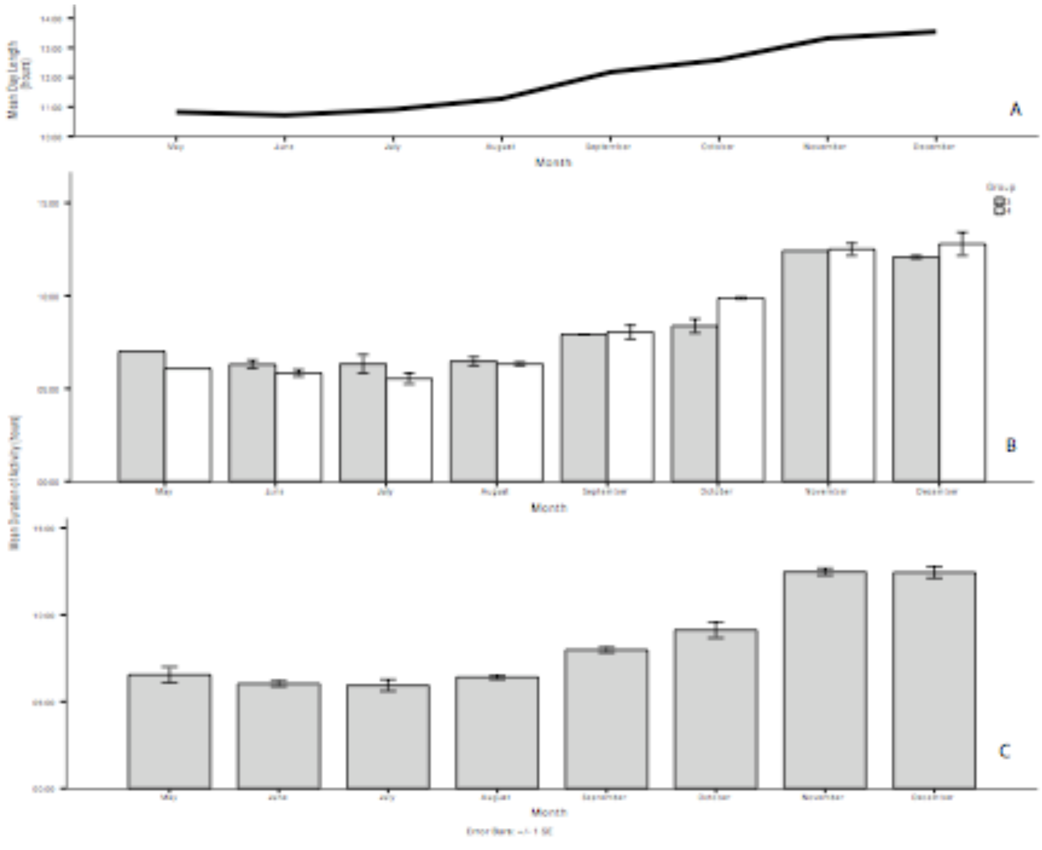


Figure 34 A: Mean monthly day length over the eight-month study period at KMNP. B: Mean daily duration of activity of *P.verreauxi* separated by group. C: Mean daily duration of activity of *P.verreauxi* for both groups. Showing that as day length increases, so does the duration of daily activity for *P.verreauxi*.

Daily duration of activity varied greatly during the eight-month study period at KMNP. The shortest measured duration of activity was 5 hours 15 minutes (recorded in July), whilst the longest duration was 13 hours 25 minutes (recorded in December). With the onset of the dry season, duration of activity began to decrease to a mean monthly low 5 hours 56 minutes in July (Figure 34C). A gradual increase in daily duration of activity was displayed from the low in July to a mean daily duration of activity in October of 9 hours 7 minutes (Figure 34C). November and December (the onset of the rainy season), were categorised by a huge leap in daily duration of activity, with the mean of those two months being 12 hours 27 minutes. Any differences in the groups with regard to duration of activity were purely down to chance ($U = 129$, two tailed $p = 0.621$).

Comparing Figure 34A and C, there is clear relationship between day length and duration of activity. A regression analysis gave a positive correlation for these two variables, producing a line of best fit with a formula: Activity duration = -19.009 + ($2.292X$). A relationship that proved to be significant ($t(32) = 17.843$, $p < 0.0001$, $R^2 = 0.909$) and with an R^2 value of 0.909 there is very little variation about the regression line, suggesting a strong correlation between day length and duration of activity.

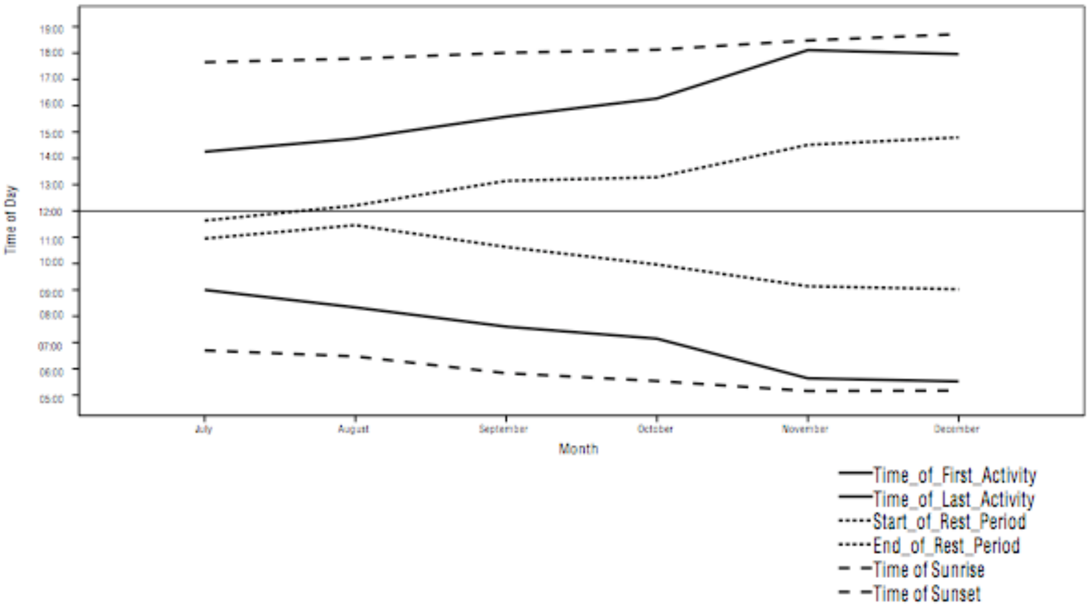


Figure 35 Monthly variation in the mean activity pattern of *P.verreauxi* including rest periods and mean day lengths. Showing an increase in duration of activity and rest periods with the onset of the rainy season.

During the start of the study period (May to July) *P.verreauxi* displayed a unimodal activity pattern with very small rest periods. From August to December an increasing level of bimodality appeared in the activity pattern of *P.verreauxi* (Figure 35). The shortest rest period was found during the month of August (30 minutes), whilst the longest (during December) was recorded at 365 minutes. At the beginning of the dry season (May) and leading into June, the activity length in both groups and overall, begins to decrease. As the dry season continues (July to October) a steady increase in activity length was observed. Whereas from October to November, a sharp increase in activity length appears (Figure 35), and then decreases slightly with the onset of December. Peak daily temperature occurs around midday and increases with the onset of the rainy season. A pattern of increasing rest period length can also be seen with the onset of the rainy season (Figure 35). These two variables correlate positively (Rest period = -636.945 + (24.010*X*) and show a significant relationship ($t(18) = 3.004$, $p = 0.008$, $R^2 = 0.334$), although the low R^2 value shows a high amount of variation around the regression line.

Discussion

Key Findings

- *P. verreauxi* has a much larger home-range within Kirindy Mitea National Park than in other more fragmented forests.
- Daily activity and ranging patterns decreased dramatically during the height of the dry season, suggesting that *P. verreauxi* conserves energy during periods of food scarcity.
- Increased ranging and length of daily activity during the rainy season suggest that *P. verreauxi* aims to increase body mass during periods of food abundance in preparation for the breeding season.

Overall Discussion

The finding that *P.verreauxi* has a mean home-range size of 15.7ha seems to be much larger than other studies performed on the same species. In other dry forest areas *P.verreauxi* ranges have varied from 4.0ha up to 10.1ha (Benadi et al. 2008; Harvey and Cluttonbrock 1981; Richard et al. 1993). The upper limit of 10.1ha is only marginally smaller than the home-range of group 3 in this study. The lower limit of 4.0ha (Richard, Rakotomanga et al. 1993), also comes from a study which has a very densely populated area of 80ha containing 27 different groups of *P.verreauxi*. Nevertheless, our result could be a consequence of the forest damage caused by cyclone Fanele, which is known to have dramatically affected the forest and has led to a 13.4% reduction in biomass (Lewis and Bannar-Martin 2011). It could also be a result of having almost no rain between the period of May to November 2010 (Figure 30), which caused the animals to range further in search of food and not be able to rely on known sources of nutrition within their usual range. The level of overlap reported in this study is much lower than the 36.5-63.7% reported by Benadi et al (2008). The difference is due to only two groups being studied, but it is known that the boarders of both groups are shared with at least three groups, which would place our value of between 6.1-9.9% for one groups overlap, within the same range. Other species within the *Propithecus* genus have also been shown to have considerably smaller and larger ranges than that of *P.verreauxi*. *P.diadema perrieri* has been reported to have a home-range of between 1.0 and 1.1ha (Lehman and Mayor 2004), whilst *P.diadema* has been shown to have a range of up to 27.0ha (Blanchard 2007). The fragmented and very much limited area of the habitat in which it lives can explain the tiny range of *P.diadema perrieri*. Whereas the larger range of *P.diadema* can be put down to it having a more frugivorous diet than that of *P.verreauxi* (Powzyk and Mowry 2003) and frugivory often demonstrates a strong correlation with large home range size among primates (Milton and May 1976). *Eulemur fulvus rufus* is a sympatric species in the Kirindy Mitea National Park and has been studied extensively at Kirindy CFPF, a nearby forest. It has been found to have a much larger home-range than that of *P.verreauxi* and its home range size has been shown to be dependent on the proximity to a water source (Scholz and Kappeler 2004). Disparities in home range size may be due to the need of *E. fulvus rufus* to drink during the dry season, whereas *P.verreauxi* has been shown not to drink during the dry season (Simmen, Hladik et al. 2003).

P.verreauxi displays very small daily ranges in the Kirindy Mitea National Park, with a mean daily range of 657m. Very similar results were displayed for *P.verreauxi* in the nearby Kirindy forest (CFPF) with small daily ranges during the height of the dry season, whereas ranging showed a jump in mean distance at the end of the dry season (Benadi, Fichtel et al. 2008). Whereas, meta-analyses of the role of folivory in daily ranging, quote the figure of 850m (Cluttonbrock and Harvey 1977) for daily ranging in *P.verreauxi*. In the Western dry forests *P.verreauxi* displays much lower daily ranging distances than most other members of the indriid family. Blanchard (2007) showed a mean daily range for *P.diadema* of 902m, whilst Warren and Crompton (1997), studying *Avahi occidentalis* had a mean daily range of 1175m. Other strepsirrhines also display much larger mean daily ranges, *Tarsius bancanus* has a mean daily range of 1765m (Crompton and Andau 1987); and also showed sex-differences, with males ranging further than females.

There are many conflicting theories surrounding the role of folivory and seasonal food scarcity pertaining to ranging distances. The findings that folivorous primates will have smaller home ranges (Milton and May 1976), also implies that daily ranging will be less. Studies comparing fragmented forests, with less food availability, with continuous tracts of forest; have found that food scarcity leads to a decrease in daily ranging (Irwin 2006). Whereas in studies of old world monkeys, daily ranging during times of food scarcity has increased (Mckey and Waterman 1982). The conclusion of this must be that different primates utilise different strategies in order to survive periods of food scarcity. In this case, *P.verreauxi* limits

its daily ranging behaviour in order to conserve energy when food is scarce; rather than ranging further in order to locate food. In addition to food scarcity, the birthing season of *P.verreauxi* also falls in July, the month of the lowest mean path length. It has previously been shown that primates who carry their young, such as *P.verreauxi*, will have smaller day ranges (Ross 2001). Carrying young may also contribute to the low levels of ranging displayed during the peak of the dry season. The impact of cyclone Fanele must also, not be underestimated. The 13.4% reduction in biomass (Lewis and Bannar-Martin 2011), could lead to even greater levels of food scarcity which will cause smaller path lengths. The likelihood is that all of these factors will play a role in *P.verreauxi* displaying very small daily ranging distances in comparison to those of other strepsirrhines and indriids.

The reduction in the mean daily area of the home range covered also backs up the decrease in daily ranging data, showing a decrease in area covered during the long dry season. Both of these results point to the theory that *P.verreauxi* employs the tactic of reducing its metabolic costs by ranging smaller distances in order to conserve energy. There is also an increase in ranging and area covered by *P.verreauxi* with the onset of the rainy season in the Kirindy Mitea National Park. Increased ranging may be apparent due to the obvious increase in leaf production which transforms Kirindy Mitea National Park during the rainy season. It has been indicated that during the months of October and November that there is a drastic increase in the proportion of young leaves that contribute to the diet of *P.verreauxi*, whilst the consumption of some fruits also occurs during this period (Yamashita 2002). An increase in the quality of diet is also essential to females during this period in order to increase their body mass for the onset of the breeding season, which for *P.verreauxi* takes place during the months of January and February (Brockman 1999). Higher body mass has been shown to positively correlate with success in breeding (Lewis and Kappeler 2005), which therefore leads to the increased ranging activity which is seen during this period in the year. These factors indicate that *P.verreauxi* conforms to the 'classic' breeding strategy, common among many primates which inhabit strongly seasonal environments (Schaik and Noordwijk 1985). This strategy is characterised by the females condition, which in turn has been influenced by food availability in the previous period of food abundance, which, in the case of Kirindy Mitea National Park is the rainy season.

There was a very large disparity during the month of November where the mean area covered by group four was much larger than the equivalent result for group three. Studies have shown that in some cases, making generalisations of a single species can be very inaccurate with regard to ranging behaviour (Chapman 1988). This is because it is sometimes apparent that species may not necessarily conform to the expected changes due to food availability or season. Although this may be the case in many rainforest studies, where masting events can quickly alter the ranging pattern of a given group of primates and seasonality is much less pronounced. When studying a primate which is described as obligate folivore, in a dry deciduous forest, which displays such strong seasonality, singular events such as occur much less regularly. Although the given discrepancy may be explained by such an event, where on one of the days sampled in November, it was noted that the group encountered rival groups of *P.verreauxi* on two different occasions during the given day of sampling. These encounters led to extended territorial disputes, which dramatically increased the day range and ranging area of this group on the given day.

With regard to day length and activity patterns, these data showed *P.verreauxi* to have a mostly unimodal activity pattern during the dry season (aside from very small rest periods). Unimodal activity patterns developed with the onset of the rainy season into a strongly bimodal pattern of activity. These animals are described as strictly diurnal with previous studies, which utilised twenty four hour monitoring showing that only 10% of activity was recorded during the night (Erkert and Kappeler 2004). These nightime movements were attributed to occasional sleeping movements or change of position during sleep, rather than any extended periods of motor activity. Also during consecutive day follows in this research, second day follows were located in the same sleep tree as they had been left in during the previous days data collection.

The increase in duration of rest periods from the onset of the rainy season could be attributed to an increase in temperature during the same period. These rest periods were all concentrated around the hottest part of the day and the hottest daytime temperature recorded during the study period was during December and was forty four degrees Celsius. Therefore this rest period may be a thermoregulatory tactic in order to reduce energetic cost in order to maximise body mass in preparation for the oncoming breeding season. The only other study involving activity patterns in *P.verreauxi* identified a complete opposite with rest periods being taken during the dry season and a unimodal pattern of activity during the rainy season (Erkert and Kappeler 2004).

In conclusion, the results of this long term study indicate that in the Kirindy Mitea National Park *P.verreauxi* shows high levels of adaptation to a highly seasonal environment. It does this by maintaining a relatively small home range, reducing daily ranging behaviour and limiting its periods of activity during the long dry season, characterised by food scarcity. Whilst during the rainy season, activity levels increase, ranging increases and longer rest periods during the hottest part of the day. These behavioural adaptations enable the sifaka to increase body mass rapidly during periods of food abundance, which allows females to increase body mass for the oncoming breeding season.

Chapter 4

The Use of Accelerometry to Monitor Locomotion the Locomotion of *Propithecus verreauxi* in Both a Captive and Wild Setting

Introduction

Primates are most notably known as an arboreal (although exceptions to this are clearly evident) order, necessitating the navigation of a three dimensional, discontinuous and very complex environment. If these factors are combined with the need to locate low quality readily available foodstuffs, such as leaves, and patchy separated nutrition found in fruit trees and insects. It is not surprising that this order has developed an array of locomotor modes to navigate through such a habitat. As a result of this arboreal lifestyle, and as the discontinuities between available supports increase, many primates have developed a leaping strategy in order to negotiate their environment. Therefore is a need for a high degree of postural and dynamic control. Although, even with such a high level of competence for arboreal locomotion it has been found that many primates carry injuries from falls, such as fractures, which have healed and this number can be as high as one in five adult individuals (Arlet, Carey et al. 2009).

Primates also display a huge degree of mass differences, ranging from 25 gram mouse lemurs up to adult male gorillas, which can attain a mass of up to 200 kilograms. The strepsirrhines alone span a 50-fold range in body mass, from the tiny mouse lemur up to the indri weighing in at seven kilograms. They also display a huge diversity in behaviour, from nocturnal, diurnal and cathemeral activity patterns. Diets ranging from insectivory and animalivory, to obligate folivores, feeding on nothing but leaves.

Monitoring locomotion in a non-captive environment has traditionally been performed by an observer, using a notepad and pen. Similar methods have also been used by observers, whilst more in depth captive studies have utilised camera equipment in order to capture images and analyse them using computer software. Most observer based wild studies of primate locomotion have used a method of sampling, called scan sampling, where any subject within a group can be sampled and the data is then collated in order to answer questions relating to a species (Crompton 1983; Crompton and Andau 1987; Blanchard 2007). Altman (1974), who suggested the scan sampling methods, also mentioned a method called focal sampling, where an individual is followed and only data pertaining to that subject is collected. Although, the drawbacks of this method, until now is that it always yields far less data than scan sampling and can cause issues of identifying a given member of a group, showing very little sexual dimorphism, therefore leading to collecting data from more than one individual.

Although observational techniques are still the norm with regard to wild primate research, it is now within the realms of possibility to obtain data from wild free roaming primate species of a more biomechanical nature. Measurements including the forces that muscles have to endure when locomoting in a three dimensional forest environment and also more accurate quantative measures of velocity and acceleration. Measurements such as these would allow researchers to see if, as expected, primates are strongly selected for efficiency of movement, either to optimise performance or to minimize the cost of locomotion. Folivory is heavily linked to a depressed metabolic rate due to the high cellulose content of leaves. *P. verreauxi* is an obligate folivore therefore it would be expected that a lower metabolic rate, would lead to this species displaying a mode of locomotion that is more energy efficient. Previous studies on other indriids has shown that locomotion only contributes 2% to the total daily metabolic energy costs (Dorcas Warren and Huw Crompton 1998), although the efficiency came as a consequence of such small daily ranging habits.

The use of accelerometers in order to monitor locomotion in free-ranging wild primates has, until now been prohibited by many factors, including cost, size, battery power and practicality. Traditionally, accelerometers have been used in more clinical environments to measure human movements, as it is a non-invasive technique and human subjects were large enough to be able wear multiple accelerometers without it impeding their ability to locomote freely (Morris 1973). Accelerometry had been limited to laboratory environments as there was no technology that enabled the data to be stored on the accelerometer, such as a micro SD card. More recently, data on animal and human movements has been recorded with accelerometers combined with walking on treadmills in order to analyse gait changes and speeds (Bidder, Soresina et al. 2012). The subjects used in these investigations were mainly birds and quadrupedal mammals, where the accelerometers were attached by harnesses or tape in order to keep them in place. The subjects in these studies were also captive animals from Buenos Aires zoo which were already habituated to human presence and had some form of training from the zoo staff. Studies on primates using accelerometers have so far been very limited (Erkert and Kappeler 2004; Sellers and Crompton 2004), with one of these studies being performed on captive lemurs and the other studying wild brown lemurs, but relating accelerometer data to activity rhythms. The only study using a similar methodology to this which has been performed looked at take off and landing forces in Malayan colugo, which can be extracted from the tree holes in which it lives (Byrnes, Lim et al. 2008).

Currently there is very little data surrounding the monitoring of wild and captive primate species using accelerometry techniques. At present there is only one study presenting data on the possibility of using accelerometer traces to recognise different modes of locomotion in captive lemurs (Sellers and Crompton 2004). A similar technique has also been used to monitor circadian rhythms rather than locomotion in wild *P.verreauxi* (Erkert and Kappeler 2004) and due to the reduction in sampling events, this allowed for a much longer battery life. Almost all comparable data sets have been obtained utilising the scan sampling methods described by Altmann (1974). Whilst this is a very widely used and accepted method of data collection, it relies heavily on the ability of a given observer to accurately estimate heights, distances and modes of locomotion and if there are several different observers collecting a given data set it must be ensured that they are collecting data in exactly the same fashion in order to prevent any bias within the data set.

With the advent of new technologies, such as micro SD cards for data storage and more powerful and compact lithium ion batteries, this study is looking to build on the small current data set that has been established on monitoring locomotion using accelerometers. It is hoped that techniques that have been previously limited to laboratory and captive environments will be adapted to enable data collection to take place in a wild free roaming environment. The progression into wild data collection will be facilitated by establishing a sound methodology in a captive environment, which will then be adapted to enable a smooth transition into the field environment. The data collected will not only be novel and the first of its kind to be collected in a wild setting using a primate subject, but it will also enable direct comparisons with observer based studies. The traces that are collected from the acceleration readings will be used to identify certain modes of locomotion. After this recognition has taken place, it will allow us to build a better picture of how often these animals use certain modes of locomotion to navigate their way in a three dimensional environment.

Materials and Methods

Data collection for this project took place in two different locations. Firstly permission was granted by the Cottswold Wildlife Park to gather data using their black lumurs (*Eulemur macaco*), although it would have been preferable to use a species at least in the same genus as *P.verreauxi*. The difficulty of using any members of the indriid family in captive research is that they are obligate folivores and the husbandry for such species is extremely difficult. The largest of the lemur species *Indri indri*, has in fact never been successfully kept in captivity. Therefore all captive indriids are very important to their establishments for captive breeding programs. For these reasons, zoos are understandably very protective of Indrrid specimens and any form of 'hands on' research is almost always forbidden. Therefore the Cottswold wildlife park offered access to *E.macaco*, as these specimens were past breeding age and had been in captivity for a long period and were well acclimatised to human contact.

Field data was collected in the Kirindy Mitea National Park, located in southwestern Madagascar (around 70km south of Morondava). The subject for this study was the indriid primate *P.verreauxi*, also known as the sifaka. Kirindy Mitea National Park was chosen as it is a well established field station with several groups of habituated sifakas and the fact that there were no other groups performing research at the site at the same time. High levels of seasonality define the site, ranging from a short, hot rainy season from December until April; to a long, cool dry season from May to November. Data collection took place between April 2010 until January 2011, a full year was the anticipated length of the field season, but a military coup in Madagascar delayed departure for a couple of months.

Equipment Design

Data loggers were ordered from Sparkfun, which log three axis accelerometery, pressure and GPS. The data loggers were re-programmed to enable acceleration samples to be taken 50 times per second, with GPS readings being taken once per second and pressure sampled ten times per second. To ensure that the data loggers are not damaged by water a Lava V300 vacuum packager was purchased. The vacuum packer was used to vacuum pack the data loggers and batteries in a neat water-tight package which will be attached to the target species. To secure the data logger on the target species, a ferret harness, purchased from a pet shop, was adapted slightly and the data logger secured to the harness with duck tape.

Locomotor Study at Cottswold Wildlife Park

Figure 36 Left = clockwise from top left: data logger, lithium ion battery, GPS. Right = black lemur (*Eulemur macaco*) wearing data logger harness.

Firstly a laboratory test was performed, whereby the data loggers (in the setup described above) were: shaken, left at rest on a bench and also thrown into the air. Providing some crude preliminary results to show what the accelerometer trace may look like when attached to the target species while the animal is at rest or performing a leap. The shake test was performed to provide a clear reference point at the beginning of the data set, which all timings can be related to.

A captive study was then performed at the Cottswold Wildlife Park. A data logger was attached via the harness to an adult male black lemur (*Eulemur macaco*)(Figure 36). Prior to this the data logger system was weighed in its entirety to ensure that the weight of the system would not compromise or affect the subjects locomotion (10% of the animals body weight is the accepted limit). A shake test was performed prior to attaching the data logger to provide a clear reference point on the accelerometer trace. The lemur was then released into its enclosure and allowed to roam freely. The animal was observed in its enclosure and all locomotion was recorded using a Sony Handycam. Recording the animal while collecting data enabled us to match the film that was recorded with the acceleration traces, this showed exactly what the animal was doing at set time points on the acceleration trace. The process was repeated on two consecutive days on the same animal, and the harness remained on the animal for an eight-hour period during the day. The black lemur was used as the subject as there are very few sifakas in captivity in the United Kingdom, and permission to perform the study on these specimens was denied.

Locomotor Study Kirindy Mitea National Park

Figure 37 ***P.verreauxi*** **being fitted with an accelerometer in Kirindy Mitea National Park.**

The methodology used in Madagascar was adapted from that which was used in the zoo environment. These changes were brought about due to the necessity to tranquilise the animals. Firstly, the animals were tracked using a Sika VHF receiver, as one animal in every group was fitted with a brass radio collar (Biotrack, Dorset UK). Tracking was performed in the morning so that, once captured, the sifakas were not tranquilised during hottest part of the day, but also it gives the longest amount of time before darkness falls for the animal to recover from the anaesthetic. Specialist Malagasy darters were hired to perform the captures as per the request of

Madagascar National Parks. Animals were darted in the thigh with a blowpipe using the telinject darting system for anaesthetic delivery. Once the animal had been darted, members of the field crew would follow the subject with a blanket to catch it in once it fell from the branches. Individuals were darted using disociative anaesthetics, the two most commonly used in Madagascar are telazol and ketamine. The ketamine comes in liquid form at a set concentration and can be loaded directly into the dart to be administered. Telazol on the other hand has to be mixed to a set concentration with distilled water before it can be loaded into a dart. The dosages and concentrations administered adhered to accepted guidelines used in previous periods of capture using closely related species (Burroughs 1993; Medicine 2001). Once immobilised the captured animal was taken to a shady field laboratory nearby. Core temperature of the individual was monitored using a rectal thermometer and if the animal was overheating, it would be cooled by pouring small amounts of water on its chest, until the temperature was back within the accepted range. To prevent any further stress to the animal, rather than fitting the animal with a harness, the accelerometer was fitted using Locktight superglue. Adhesive prevented the necessity of capturing the animal for a second time to remove the harness, as, once the glue had worn off, the accelerometer would simply fall off. The animal was then placed into an empty pillow case in a quiet shady area to enable it to recover from the anaesthesia. If at any point during the fitting of the accelerometer an animal became overly active and seemed to be recovering from the anaesthetic too quickly, a second dose of anaethestic was administered using a syringe in order to prevent any unnecessary stress to the animal. Accelerometers were placed as close to the cetre of mass of the animal as possible, therefore the area chosen was just above the pelvic girdle on the dorsal side of the animal (Figure 37).

Once the animal had recovered sufficiently from the anaesthesia, the rest of the sifakas group was re-located using the radio collar. The animal was then released onto a nearby vertical support. All animals recovering from anaesthesia were followed until the observer was sure that the individual had re-joined the group and was feeling no ill effects from the anaesthesia and was locomoting freely. Once the animal had been released, the same methodology as the captive project at Cotswold Wildlife Park was utilised where the animal wearing the accelerometer was followed and filmed using a Sony Handycam.

All animals wearing accelerometers, even after the battery power had been exhausted, were checked daily to see if the accelerometer had detached itself from the subject. To ensure that all accelerometers were relocated, radiotracking beads were glued to the accelerometer before the unit was vacuum packed. In order to maintain the maximum range on the tracking bead, it was necessary to keep the aerial for the bead as straight as possible. Once the accelerometer had fallen from the animal it was relocated using the Yagi flexible antenna and Sika radio tracking unit.

Data Analysis

The video footage that was captured was converted from its raw format into MP4 format using iSkysoft video converter. The MP4 video footage could then be analysed using editing software from Avidemux. For analysing the video, very broad locomotor categories were chosen: resting, slow terrestrial quadrupedalism, fast terrestrial quadrupedalism, slow arboreal quadrupedalism, fast arboreal quadrupedalism, climbing and leaping. The timings of these events on the video were then recorded. The information on the data loggers was uploaded into Matlab 7.4 and acceleration traces were created. The traces were then linked to the locomotor behaviours, which were viewed in the video data. Data smoothing was performed on the data, using a moving average smoother in MatLab, to attempt to remove some of the high frequency noise from the traces. A fast fourier transform (FFT) was performed using the MatLab signal processing toolbox to attempt to find the fundamental frequency of some of the locomotor modes (Sellers and Crompton 2004). Lastly the frequency of the locomotor bouts was calculated in the form of a percentage to investigate which locomotor modes were preferred by *Eulemur macaco*. The amount of time spent performing each different form of locomotion was calculated from the video data, and then the percentage of time spent locomoting in this fashion was then calculated.

Results

Captive Study Results

Over eight hours of video data and 15 hours of accelerometry data was collected over a two-day period. The explicit aim of collecting the data was to test if the accelerometer was sensitive enough to recognise changes in locomotor behaviour in a black lemur (*Eulemur macaco*).

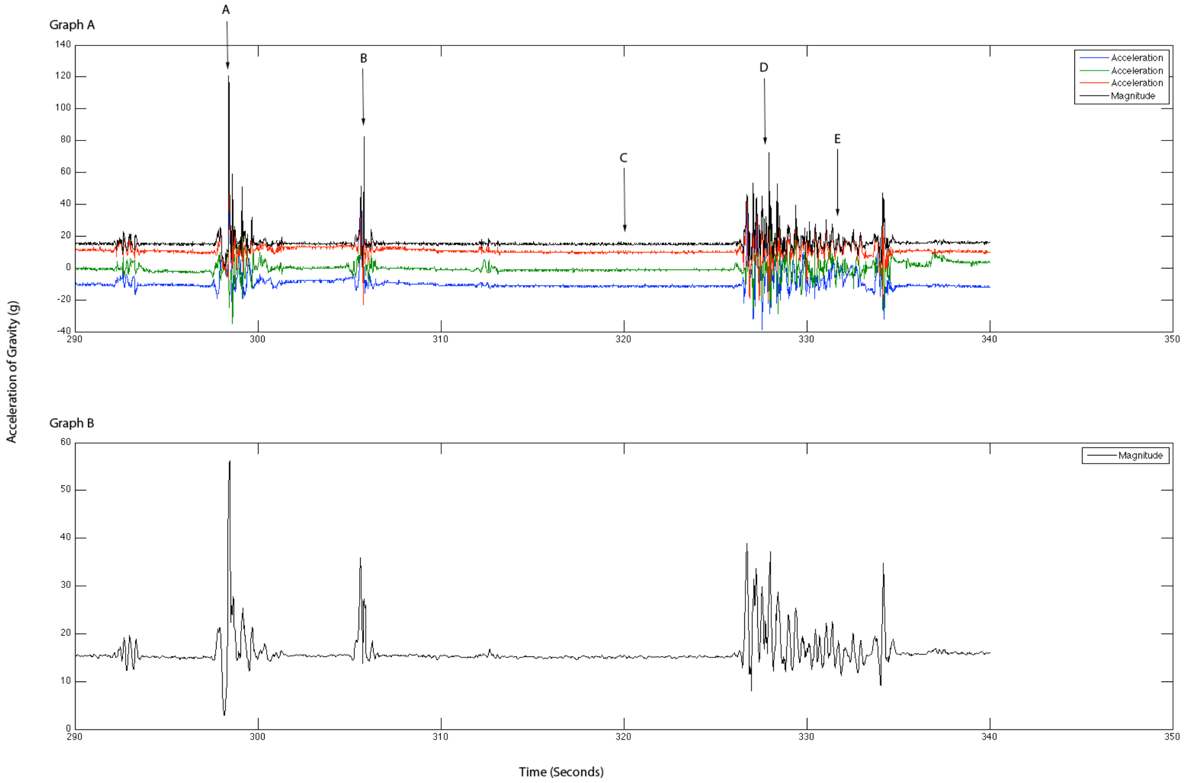


Figure 38. Graph A: 50-second extract from the accelerometry data displaying locomotor patterns. A = leap, B = leap, C = rest, D = three successive leaps, E =

fast quadrupedalism. Graph B, the same 50-second section with the magnitude smoothed

Figure 10 demonstrates the general accelerometer patterns which are shown on the trace when the black lemur engages in leaping behaviour (A, B and E, Figure 38). A and B show two single leaps and clearly display the sudden increase in acceleration that would be expected when an animal propels itself off of the ground. D represents a group of three successive leaps hence the increased duration of high amplitude peaks seen at this point. These three leaps are immediately followed by a period of slightly reduced amplitude cyclic readings that was recognised on the video data as a period of fast quadrupedalism (E, Figure 38), lasting around five seconds. Leaping can clearly be differentiated from other forms of behaviour, such as rest (C, Figure 38). Rest is categorised by a period of no acceleration and baseline measures as the animal is not moving, apart from to breathe. Leaping traces cannot be separated into clear sections, of take-off, flight and landing, due to the presence of high frequency noise in the data. To try and depict a clearer version of events smoothed versions of the magnitude traces are depicted (graph B, Figure 38), which give a clearer depiction of more cyclic behaviours.

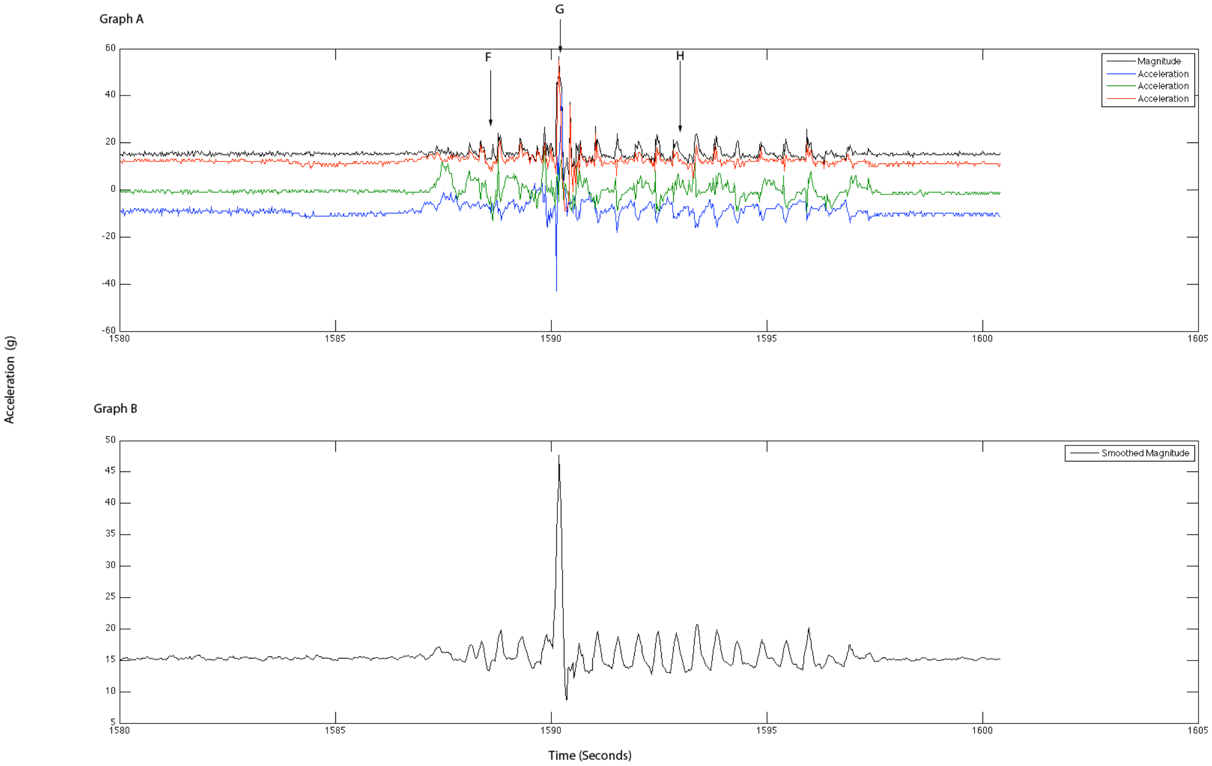


Figure 39, Graph A 20-second extract of accelerometer data showing two separate locomotor behaviours, F and H = quadrupedalism and G = leap. Graph B smoothed magnitude trace of the magnitude line in graph A.

Quadrupedalism is a cyclic behaviour that is depicted at points F and H (Figure 39). Quadrupedalism produces an oscillating trace which can be viewed more clearly in the smoothed magnitude graph (graph B, Figure 39). Point G shows the stark contrast in amplitude between leaping and quarupedalism, with the large amplitude single spike of the leap in comparison to the small amplitude cyclical nature of quadrupedalism.

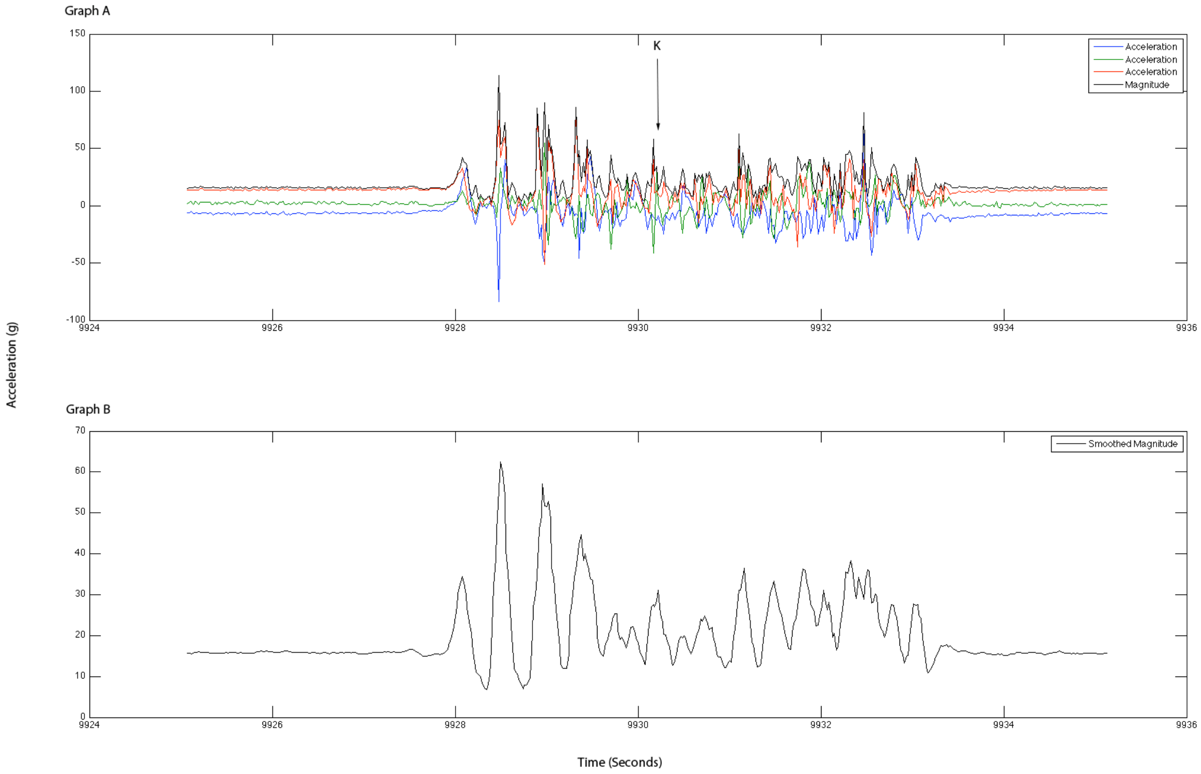


Figure 40 Graph A, 12 second extract from the accelerometer depicting fast quadrupedalism (K). Graph B, a smoothed version of the magnitude trace shown in grpah A.

Fast quadrupedalism (point K, Figure 40) is demonstrated by an oscillating trace of much larger amplitude than was demonstrated in quadrupedalism. The increase in acceleration is expected, due to the fact the animal is traveling much faster during fast quadrupedalism. The amplitude of the oscillations also decreses at point K, which is due to a decrease in speed at which the animal is traveling.

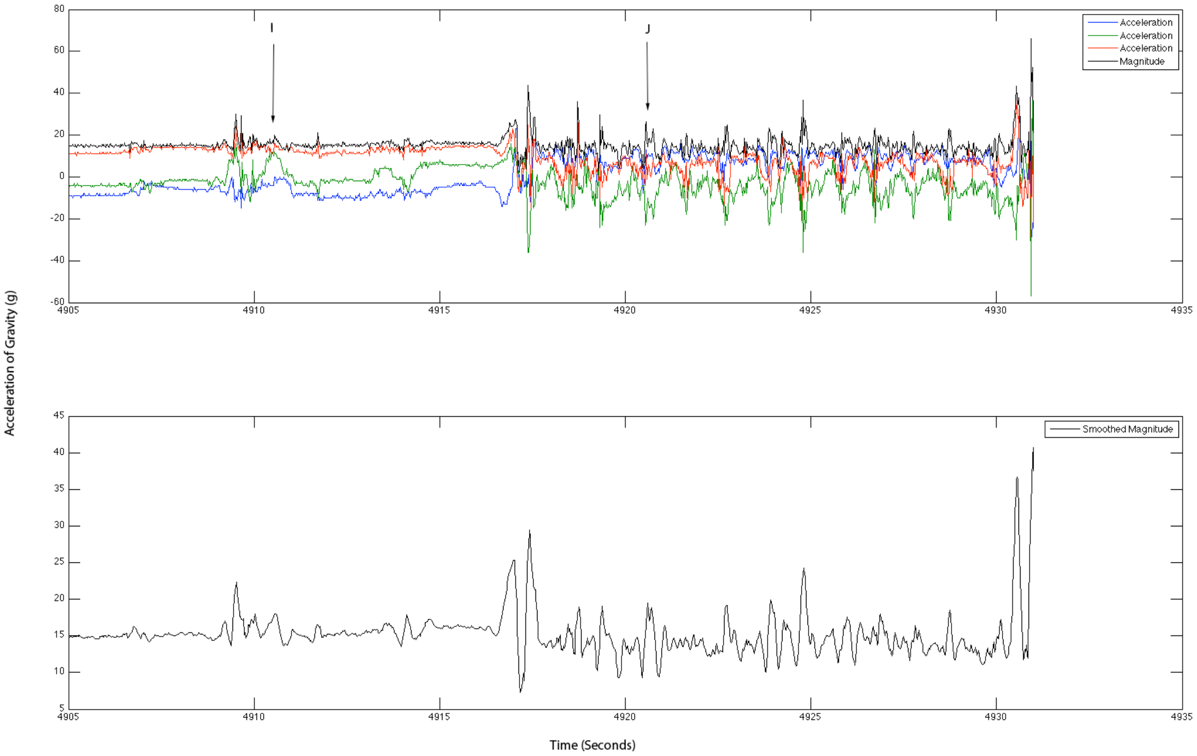


Figure 41. Graph A, a 26 second extract from the accelerometer, I and J = climbing. Graph B A smoothed version of the magnitude trace in graph A.

Climbing (I and J, Figure 41) gives a very similar trace to that of quadrupedalism and is demonstrated by a small amplitude oscillating trace. At point I, the animal was observed to be climbing up a fence. Followed by a period of rest, then the animal began to climb across the fence, which changes the orientation of the accelerometer. A change in orientation led to a drop in the values for the red and green axes of acceleration, whereas the axis depicted in blue increased.

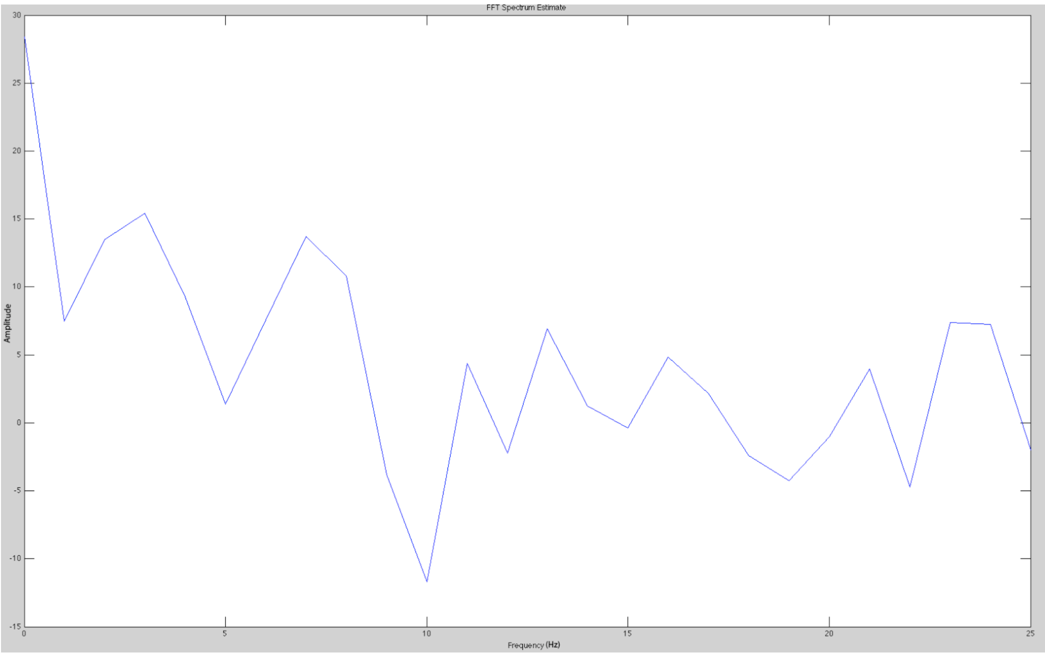


Figure 42. Fast Fourier transformation of a 5 second extract of acceleration data during fast quadrupedalism

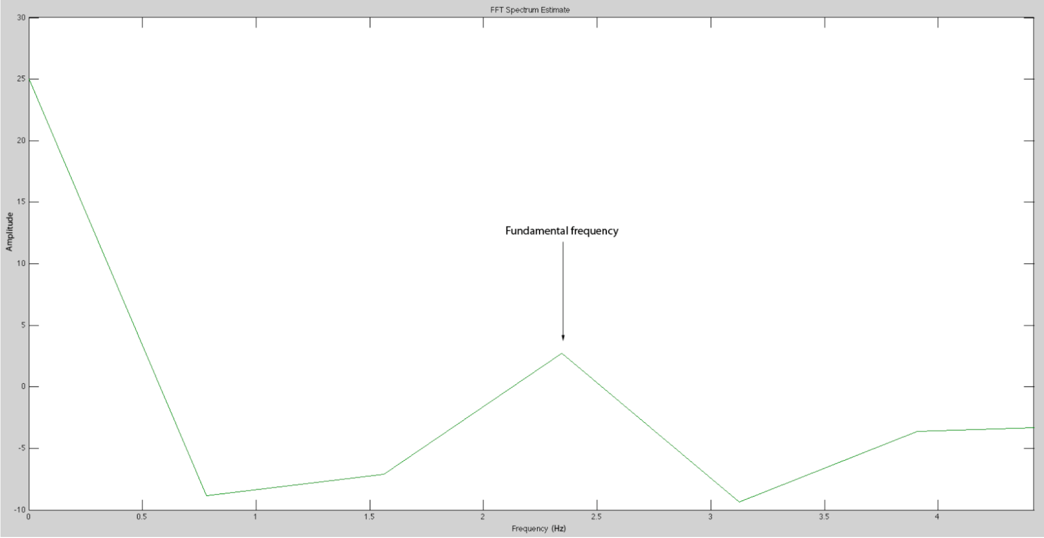


Figure 43. Fast Fourier transformation of a 5 second extract of acceleration data during quadrupedalism

Fast Fourier transforms were performed on five-second data segments of continuous data for quadrupedalism (Figure 43) and fast quadrupedalism (Figure 42). The amplitude peak shows the fundamental frequency for quadrupedalism is 2.3Hz, which means that the time for one complete oscillation of quarupedal locomotion to occur is around 0.43 seconds. Whereas, no fundamental frequency could be deduced from the fast quadrupedalism Fourier analysis due to there being no clear peak representing a fundamental frequency.

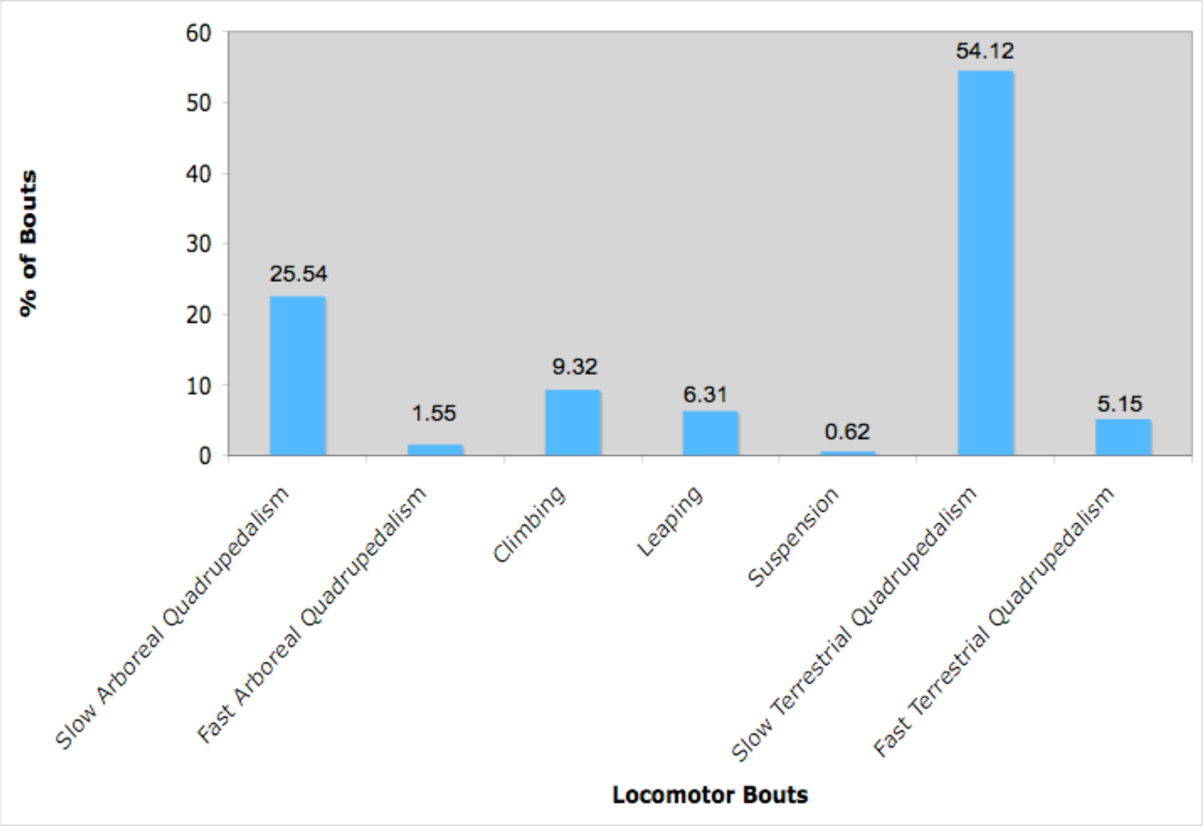


Figure 44 Locomotor frequencies for different locomotor bouts in Eulemur macaco.

From Figure 44, it is clear the quadrupedalism is the most frequently used mode of locomotion in the black lemur. In total 86.36% of all locomotion was quadrupedal with 62.67% of all quadrupedalism being slow terrestrial quadrupedalism. In terms of slow quadrupedalism there was a clear preference shown for this form of locomotion in both the arboreal and terrestrial habitat, with slow quadrupedalism accounting for 92.24% of all quadrupedal events. In terms of leaping, an event that lemurs are most known for, this only accounted for 6.31% of all locomotion.

Accelerometer Results from Kirindy Mitea National Park

No analysable results were collected from the accelerometer data loggers that were attached to *P. verreauxi* during the field study in Kirindy Mitea National Park. Although, over the field season five accelerometers were attached to individuals for data collection purposes, none of these yielded any useable data. The reasons for this lack of data collection will be reviewed in the discussion for this chapter.

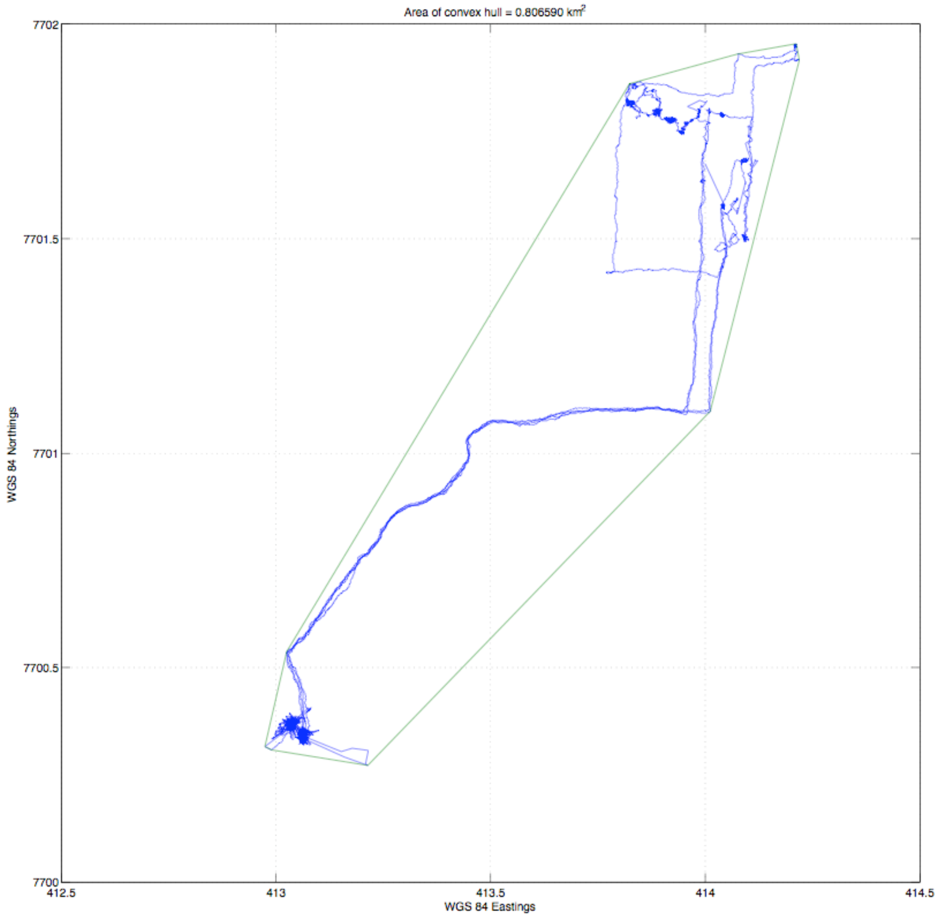


Figure 45 GPS recording from an accelerometer

The only data collected from any of the data loggers attached to the lemurs was a GPS trace (Figure 45). Unfortunately almost all of the ranging behaviour that is displayed is from researchers transporting the animal back to the camp for an overnight stay as the sifaka had taken an extended period to recover from the anaesthesia. The animal was then transported back into the forest the following morning, where thirty minutes after it was released, the battery life of the data logger expired.

Discussion

Key Findings

Findings from the captive study suggest that accelerometry is a useful tool for remotely monitoring primate locomotion. Different modes of locomotion can clearly be defined from the acceleration traces. Several unavoidable and unpredictable factors prevented the replication of the results of the captive study within a wild setting.

Overall Discussion

The main aim of this study was to demonstrate that an accelerometer can be used to recognise pre-defined patterns of locomotion. Leaping is clearly visible as a very short period of high acceleration that shows a high amplitude peak in graphical form. More cyclic locomotor patterns such as climbing and quadrupedalism display very similar acceleration patterns, although the orientation of the accelerometer changes the strength of the signal in the different axes. Axial differences allow for differentiation between locomotor modes which produce a signal with very similar axial oscillations. The differences between slow quadrupedalism and fast quadrupedalism are shown by a large change in amplitude of the trace. Fast quadrupedalism shows more oscillations for a given period of time than quadrupedalism. These results compliment the results of similar studies of remote monitoring using accelerometers (Sellers, Varley et al. 1998; Sellers and Crompton 2004). Even though the accelerometer used in this study only samples at half the rate of the previous investigations, similar patterns in the acceleration trace were still viewed but this accelerometer samples in three axes rather than just one.

Some of the locomotor behaviours that were listed to be recognised in the materials and methods section, such as arboreal quadrupedalism, fast arboreal quadrupedalism and suspension, could not be visualised on the traces. The failure to recognise these patterns was due to the fact that there were not long enough periods of each of these behaviours to recognise a pattern or signal within the data; mainly due to the lack of trees present in the animal's enclosure. Even if arboreal quadrupedalism had occurred enough to see a trace, the thickness of the branch and its compliant nature (if very thin) may have changed the trace slightly.

Fast Fourier transforms were performed on the data in an attempt to discover the fundamental frequency of each locomotor activity. The fundamental frequency of quadrupedalism was recorded at 2.3 Hz, whereas the fundamental frequency of fast quadrupedalism was not clear. There were many peaks within the Fourier analysis for fast quadrupedalism, this may be caused by the animal adjusting its speed during the period analysed, creating many different peaks for the varying velocity observed. Other locomotor behaviours, such as arboreal quadrupedalism and climbing could not be analysed as not continuous length of continuous climbing or arboreal quadrupedalism could be identified in the data, which was long enough to analyse.

High frequency noise was ever-present in the data; this can be attributed to the fact that the animal was wearing a harness with the accelerometer attached. However tightly you fit the harness to the animal, it will still bounce around in addition to the animal's movements. Therefore lots of smaller acceleration peaks are created due to the effect of this bouncing. Signal interference was tackled in the analysis by smoothing the data to present a clearer image of the behaviours demonstrated, as in (Sellers and Crompton 2004). To try and prevent this bouncing effect when in the field, the accelerometer will be glued to a shaven area of the animal's skin as in (Byrnes, Lim et al. 2008), which produced more accurate data collection. The position of the accelerometer on the animal (Figure 9) also may also have caused some noise within the data. The harness sat very high up on the animals back, between the shoulder blades. Positioning such as this meant that any movement of the head or shoulders of the animal would have been recorded. A better method is to place the accelerometer dorsally, as close to the centre of mass as possible, which is around the base of the spine. Dorsal placement would pick up much less irrelevant data, such as minor head movements or upper body rotation.

With lemurs so regularly being studied for their leaping ability (Oxnard, German et al. 1981; Demes, Jungers et al. 1996; Crompton and Sellers 2007), the amount of time spent performing leaping was surprisingly low. Although in terms of purely the amount of leaps performed, there were 102 individual leaps performed during observations compared to 188 occurrences of slow quadrupedal locomotion, but the time taken to leap is much less than quadrupedal locomotion, which can continue for a very long period of time and not just as far as the animal can propel itself. Still, a very small amount of time that has been spent leaping compared with other investigations, which suggest a leaping frequency of between 28% and 58% (Gebo 1987; Tilden 1990; Sellers and Crompton 2004). These investigations were also carried out over a larger period of time and also some used different sampling techniques of switching subjects if no locomotor incidents occurred after a minute (Gebo 1987). During the fieldwork data collection, data will be collected over a twelve month period, allowing for a much more accurate representation of how often wild lemurs perform different locomotor bouts.

With no analysable data collected from the accelerometer data collected during the wild field study in Kirindy Mitea National Park, it is only correct to discuss the problems faced in terms of methodology in an attempt prevent any future data collection using similar methods to fall foul of these issues. The first thing to discuss would be the accelerometer unit itself. Although the accelerometer itself is small, there were four different components which needed to be attached together in order for the methodology to work in the wild: the accelerometer, GPS unit, battery and radio tracking bead. Albeit the components were glued together, the connectors that linked the systems together were very fragile. Fragility led to connections being lost between the battery and the accelerometer or GPS meaning that the sampling was heavily reduced. Also, these components had to be placed in a certain layout in order for the items that needed to receive or emit a signal to function correctly. These components were the GPS unit, which needs to gain signals from satellites in order to pinpoint its position. Also, the radio-tracking bead, which emitted a VHF signal via an aerial, needed the aerial to be as straight as possible in order to gain the greatest range (1km) on the signal emitted. If this is added to the fact, that in order to get a relatively large, flat surface area upon which to secure the unit to the animal, meant that the most robust piece of the equipment, the battery, was located on the dorsal surface of the animal, which was the most protected. Therefore the most fragile components of the accelerometer unit were the most exposed.

With such fragile electrical components highly exposed and only being protected by the plastic of the vacuum packing bag, this led to them being damaged. Lemurs are known amongst primate species for being for being the least dextrous order in comparison to apes, old and new world monkeys (Torigoe 1985). Within this order, *P.verreauxi* and *D.madagascarensis* show the greatest level of manual dexterity (Pellis and Pellis 2012). High levels of dexterity would certainly enable them to manipulate the accelerometer and damage it by removing components or disrupting the connections between the given components. A study with incredibly similar methodology (Byrnes, Lim et al. 2008) conducted a survey on the Malayan colugo *(Galeopterus variegates*), had much more promising results investigating this species. These results may be due to the fact that the Malayan colugo has claws rather than nails which are designed to grip tree trunks, preventing this species from interfering with the components.

Given the success of the captive study at Cottswold Wildlife Park, where animals wearing the harnesses showed no interest in the harnesses being worn or the accelerometers, it was assumed that their wild counterparts would show a similar level of disinterest. Although the placement of the accelerometer had to be adjusted slightly to accommodate the more slender frame of *P.verreauxi* in comparison to *E.macacao*, it was not anticipated that this minimal adjustment in placement would affect the animal's attitude towards the accelerometer. But individuals fitted with the accelerometers were regularly observed attempting to manipulate or remove them with both their forelimbs and their teeth. The other issue that let to the loss of two accelerometers, was that the most prominent component of the accelerometer unit was the radio tracking bead. The bead produced a VHF signal, which was the only means of locating the accelerometer once it was detached from the animal. Due to the need for a clear signal this made it the first thing that the lemurs came into contact with when interfering with the unit, it was also very small, so only a limited amount of glue could be used to attach it to the accelerometer. Leading to the animal removing this part of the accelerometer before the entire unit detached, meaning that the unit was never recovered.

Normally, this would lead to a return to the laboratory in order to re-design the equipment, packaging or adjust the placement on the animal. Unfortunately, prior to departure the idea of re-packaging the accelerometer in a hardier casing was discussed at length, but no better solution could be found. The proposition of encasing the accelerometer in epoxy resin was rejected as it would add far too much weight to the accelerometer, which would then exceed the accepted 10% of the animals adult body weight. The density of the resin would also prevent the GPS unit from gaining a signal from satellites and render it useless. The adaptations to the epoxy would have lead to large holes in the resin for GPS, the tracking beads VHF signal, the battery recharging port and access for the micro SD card. Meaning, that if it rained after the accelerometer fell from the animal and was waiting to be found, that this would damage the electrical circuits and render any stored data irretrievable.

Other methods have been used to attach accelerometer to *P.verreauxi* in the nearby forest of Kirindy (Erkert and Kappeler 2004). Although the equipment used was similar, the focus of the research was very different. The accelerometers in this study were used to monitor activity rhythms, rather than locomotion. Therefore it was viable for the researchers of this investigation to encase the accelerometers in a metal box and attach them to collars which were worn around the animal's neck, in a almost identical fashion to the widely used radio-collars. A methodology such as this was just not viable for this investigation. Firstly, the sampling frequency was heavily reduced, this meant that the battery life for the accelerometer was increased drastically, so the collars were worn over a much longer period of time. Secondly, any background noise created by the collar moving independently of the animal was not an issue in the study as it was not attempting to pick out individual modes of locomotion, just indicate of the animal was active or inactive. Therefore, a methodology such as this was just not suitable for a study collecting data on locomotion. The only adjustment that could be made given the remoteness of the field site and the limited availability of any useful products to amend the set up, was to encase the entire vacuum packed unit in duck tape in an attempt to reduce the damage caused by the lemur.

Other unforeseen factors also affected the amount of data collection using the accelerometers. Due to the necessity of capture it was required that permission was gained from Madagascar National Parks, prior to arrival, for periods of capture to be performed at the field site. Authorisation was granted, but with the proviso that a local resident would have to be trained to perform these captures in order to provide employment in the local area as there were no experienced personnel within reasonable traveling distance of Kirindy Mitea National Park. Therefore, for the first capture period, a specialist darter was flown in from Beza Mehafaly, a research station located 600km to the south of Kirindy Mitea National Park. The specialist performed the first period of capture whilst training a local resident recommended by the camp manager. Training was due to continue with the local resident returning to Beza Mehafaly with the darter in order to gain more experience. Unfortunately, Madagascar National Parks had amended the original agreement and said that rather than a local resident it would have to be a parks employed agent who performed capture within the park as it had come to light that elsewhere in Madagascar, local residents had used learned capture skills for hunting purposes and this would not happen if the darter trained, worked for the National Parks agency. Recruiting a suitable individual delayed any further periods of capture whilst a candidate was chosen and then travel arrangements were planned.

Unfortunately, the chosen candidate did not have sufficient time training with the expert, due to his other work commitments with Madagascar National Parks in Kirindy Mitea National Park. Therefore when he was hired for a capture period, it was realised that he did not possess the required skill level to perform captures without there being an increased risk to the animals. Hence, it was decided that this individual could no longer be used to aid in capture periods. At this time, there was also a blanket ban placed on the capture of lemurs across the entirety of Madagascar. These factors all added to the limited number of individuals that were fitted with accelerometers during the field season. The only other period of capture occurred when the blanket ban on capture was lifted and there was an opportunity to collaborate with a qualified Malagasy veterinarian, who aided in a capture period where three lemurs were fitted with accelerometers.

Other issues which limited the data collection stemmed from three issues that combined to reduce levels of data drastically. Firstly, the recovery from the anaesthesia was a long process. Using a blowpipe is certainly not an exact science, and the main concern during a period of capture is reducing as many of the risks to an animals health as much as possible. Although capture was started as early as possible, it often took a long period of time to have a given individual in a good position in an attempt to secure a good shot into the upper hindlimb. Due to *P.verreauxi* being arboreal, a large enough dosage is required to cause the animal to fall from the tree and often when a dart hits, the full dosage is not administered necessitating a second dart to be administered. Two darts often lead to the animal receiving a larger dosage that in turn leads to an increased recovery period. Necessitating animals being returned to camp overnight in order for them to fully recover from the effects of the anaesthesia. One of the major factors that could attribute to elongated recovery periods is that *P.verreauxi* is an obligate folivore, which means that it has a much lower metabolic rate which means it takes longer to metabolise the anaesthesia. Overnight observation is not an uncommon event during capture periods (Cuozzo, Sauther et al. 2010), but had a large knock on effect on the sampling period due to battery life.

To prevent the unit from weighing too much, lithium batteries were used to power all of the components. The choice of battery was also limited by this factor therefore the battery life was limited. During preliminary testing, the longest the battery lasted before exhaustion was 28 hours. Obviously this is the optimum and battery life can be much shorter than this. If this is combined with the fact that recovery periods can be more than fifteen hours in length, if an overnight period is required, then the sampling period can be drastically reduced. Other studies have been shown not to require anaesthsia, due to animals such as the colugo (Byrnes, Lim et al. 2008) not only being relatively small, but spending daylight hours in a specific tree hole which they can be captured from by hand. Prior to departure to the field alternative capture methods were discussed, such as trapping. But these ideas were rejected due to the fact that *P.verreauxi* is a folivore and therefore eats a readily available food source so would therefore not be easily tempted into a trap. Also, sifakas are a large arboreal primate, so securing a large enough trap in an arboreal environment would be a very difficult task. Lastly, capturing an animal in a wild environment is a very stressful event for the animal, so in an attempt to reduce stress levels as much as possible it was decided to use anaesthetic as attempting to manipulate a sifaka without the use of anaesthesia would be far too stressful for the animal.

The final problem that added to the problems of battery power and anaesthesia recovery was that of the animals response to human presence post capture. During a normal capture, such as that for fitting of a radio collar, morphometric measurements or collection of blood samples; there is no need for the captured animal to be followed immediately post-capture. Normally any group of animals which have any individuals captured are left alone for at least a twenty four hour period so as not to stress the animals any further. Unfortunately with the combined effects of the anaesthetic recovery and short battery life, it was necessary to follow the groups as soon as possible after release. Leading to fleeing responses being displayed in the presence of an observer and this severely hampered any attempts to gain video footage simultaneous with accelerometer data.

Overall, the positive results gained in the Cottswolds Wildlife Park and other captive studies performed on lemurs (Sellers and Crompton 2004), led to the belief that the wild study in Kirindy Mitea National Park would gain similar results. Unfortunately the reaction to wearing the accelerometer of wild *P.verreauxi* was not expected and the possibility of attaching the unit to a harness was not an option in a wild scenario due to the need to recapture the animal after such a short period of time. Other more beauraucratic factors led to far less sampling than was anticipated. Lastly the combination of battery life, anaesthesia recovery and group responses led to a very small data collection window.

Even though the issues discussed hear sound as if they condemn the methodology, there are positives to be taken from this investigation. During the captive study there were clear definitions between different locomotor modes, which means that it would be possible to recognise these same definitions in wild subjects. Since the field season finished in 2011, there have already been advances in accelerometer technology, making the unit smaller and possibly less noticeable when attached to the individual leading to less attempts to remove the accelerometer. In the long term, finding a methodology which produces results in this field would enable complete remote monitoring of a given species locomotion. Accelerometry would produce huge quantities of data on a single animal in comparison to focal sampling or scan sampling. It would also not require a given group to be habituated in order to collect data from them and multiple accelerometers could be attached simultaneously to enhance data collection.

Chapter 5

Discussion

General Discussion

Key Findings

- *P. verreauxi* relies heavily on leaping as its main mode of locomotion to navigate within the forest environment. Utilising mid-range diamter, upright supports, it is correctly classified as a vertical clinger and leaper.
- In Kirindy Mitea National Park, *P. verreauxi* shows a relatively large home range in comparison to studies in other forests. Although large, this home range is only fully exploited during the rainy season. During the dry season, a lack of nutrition leads the sifaka to conserve energy by ranging less.
- The use of accelerometry demonstrated, that under captive conditions, it can be a useful tool for monitoring locomotion. A differenct set of factors prevented the replitcation of the success shown in the captive study, within a wild setting.

General Conclusions

The research in this thesis has described how *P. verreauxi* locomotes within an arboreal environment. What modes of locomotion it utilises to navigate within this environment and what activities those forms of locomotion are used to perform. It also investigates home range, daily path lengths and activity patterns, discussing how all of these behaviours are affected by a highly seasonal environment. Lastly, it attempted to use a novel method of accelerometry to also quantify how *P. verreauxi* locomotes.

The locomotion if *Propithecus verreauxi*

The first chapter of the thesis investigated what modes of locomotion *P. verreauxi* uses to locomote within a forest environment, how often they are performed and what substrates are most often exploited. These investigations have provided quantitative data that supports previous findings that *P. verreauxi* relies heavily on leaping as its main mode of locomotion to move around the forest (Dagosto 1995). This study employed traditional scan sampling methods (Altmann 1974), making it highly comparable to similar locomotor studies performed on strepsirrhine primates. The findings of this first chapter were important to developing a greater understanding of sifaka locomotion, substrate use and activity.

Home range and daily path lengths

Data presented in the second chapter of this thesis investigated the home range size, daily ranging distances and activity patterns of *P. verreauxi* within Kirindy Mitea National Park. Chapter two demonstrates that within Kirindy Mitea National Park, these primates show a larger home range area than other sifaka species (Wright 1995; Nagy 2007; Benadi, Fichtel et al. 2008). The increase in home-range at KMNP may be due to other locations facing overpopulation or increasing fragmentation of forested areas due to deforestation (Irwin 2008), whereas Kirindy Mitea National

Park is the largest remaining tract of continuous dry-deciduous forest in Madagascar (Whitehurst, Sexton et al. 2009). Research into daily ranging behaviour demonstrated that daily path lengths vary throughout the annual cycle and whereas some sympatric species, such as *Eulemur fulvus rufus* increases its daily ranging during the dry season (Scholz and Kappeler 2004), the complete opposite is displayed by *P. verreauxi* during this period. The results of this chapter give quantitative results on home range and ranging behaviour, which can help in the understanding of the locomotor ecology of this species.

The affect of seasonality

The first two chapters of this thesis also investigated how the locomotor ecology of *P. verreauxi* was affected by living in a highly seasonal environment. These investigations have provided data that supports previous theoretical explanations on how lemurs in general have evolved to cope with the stresses associated with extended periods of food scarcity (Wright 1999). These chapters demonstrate that lemurs reduce their traveling behaviour, activity lengths and path lengths during the long dry season, characterised by a period of food scarcity. The findings of these first two chapters help to develop a greater understanding of how lemurs adapt their behaviour during the annual cycle, in response to a variable environment.

Remote monitoring of locomotion

The final chapter of this thesis attempted to use accelerometry in both a wild and captive setting in order to remotely monitor locomotion. Forms of monitoring, such as this, for locomotion studies have only been used once in a wild environment (Byrnes, Lim et al. 2008) and once before in a captive setting using a lemur model (Sellers and Crompton 2004). Although problems were encountered using this methodology during the field research, the captive study demonstrated that specific modes of locomotion could be recognised from acceleration traces.

The energy conservation hypothesis versus the evolutionary disequilibrium hypothesis

Over the last twenty years, there have been two main hypotheses which have attempted to partially explain the diveregent evolution of certain traits which lemurs possess making them so different from anthropoid primates. Firstly, the evolutionary divergence hypothesis, which suggests that a mass extinction of diurnal predators around the time of human arrival had a profound effect on certain behavioural and physiological traits of lemurs (van Schaik and Kappeler 1996). Extinction allowed for what were considered to be nocturnal lemurs to become much more diurnal. The evolutionary disequilibrium hypothesis states that the presence of cathemerality amongst some extant *Eulemur* species suggests a transitional state where these species are moving towards becoming diurnal.

The second proposal, is that of the energy conservation hypothesis which attempts to explain the physiological and behavioural differences between lemurs and other anthropoids using the environment in Madagascar (Wright 1999). The energy conservation hypothesis states that there is a higher degree of seasonality shown in Madagascar than in comparable tropical forests located in Asia, mainland Africa and

South America (Morland 1991; Dewar and Richard 2007). It goes on to state that due to these high levels of seasonality, lemurs in Madagascar are subjected to long periods of extreme food scarcity that are not found in tropical forests containing anthropoid primates (Wright 1999). Thus, this high degree of seasonality has led to the development of certain traits which help lemurs to cope with these extended periods of food scarcity.

Neither of these theories discuss locomotion, ranging and activity patterns as traits that have evolved in response to either a lack of diurnal predators, or due to extreme seasonality. The evolutionary disequilibrium hypothesis states that developed traits such as cathemerality are a step in the direction towards lemurs becoming more anthropoid-like. Whereas certain other traits, such as female dominance (Radespiel and Zimmermann 2001) and smaller group sizes (Curtis 2004) or pair bonding (Godfrey, Jungers et al. 2007) are primitive retentions which are in the process of being selected out, as lemurs are evolving to become more anthropoid in nature. The only way to attempt to relate the locomotor behaviour of *P. verreauxi* to the evolutionary disequilibrium hypothesis, would be to compare current modes of locomotion with that of the extinct subfossil lemurs. If this comparison were to hold true, you would expect the locomotor repetoires of the extinct lemurs to be very different to that of the extant *P. verreauxi*.

The extinct sister clade of the family Indriidae is that of the Paleopropithecidae, which are known more commonly as the sloth lemurs (Karanth, Delefosse et al. 2005). The Paleopropithecidae are known to have survived the advent of human colonisation, as there is evidence of human butchered sloth lemur skeletons dating more than 2000 years old (Gould and Sauther 2007). Paleopropithecidae extinction dates at roughly the same time as that of the predators, which according to the evolutionary disequilibrium hypothesis, allowed for lemurs to become more diurnal. These animals are known as sloth lemurs mainly due to their locomotion. They were large bodies lemurs (weighing upwards of thirty five kilograms) and mainly used climbing and suspensory movements to locomote in the canopy (Godfrey, Jungers et al. 2007). The issue with attempting to compare the extant Indriidae family with the extinct Paleopropithecidae in an attempt to fit the evolutionary disequilibrium hypothesis is that it simply does not work. The evolutionary disequilibrium hypothesis relies on the fact that certain characteristics and behaviours evolved as a result of predator extinctions around 2000 years ago. Firstly, vertical clinging and leaping was first recognised in the fossil record during the Eocene period between thirty-four to fifty-six million years ago (Napier 1967). Suggesting that *P. verreauxi* and other members of the Indriidae family, were already highly reliant on leaping as a means of locomotion before the extinction of predators occurred. Members of the Paleopropithecidae, along with other extinct subfossil lemurs have also been suggested as already being diurnal, due to their optic foramen index (a ratio of the size of the optic canal, compared to that of the orbit) being similar to that of both extant diurnal lemurs and anthropoids (Gould and Sauther 2007).

Clearly, certain modes of locomotion seem not to have evolved in response to a mass extinction of diurnal predators. But many of the other listed traits claimed by the evolutionary disequilibrium hypothesis to have been caused by these extinction events have also proved controversial within the scientific community. The postulation that is key to the evolutionary disequilibrium hypothesis, is that of cathemerality being a transitional state. If this were the case then it would be expected that the diurnal lemurs, such as the indriids would display an eye morphology similar to that of the anthropoid primates that the evolutionary disequilibrium hypothesis suggests that they are evolving towards. Diurnal lemurs have in fact evolved an eye morphology that is more similar to that of other diurnal mammals and not that of anthropoid primates. Diurnal anthropoid primates display a reduced cornea size relative to other diurnal mammals, whereas diurnal strepsirrhine primates display a similar cornea size similar to that of diurnal mammals such as the *Sciurids* (Kirk 2006). The reduced cornea size is said to be an adaptation to increase visual acuity in photopic conditions.

Another trait used to explain differences between anthropoids and strepsirrhines is the presence of female dominance in Malagasy lemurs. The evolutionary disequilibrium hypothesis suggests that the presence of female dominance is a trait which has been retained from the ancestral monogamous lemurs. If that were the case, then it would be expected that other nocturnal strepsirrhine primate would also display some form of female dominance, but this phenomenon has not been observed in tarsiers, lorises or galagos (Gursky 2007). One other assumption with regard to the evolutionary disequilibrium hypothesis and female dominance is that there is female dominance displayed by anthropoid nocturnal primates. Again, it has been shown that anthropoid nocturnal primates tend towards a social hierarchy which is based upon co-dominance rather than female dominance (Palombit 1997).

Although it is likely that that the mass extinction of diurnal predators around 2000 years ago will have had some sort of effect on lemur behaviour. The level of change suggested by the evolutionary disequilibrium hypothesis in a relatively short period of time seems to be unlikely. Currently there is not quantifiable method of measuring the effect of this extinction event in terms of lemur evolution. Clearly such a broad range of lemur traits evolving over such a small period of time would certainly be remarkable, but more comparative field data is needed to ascertain how many of these changes may have been caused by the extinction of many species of diurnal predators.

The energy conservation hypothesis, on the other hand, lends itself to the results found in this research much more favourably. The concept that many of the traits which separate lemurs from anthropoid primates such as female dominance, cathemerality and a lack of sexual dimorphism; have evolved as a consequence of Madagascar's harsh and unpredictable environment. With Kirindy Mitea National Park being a dry deciduous forest, located in south-western Madagascar, the level of seasonality displayed is much more pronounced than that of the rainforests located in eastern Madagascar (Lewis and Kappeler 2005). It is also located in a coastal region which is known for regular cyclones during the rainy season (Lewis and Bannar-Martin 2011) . The energy conservation hypothesis predicts that long periods of food scarcity have lead to the development of certain traits, unique to lemurs, that are not present in anthropoid primates.

For the results of this investigation to complement the energy conservation hypothesis, it would be expected that all of the results analysed during the dry season would conform to a pattern of frugality in relation to energy expenditure. Whilst this behaviour would see a gradual change with the onset of the short rainy season during which time food is abundant to a less energy constrained lifestyle.

From the pattern of results seen in this investigation, the difference in seasonal behaviour clearly demonstrates that *P. verreauxi* is highly adapted for life in an incredibly seasonal environment. If some of the results are combined to give an overall picture of how *P. verreauxi* behaves and adapts its behaviour seasonally, a pattern of behaviour emerges that complements the expected behaviour outlined by the energy conservation hypothesis. Firstly, the ranging data presented demonstrates that during the dry season, *P. verreauxi* travels less than during the onset and ending of the rainy season. The fact that *P. verreauxi* is a folivorous primate does imply that daily ranging will be less than that of an equally sized frugivorous primate (Milton and May 1976). But the variation in daily ranging, with greater daily distances being displayed during the onset and end of the short rainy season suggest that *P. verreauxi* does limit the distances that it ranges in a day during the long dry season which is characterized by food scarcity.

Activity data also seems to complement the notion of energy conservation, with more bouts of locomotion leading to rest periods during the dry season, whilst during the rainy season a higher proportion of bouts of locomotion led to travelling behaviour. Activity rhythms also follow a very similar pattern with very short periods of activity at the height of the dry season with an increasing period of activity with the onset of the rainy season. The only form of activity that does not fluctuate seasonally is that of feeding behaviour. There is an explanation for why this may be the case. Firstly, the activity data is calculated as a proportion of entire daily activity. If the animals are active for longer periods during the day, then they are spending more absolute time feeding during the rainy season, even though the proportion of that activity period spent feeding was similar. Secondly, the actual nutritional value of the leaves that are consumed varies dramatically throughout the seasons (Ganzhorn 1992). During the height of the dry season, in a deciduous forest the nutritional value of the remaining leaves is much less than at the height of the rainy season, when there are young nutritious leaves present. Therefore, although *P. verreauxi* may be consuming a similar amount of leaf matter throughout the annual cycle, the nutritional value of what is being consumed varies throughout that period.

One of the primary postulations from the energy conservation hypothesis is that a lot of the traits that have developed to enable the evolution of female dominance in lemurs. Dominance enables females to time the birth of their offspring to coincide with the start of the rainy season, when food is more plentiful (Richard, Dewar et al. 2000). The energy conservation hypothesis has been further expanded, stating that extended period of food scarcity, due to the harsh, but predictable seasonality present in Madagascar has led the Malagasy primates to evolve behavioural traits which are adapted towards conserving energy (Wright 1999). The evidence presented in this study certainly complements the ideas put forward by the energy conservation hypothesis, showing decreases in ranging, travel behaviour and daily activity lengths during the long dry season, which is categorised by an extended period of food scarcity.

The energy conservation hypothesis is based on the idea of frugality, but one aspect of the locomotion and behaviour of *P. verreauxi* that certainly does not seem to concur with this is their propensity for saltatory locomotion. Leaping as a mode of locomotion has a high energetic cost, compared to certain other modes of locomotion, such as quadrupedalism or suspensory locomotion. It would be expected that if *Propithecus verreauxi* is attempting to conserve energy during extended periods of food scarcity that it would also have evolved to use a less energetically costly mode of locomotion. Certainly member of the extinct sub fossil sister clade of *P. verreauxi*, the sloth lemurs (Paleopropithecidae), were known to have utilised a suspensory mode of locomotion (Godfrey, Jungers et al. 2007). Although, there are a range of reasons as to why leaping may in fact be more energy efficient than other modes of locomotion in the forests of Madagascar.

Firstly, the forest architecture in Madagascar is considered somewhat unique in comparison to similar tropical forests found in South America and Asia. The average crown diameter of trees found in the tropical forests of Madagascar has been found to be much less than that of the equivalent forests found in Asia and South America (Ganzhorn 1988). Crown diameter differences are thought to be an evolutionary adaptation of Malagasy trees in order to survive the high winds during a cyclone, whilst incurring minimal damage (Wright 1999). A smaller crown diameter presents smaller surface area for the wind to hit the tree, therefore, reducing the likelihood of a tree being felled during a cyclone. Small crown diameters lead to the canopy not interlinking to such a high degree as in other tropical forests, creating a higher amount of discontinuous supports. High levels of discontinuity within the canopy may have led to selection against other forms of locomotion. Cyclone damage that does occur, also leads to there being large patchy areas of forest, which would necessitate leaping as a means of locomotion to travel between discontinuous supports.

P. verreauxi is noted as an obligate folivore, leading to the majority of nutrition being located in the canopy (Hemingway 1998). Other species which are more frugivorous are able to forage for fruit which has fallen from trees as well as fruit which is still attached to trees (Pride 2005), whereas leaves are almost exclusively located in the canopy of trees. Food location combined with the fact that there are a higher proportion of discontinuous supports present in trees in Madagascar mean that leaping may in fact be a more energetically efficient mode of locomotion. For example, if *P. verreauxi* had to climb down from a canopy where it was feeding and locomote to the next feeding tree and climb back up to the canopy, this may be more energetically costly than leaping from one tree to the other (Crompton and Sellers 2007). These factors combined, suggest that leaping as a main form of locomotion may actually be a more energy efficient way of travelling within the forest environment of Madagascar than other forms of locomotion. It should also be noted, that once within a tree canopy, less strenuous forms of locomotion, such as foliage crossing and suspension are used whilst feeding. Leaping was noted within this thesis as being the predominant mode of locomotion for travelling, rather than feeding behaviour.

The evolution of leaping as a mode of locomotion may have also have evolved in response to other selection pressures. Predation from the remaining diurnal raptors from above and viverrids such as the fossa (*Cryptoprocta ferox*) which is comfortable in both an arboreal environment and terrestrially (Hawkins and Racey 2005) may have also impacted upon the way that *P. verreauxi* locomotes. Therefore, if locomoting quadrupedally or bipedally terrestrially imposes a greater risk of predation; or using suspension, brachiation or cantilevering, high in the canopy then an adaptation towards leaping within the understory may have evolved.

All of these factors suggest that the locomotor ecology of *P. verreauxi* lends itself to surviving long periods of food scarcity within a highly seasonal environment. Survival is achieved by decreasing daily ranging, daily activity and travel activity during the dry season. The findings presented clearly complement the energy conservation hypothesis, but that is not to say that energy conservation is the sole reason for *P. verreauxi* evolving the locomotor patterns, activity patterns and ranging behaviour displayed. Clearly the mass extinction of diurnal predators suggested by the evolutionary disequilibrium hypothesis will have had an effect on lemur behaviour, but the extent to which this is the case is currently unknown. Also, to suggest that the locomotor ecology of *P. verreauxi* evolved purely in response for the need to conserve energy would be credulous. Other factors, such as the risk of predation, may have also caused *P. verreauxi* to evolve saltatory movement patterns for locomoting in a forest environment.

Thesis limitations

There are limitations to the results which are presented within this thesis. Clearly, when conducting field based behavioural studies, it is impossible to replicate the same level of control over different variables that is expected within a laboratory environment. Therefore, it is necessary to simplify data collection techniques in order to cope within a field environment. Data collection whilst in the field poses a set of challenges which are not faced within the laboratory setting, subsequently, within this thesis there are some limitations.

Sampling methods

The scan sampling methods which were adapted from Altmann (1974)are not without their own shortcomings. Scan sampling data collection, sampling from a whole group of subjects, has proved a popular methodology among field scientists investigating behaviour (Crompton 1983; Crompton and Andau 1986; Crompton and Andau 1986; Tilden 1990; Dagosto 1995). But there are certainly some issues with the accuracy of data collection. Firstly, all heights and distances are not measured, but estimated by eye. Obviously, this is never going to be as accurate as would be expected within a laboratory setting. If every piece of collected data was measured more accurately, it would require far too much equipment and would reduce data collection drastically. There are also issues with this method of sampling with regards to sampling ratios, with some individuals being more readily observable than others within a group situation. For example, during the breeding season, males often leave the group in an attempt to breed with other females, therefore taking them out of the sampling regime for a period of time. The lack of sexual dimorphism shown in lemurs (Wright 1999) also means that variables, such as gender, could not be investigated within this study.

The other option relating to data collection for this study was focal sampling, where data from a single individual is collected. Focal sampling is also not without its shortcomings. Sampling from a single individual suggests that you are capturing every movement that individual makes throughout the day, this is not a possibility as transcribing the data takes your attention away from the focal individual. There may also be long periods of no sampling if an individual cannot be located within a group and is also not fitted with a radio collar. The issue of recognising an individual within a group may also prove difficult due to the lack of sexual dimorphism displayed by lemurs. Lastly, focal sampling also yields much lower amounts of data than scan sampling. For the reasons listed previously, this is why a scan sampling methodology was chosen, but as explained, this method is also not without its shortcomings.

Accelerometer

This study did not manage to replicate the results obtained from the accelerometry in the Cottswolds Wildlife Park within a wild setting. Although, this is not completely without precedent, as the only other locomotor study involving lemurs using this methodology was also performed within a captive environment (Sellers and Crompton 2004). Wild studies using accelerometers to monitor lemurs have related to activity rhythms, which allowed the accelerometer to be attached to collars (Erkert and Kappeler 2004) and this method would have produced far too much background noise within the signal to have been a possible methodology for this study. Successful collection of accelerometry data would have allowed a comparison to be made with the more traditional sampling methods performed in chapter one of this thesis. If more research into accelerometry is to be performed it may be necessary to design a less obtrusive and smaller data logger, with a longer battery life. The other option would be to chose a larger target species to sample from, which may not find the data logger so restrictive.

Future work

During the completion of this thesis, future avenues of research have become apparent. These new questions are not within the remit of this thesis, although the ideas are born from the results obtained from it.

Investigating habitat structure

It would be of some interest to extend the locomotion study to include support availability. Many previous studies have investigated how positional behaviour varies in relation to species, age, gender and season (Crompton 1983; Tilden 1990; Dagosto 1995; Gebo and Chapman 1995), but very few have investigated how habitat structure can affect positional behaviour and locomotion (Dagosto and Yamashita 1998). Primates of the same species have been investigated in different geographic locations and the results show geographic variation in relation to positional and locomotor behaviour (Mendel 1976; Gebo 1992). These results may not be caused by differences in habitat structure, but this variable was not considered and therefore habitat structure could possibly play a role in determining locomotor patterns.

A greater understanding of the forest architecture within Kirindy Mitea National Park may shed light on the locomotor repertoires and support usage of *P. verreauxi*. Previous studies of nocturnal indriids (Warren and Crompton 1997) have indicated that support choices do not correlate with the abundance of support type available. Nocturnal indriids have been discovered to choose small oblique and horizontal branches upon which to locomote, whilst the most numerous available supports were vertical and angled. Research of this nature could also be related to which activities are being performed on certain substrate sizes and orientation in relation to their abundance. An investigation such as this would increase the understanding of form and function relationships, but also show preferences within the natural habitat in relation to support abundance.

Energy expenditure and body composition

This thesis has gone some way in attempting to understand how *P. verreauxi* adapts its locomotor behaviour and ranging in order to cope with a highly seasonal environment. However, it would be interesting to further investigate any physiological changes that occur during, or in preparation for the changing seasons. Previous studies of mouse lemurs have displayed seasonal fattening behaviour in preparation for the dry season and periods of extended food scarcity (Atsalis 1999). Generating results on field metabolic rate, daily total energy expenditure and body composition would provide quantitative data on the physiological changes experiences by *P. verreauxi* during the annual cycle.

In order to produce data of this nature the doubly labelled water method would be utilised. The doubly labelled water method involves administering water where the hydrogen and oxygen have been replaced with isotopes for tracing purposes. The hydrogen isotope is eliminated from the body as water, whereas the oxygen isotope is eliminated as carbon dioxide. The difference in these elimination rates is proportional to carbon dioxide production and hence energy expenditure (Schoeller, Ravussin et al. 1986). Generating data of this nature could further enhance the theories of the energy conservation hypothesis as a reason as to why the Malagasy lemurs have evolved traits so different from anthropoid primates.

Concluding remarks

This thesis has presented data about the locomotor ecology of *P. verreauxi* within the Kirindy Mitea National Park. It has demonstrated that *P. verreauxi* is a committed leaper using a highly energetic mode of locomotion (leaping) within a highly seasonal environment. High levels of seasonality have led to adjustments in ranging, activity, support choice and resting behaviour during the annual cycle. By relating seasonality to locomotor ecology, this study hopes to bring greater understanding to how lemurs adapt their behaviour in order to cope with a highly seasonal environment.

References

Aerts, P. (1998). "Vertical Jumping in Galago senegalensis: The Quest for an Obligate Mechanical Power Amplifier." Philosophical Transactions: Biological Sciences **353**(1375): 1607-1620.

Alexander, R. M. (1985). "The maximum forces exerted by animals." J Exp Biol **115**(1): 231-238.

Alexander, R. M. (1995). "Leg Design and Jumping Technique for Humans, Other Vertebrates and Insects." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **347**(1321): 235-248.

Alexander, R. M. (1995). "Leg Design and Jumping Technique for Humans, other Vertebrates and Insects." Philosophical Transactions: Biological Sciences **347**(1321): 235-248.

Altmann, J. (1974). "Observational study of behavior: sampling methods." Behaviour **49**(3): 227-267.

Altmann, J. (1974). "Observational Study of Behavior: Sampling Methods." Behaviour **49**(3/4): 227-267.

Andriaholinirina, N., J.-L. Fausser, et al. (2006). "Molecular phylogeny and taxonomic revision of the sportive lemurs (Lepilemur, Primates)." BMC Evolutionary Biology **6**(1): 17.

Anemone, R. L. and H. H. Covert (2000). "New skeletal remains of Omomys (Primates, Omomyidae): functional morphology of the hindlimb and locomotor behavior of a Middle Eocene primate." Journal of Human Evolution **38**(5): 607-633.

Anemone. R, L. (1990). "The VCL hypothesis revisited: Patterns of femoral morphology among quadrupedal and saltatorial prosimian primates." American Journal of Physical Anthropology **83**(3): 373-393.

Arlet, M., J. Carey, et al. (2009). "Species, age and sex differences in type and frequencies of injuries and impairments among four arboreal primate species in Kibale National Park, Uganda." Primates **50**(1): 65-73.

Atsalis, S. (1999). "Seasonal Fluctuations in Body Fat and Activity Levels in a Rain-Forest Species of Mouse Lemur, Microcebus rufus." International Journal of Primatology **20**(6): 883-910.

Benadi, G., C. Fichtel, et al. (2008). "Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*)." American Journal of Primatology **70**(10): 956-965.

Bennet-Clark, H. C. (1975). "The energetics of the jump of the locust Schistocerca gregaria." J Exp Biol **63**(1): 53-83.

Bidder, O. R., M. Soresina, et al. (2012). "The need for speed: testing acceleration for estimating animal travel rates in terrestrial dead-reckoning systems." Zoology **115**(1): 58-64.

Blanchard, M. L. (2007). Locomotor behaviour and ecology of three sympatric lemur species in Mantadia National Park, Madagascar, University of Liverpool. **PhD**.

Blanchard, M. L. (2007). Locomotor behaviour and ecology of three sympatric lemur species in Mantadia National Park, Madagscar, University of Liverpool. **PhD**.

Blanchard, M. L. and R. H. Crompton (2011). Field Study methods for primate locomotor ecologyand biomechanics Primate Locomotion: Linking Field and Laboratory Research. K. D'Août and E. E. Vereecke. Berlin, Springer**:** 183-200.

Bloch, J. I. and D. M. Boyer (2002). "Grasping Primate Origins." Science **298**(5598): 1606-1610.

Bloch, J. I., M. T. Silcox, et al. (2007). "New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates." Proceedings of the National Academy of Sciences **104**(4): 1159-1164.

Britt, A. (2000). "Diet and feeding behaviour of the black-and-white ruffed lemur (Varecia variegata variegata) in the Betampona Reserve, eastern Madagascar." Folia Primatologica **71**(3): 133-141.

Brockman, D. K. (1999). "Reproductive Behavior of Female <i>Propithecus verreauxi</i> at Beza Mahafaly, Madagascar." International Journal of Primatology **20**(3): 375-398.

Burr, D. B., G. Piotrowski, et al. (1982). "Femoral mechanics in the lesser bushbaby (*Galago senegalensis*): Structural adaptations to leaping in primates." The Anatomical Record **202**(3): 419-429.

Burroughs, R. E. J. (1993). A summary of the practical aspects of drugs commonly used for the restraint of wild animals. The Capture and Care Manual: Capture, Care, Accommodation and Transportation of Wild African Mammals. A. McKenzie. Pretoria, Wildlife decision support services.

Byrnes, G., N. T. L. Lim, et al. (2008). "Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*)." Proceedings of the Royal Society B: Biological Sciences **275**(1638): 1007-1013.

Cannell, M. G. R. and J. Morgan (1987). "Young's modulus of sections of living branches and tree trunks." Tree Physiology **3**(4): 355-364.

Cant, J., G. H. (1992). "Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application." American Journal of Physical Anthropology **88**(3): 273-283.

Cant, J. G. H. (1986). "Locomotion and Feeding Postures of Spider and Howling Monkeys - Field-Study and Evolutionary Interpretation." Folia Primatologica **46**(1): 1-14.

Cant, J. G. H. (1992). "Positional Behavior and Body Size of Arboreal Primates - a Theoretical Framework for Field Studies and an Illustration of Its Application." American Journal of Physical Anthropology **88**(3): 273-283.

Cant, J. G. H., D. Youlatos, et al. (2001). "Locomotor behavior of Lagothrix lagothricha and Ateles belzebuth in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes." Journal of Human Evolution **41**(2): 141-166.

Cartmill, M. (1987). Rethinking primate origins. Primate Evolution and Human Origins. R. L. Ciochon and J. G. Fleagle. New York, Aldine de Gruyher**:** 14-21.

Cartmill, M. (1992). "New views on primate origins." Evolutionary Anthropology: Issues, News, and Reviews **1**(3): 105-111.

Chapman, C. (1988). "Patterns of foraging and range use by three species of neotropical primates." Primates **29**(2): 177-194.

Chouteau, P. (2006). "Influences of the season and the habitat structure on the foraging ecology of two Coua species in the western dry forest of Madagascar." Comptes Rendus Biologies **329**(9): 691-701.

Cluttonbrock, T. H. and P. H. Harvey (1977). "Primate Ecology and Social-Organization." Journal of Zoology **183**(Sep): 1-39.

Colquhoun, I. C. (2006). "Predation and Cathemerality." Folia Primatologica **77**(1-2): 143-165.

Connour, J. R., K. Glander, et al. (2000). "Postcranial adaptations for leaping in primates." Journal of Zoology **251**(01): 79-103.

Craighead, F. C., Jr. (1976). "Grizzly Bear Ranges and Movement as Determined by Radiotracking." Bears: Their Biology and Management **3**: 97-109.

Crompton, R. (1983). "Age differences in locomotion of two subtropical galaginae." Primates **24**(2): 241-259.

Crompton, R. and P. Andau (1986). "Locomotion and habitat utilization in free-rangingTarsius bancanus: A preliminary report." Primates **27**(3): 337-355.

Crompton, R. and W. Sellers (2007). A Consideration of Leaping Locomotion as a Means of Predator Avoidance in Prosimian Primates. Primate Anti-Predator Strategies. S. Gursky and K. A. I. Nekaris. New York, Springer**:** 127-145.

Crompton, R. H. (1980). *Galago* locomotion, Harvard University. **PhD**.

Crompton, R. H. (1983). "Age differences in locomotion of two subtropical galaginae." Primates **24**(2): 241-259.

Crompton, R. H. and P. M. Andau (1986). "Locomotion and habitat utilization in free-ranging *Tarsius bancanus*: a preliminary report." Primates **27**(3): 337-355.

Crompton, R. H. and P. M. Andau (1986). "Locomotion and Habitat Utilization in Free-Ranging Tarsius-Bancanus - a Preliminary-Report." Primates **27**(3): 337-355.

Crompton, R. H. and P. M. Andau (1987). "Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: a preliminary report." International Journal of Primatology **8**(1): 43-71.

Crompton, R. H. and P. M. Andau (1987). "Ranging, Activity Rhythms, and Sociality in Free-Ranging Tarsius-Bancanus - a Preliminary-Report." International Journal of Primatology **8**(1): 43-71.

Crompton, R. H., W. I. Sellers, et al. (1993). "Energetic Efficiency and Ecology as Selective Factors in the Saltatory Adaptation of Prosimian Primates." Proceedings: Biological Sciences **254**(1339): 41-45.

Crompton, R. H., W. I. Sellers, et al. (1993). "Energetic Efficiency and Ecology as Selective Factors in the Saltatory Adaptation of Prosimian Primates." Proceedings of the Royal Society of London Series B-Biological Sciences **254**(1339): 41-45.

Crompton, R. H., W. I. Sellers, et al. (2007). A Consideration of Leaping Locomotion as a Means of Predator Avoidance in Prosimian Primates
Primate Anti-Predator Strategies, Springer US**:** 127-145.

Cuozzo, F. P., M. L. Sauther, et al. (2010). "Variation in dental wear and tooth loss among known-aged, older ring-tailed lemurs (Lemur catta): a comparison between wild and captive individuals." American Journal of Primatology **72**(11): 1026-1037.

Curtis, D., J. (2004). "Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs." American Journal of Physical Anthropology **124**(3): 234-247.

Curtis, D. J. and M. A. Rasmussen (2002). "Cathemerality in lemurs." Evolutionary Anthropology: Issues, News, and Reviews **11**(S1): 83-86.

Dagosto, M. (1989). "Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar." American Journal of Physical Anthropology **78**(2): 209.

Dagosto, M. (1995). "Seasonal variation in positional behavior of Malagasy lemurs." International Journal of Primatology **16**(5): 807-833.

Dagosto, M. (1995). "Seasonal-Variation in Positional Behavior of Malagasy Lemurs." International Journal of Primatology **16**(5): 807-833.

Dagosto, M. and N. Yamashita (1998). "Effect of habitat structure on positional behavior and support use in three species of lemur." Primates **39**(4): 459-472.

Davenport, C. B. (1935). "Variation in Proportions among Mammals, with Special Reference to Man." Journal of Mammalogy **16**(4): 291-296.

De Villiers, P. A. and O. B. Kok (1997). "Home range, association and related aspects of elephants in the eastern Transvaal Lowveld." African Journal of Ecology **35**(3): 224-236.

Delpero, M., J. C. Masters, et al. (2001). "Phylogenetic relationships among the Malagasy lemuriforms (Primates: Strepsirrhini) as indicated by mitochondrial sequence data from the 12S rRNA gene." Zoological Journal of the Linnean Society **133**(1): 83-103.

DelPero, M., L. Pozzi, et al. (2006). "A Composite Molecular Phylogeny of Living Lemuroid Primates." Folia Primatologica **77**(6): 434-445.

Demes, B., J. G. Fleagle, et al. (1999). "Takeoff and landing forces of leaping strepsirhine primates." Journal of Human Evolution **37**(2): 279-292.

Demes, B. and M. M. Günther (1989). "Biomechanics and allometric scaling in primate locomotion and morphology." Folia Primatologica **53**(1-4): 125-141.

Demes, B., W. L. Jungers, et al. (1996). "Body size and leaping kinematics in Malagasy vertical clingers and leapers." Journal of Human Evolution **31**(4): 367-388.

Demes, B., W. L. Jungers, et al. (1995). "Kinetics of Leaping Primates - Influence of Substrate Orientation and Compliance." American Journal of Physical Anthropology **96**(4): 419-429.

Demes, B., W. L. Jungers, et al. (1995). "Kinetics of leaping primates: influence of substrate orientation and compliance." Am J Phys Anthropol **96**(4): 419-29.

Demes, B., S. G. Larson, et al. (1994). "The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered." Journal of Human Evolution **26**(5-6): 353-374.

Dewar, R. E. and A. F. Richard (2007). "Evolution in the hypervariable environment of Madagascar." Proceedings of the National Academy of Sciences **104**(34): 13723-13727.

Dirzo, R., H. S. Young, et al. (2011). Introduction. Seasonally dry tropical forests : ecology and conservation. R. Dirzo, H. S. Young, H. A. Mooney and G. Ceballos. Washington, Island Press**:** xi-xiii.

Doran, D., M. (1993). "Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion." American Journal of Physical Anthropology **91**(1): 83-98.

Dorcas Warren, R. and R. Huw Crompton (1998). "Diet, Body Size and the Energy Costs of Locomotion in Saltatory Primates." Folia Primatologica **69**(Suppl. 1): 86-100.

Dunbar, D. C. (1988). "Aerial maneuvers of leaping lemurs: The physics of whole-body rotations while airborne." American Journal of Primatology **16**(4): 291-303.

Erkert, H. G. and P. M. Kappeler (2004). "Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (Propithecus v. verreauxi; Primates : Indriidae)." Behavioral Ecology and Sociobiology **57**(2): 174-186.

Erkert, H. G. and P. M. Kappeler (2004). "Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae)." Behavioral Ecology and Sociobiology **57**(2): 174-186.

Fashing, P. J. (2001). "Activity and ranging patterns of guerezas in the Kakamega Forest: Intergroup variation and implications for intragroup feeding competition." International Journal of Primatology **22**(4): 549-577.

Fietz, J. and J. r. U. Ganzhorn (1999). "Feeding ecology of the hibernating primate Cheirogaleus medius: how does it get so fat?" Oecologia **121**(2): 157-164.

Fleagle, J. G. (1988). Primate Adaptation and Evolution. San Diego, Academic Press Inc.

Fleagle, J. G. and F. Anapol (1992). "The indriid ischium and the hominid hip." Journal of Human Evolution **22**(4-5): 285-305.

Fleagle, J. G. and R. A. Mittermeier (1980). "Locomotor Behavior, Body Size, and Comparative Ecology of 7 Surinam Monkeys." American Journal of Physical Anthropology **52**(3): 301-314.

Fontaine, R. (1990). "Positional Behavior in Saimiri-Boliviensis and Ateles-Geoffroyi." American Journal of Physical Anthropology **82**(4): 485-508.

Fragaszy, D. M., S. Boinski, et al. (1992). "Behavioral Sampling in the Field - Comparison of Individual and Group Sampling Methods." American Journal of Primatology **26**(4): 259-275.

Franz, T. M., B. Demes, et al. (2005). "Gait Mechanics of lemurid primates on terrestrial and arboreal substrates." Journal of Human Evolution **48** 199-217.

Franzen, J. L., P. D. Gingerich, et al. (2009). "Complete Primate Skeleton from the Middle Eocene of Messel in Germany: Morphology and Paleobiology." PLoS ONE **4**(5): e5723.

Gander, P. H. and M. C. Moore-Ede (1983). "Light-dark masking of circadian temperature and activity rhythms in squirrel monkeys." American Journal of Physiology - Regulatory, Integrative and Comparative Physiology **245**(6): R927-R934.

Ganzhorn, J. (1992). "Leaf chemistry and the biomass of folivorous primates in tropical forests." Oecologia **91**(4): 540-547.

Ganzhorn, J. (2002). "Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics." Oecologia **131**(3): 427-435.

Ganzhorn, J. U. (1988). "Food partitioning among Malagasy primates." Oecologia **75**(3): 436-450.

Garber, P. A. and J. D. Pruetz (1995). "Positional Behavior in Moustached Tamarin Monkeys - Effects of Habitat on Locomotor Variability and Locomotor Stability." Journal of Human Evolution **28**(5): 411-426.

Gebo, D. L. (1987). "Locomotor Diversity in Prosimian Primates." American Journal of Primatology **13**(3): 271-281.

Gebo, D. L. (1992). "Locomotor and postural behavior in Alouatta palliata and Cebus capucinus." American Journal of Primatology **26**(4): 277-290.

Gebo, D. L. and C. A. Chapman (1995). "Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys." American Journal of Physical Anthropology **96**(1): 73-82.

Gebo, D. L. and C. A. Chapman (1995). "Positional behavior in five sympatric old world monkeys." American Journal of Physical Anthropology **97**: 49-76.

Gebo, D. L., M. Dagosto, et al. (2000). "The oldest known anthropoid postcranial fossils and the early evolution of higher primates." Nature **404**(6775): 276-278.

Gibbons, A. (2009). "Celebrity Fossil Primate: Missing Link or Weak Link?" Science **324**(5931): 1124-1125.

Gingerich, P. D. and A. Arbor (1980). "Dental and cranial adaptations in Eocene Adapidae." Z Morphol Anthropol **71**: 135-142.

Glessner, K. D. G. and A. Britt (2005). "Population density and home range size of Indri indri in a protected low altitude rain forest." International Journal of Primatology **26**(4): 855-872.

Godfrey, L. R., W. L. Jungers, et al. (2007). Ecology and Extinction of Madagascar's Subfossil Lemurs. Lemurs: Ecology and Adaptation. L. Gould and M. L. Sauther. New York, Springer**:** 41-64.

Godfrey, L. R., S. K. Lyon, et al. (1993). "Sexual dimorphism in large-bodied primates: The case of the subfossil lemurs." American Journal of Physical Anthropology **90**(3): 315-334.

Godinot, M. (2006). "Lemuriform Origins as Viewed from the Fossil Record." Folia Primatologica **77**(6): 446-464.

Goodman, S. (1994). "The enigma of antipredator behavior in lemurs: Evidence of a large extinct eagle on Madagascar." International Journal of Primatology **15**(1): 129-134.

Goodman, S. M. and J. P. Benstead (2005). "Updated estimates of biotic diversity and endemism for Madagascar." Oryx **39**(1): 73-77.

Gorenflo, L. J., C. Corson, et al. (2011). Exploring the Association Between People and Deforestation in Madagascar
Human Population. Human Population: Its Influences on Biological Diversity. M. M. Caldwell, G. Heldmaier, R. B. Jacksonet al, Springer Berlin Heidelberg. **1650:** 197-221.

Gould, L. and M. Sauther (2007). Anti-Predator Strategies in a Diurnal Prosimian, the Ring-Tailed Lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. Primate Anti-Predator Strategies. S. Gursky and K. Nekaris. New York, Springer**:** 275-288.

Grassi, C. (2006). "Variability in habitat, diet, and social structure of Hapalemur griseus in Ranomafana National Park, Madagascar." American Journal of Physical Anthropology **131**(1): 50-63.

Groves, C. (2000). "The Genus Cheirogaleus: Unrecognized Biodiversity in Dwarf Lemurs." International Journal of Primatology **21**(6): 943-962.

Gunther, M. M., H. Ishida, et al. (1991). "The jump as a fast mode of locomotion in arboreal and terrestrial biotopes." *Z. Morph. Anthropol.* **78**: 341-372.

Gunther, M. M., H. Ishida, et al. (1991). "The jump as a fast mode of locomotion in arboreal and terrestrial biotopes." Z. Morphol. Anthropol. **78**: 341-372.

Gursky, S., K. A. I. Nekaris, et al. (2007). Predation on Lemurs in the Rainforest of Madagascar by Multiple Predator Species: Observations and Experiments. Primate Anti-Predator Strategies, Springer US**:** 77-99.

Gursky, S. L. (2007). The Response of Spectral Tarsiers Toward Avian and Terrestrial Predators. Primate Anti-Predator Strategies. S. Gursky and K. Nekaris. New York, Springer**:** 241-252.

Hanya, G. (2004). "Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: Effects of food and temperature." American Journal of Primatology **63**(3): 165-177.

Harcourt, C. S. and L. T. Nash (1986). "Species differences in substrate use and diet between sympatric galagos in two Kenyan coastal forests." Primates **27**(1): 41-52.

Harper, G. J., M. K. Steininger, et al. (2007). "Fifty years of deforestation and forest fragmentation in Madagascar." Environmental Conservation **34**(4): 325-333.

Harvey, P. H. and T. H. Cluttonbrock (1981). "Primate Home-Range Size and Metabolic Needs." Behavioral Ecology and Sociobiology **8**(2): 151-155.

Hawkins, C. E. and P. A. Racey (2005). "Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: implications for protected area management." Oryx **39**(1): 35-43.

Heitler, W. J. (1974). "The locust jump." Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology **89**(1): 93-104.

Hemingway, C. A. (1994). "Spatial relations in three groups of the diademed sifaka, *Propithecus diadema edwardsi*, in southeastern Madagascar." American Journal of Physical Anthropology **37**(S18): 105.

Hemingway, C. A. (1998). "Selectivity and variability in the diet of Milne-Edwards' sifakas (Propithecus diadema edwardsi): Implications for folivory and seed-eating." International Journal of Primatology **19**(2): 355-377.

Hemingway, C. A. (1999). "Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance?" Behavioral Ecology and Sociobiology **45**(3-4): 311-322.

Irwin, M. T. (2006). "Leaner diet, less energy: Diademed sifakas (Propithecus diadema) in forest fragments show reduced ranging and altered activity patterns." American Journal of Physical Anthropology: 108-108.

Irwin, M. T. (2008). "Diademed Sifaka (Propithecus diadema) Ranging and Habitat Use in Continuous and Fragmented Forest: Higher Density but Lower Viability in Fragments?" Biotropica **40**(2): 231-240.

Irwin, M. T. (2008). "Feeding ecology of Propithecus diadema in forest fragments and continuous forest." International Journal of Primatology **29**(1): 95-115.

Irwin, M. T., L. Gould, et al. (2007). Ecologically Enigmatic Lemurs: The Sifakas of the Eastern Forests (<i>Propithecus candidus, P. diadema, P. edwardsi, P. perrieri,</i> and <i>P. tattersalli</i>)
Lemurs. L. Barrett, Springer US**:** 305-326.

Isaac, N. J. B., J. Mallet, et al. (2004). "Taxonomic inflation: its influence on macroecology and conservation." Trends in Ecology & Evolution **19**(9): 464-469.

Jenkins, F. A. J., A. W. Crompton, et al. (1983). "Mesozoic Mammals from Arizona: New Evidence on Mammalian Evolution." Science **222**(4629): 1233-1235.

Jolly, A. (1998). "Pair-Bonding, Female Aggression and the Evolution of Lemur Societies." Folia Primatologica **69(suppl 1)**(Suppl. 1): 1-13.

Kappeler, P. M. (1997). "Intrasexual selection in Mirza coquereli : evidence for scramble competition polygyny in a solitary primate." Behavioral Ecology and Sociobiology **41**(2): 115-127.

Kappeler, P. M. and H. G. Erkert (2003). "On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (<i>Eulemur fulvus rufus</i>)." Behavioral Ecology and Sociobiology **54**(4): 359-369.

Kappeler, P. M., J. Trillmich, et al. (2004). "Coordination of group movements in wild Verreaux's sifakas (Propithecus verreauxi)." Behaviour **141**: 1103-1120.

Karanth, K. P., T. Delefosse, et al. (2005). "Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates." Proceedings of the National Academy of Sciences of the United States of America **102**(14): 5090-5095.

Kays, R., S. Tilak, et al. (2011). "Tracking Animal Location and Activity with an Automated Radio Telemetry System in a Tropical Rainforest." The Computer Journal.

Kimura, T. (1992). "Hindlimb dominance during primate high-speed locomotion." Primates **33**(4): 465-476.

Kinzey, W. G., A. L. Rosenberger, et al. (1975). "Vertical clinging and leaping in a neotropical anthropoid." Nature **255**(5506): 327-328.

Kirk, E. C. (2006). "Eye morphology in cathemeral lemurids and other mammals." Folia Primatologica **77**(1-2): 27-49.

Kirk, E. C., M. Cartmill, et al. (2003). "Comment on "Grasping Primate Origins"." Science **300**(5620): 741b-.

Kubzdela, K. S., A. F. Richard, et al. (1992). "Social relations in semi-free-ranging sifakas (<I>Propithecus verreauxi coquereli</I>) and the question of female dominance." American Journal of Primatology **28**(2): 139-145.

Larson, S. G., D. Schmitt, et al. (2000). "Uniqueness of primate forelimb posture during quadrupedal locomotion." American Journal of Physical Anthropology **112**(1): 87-101.

Lehman, S. M. and M. Mayor (2004). "Dietary patterns in Perrier's sifakas (Propithecus diadema perrieri): A preliminary study." American Journal of Primatology **62**(2): 115-122.

Lehman, S. M., M. Mayor, et al. (2005). "Ecogeographic size variations in sifakas: A test of the resource seasonality and resource quality hypotheses." American Journal of Physical Anthropology **126**(3): 318-328.

Lewis, R. J. (2006). "Scent marking in Sifaka: No one function explains it all." American Journal of Primatology **68**(6): 622-636.

Lewis, R. J. and K. H. Bannar-Martin (2011). "The Impact of Cyclone Fanele on a Tropical Dry Forest in Madagascar." Biotropica: no-no.

Lewis, R. J. and P. M. Kappeler (2005). "Seasonality, body condition, and timing of reproduction in Propithecus verreauxi verreauxi in the Kirindy Forest." American Journal of Primatology **67**(3): 347-364.

Llorens, L., A. Casinos, et al. (2001). "A Biomechanical Study of the Long Bones in Platyrrhines." Folia Primatologica **72**(4): 201-216.

Louis, E., M. Coles, et al. (2006). "Revision of the Mouse Lemurs (Microcebus) of Eastern Madagascar." International Journal of Primatology **27**(2): 347-389.

Martin, R. D. (1968). "Towards a New Definition of Primates." Man **3**(3): 377-401.

Martin, R. D. (1990). Primate Origins and Evolution. London, Chapman and Hall.

Martin, R. D. (1993). "Primate origins: plugging the gaps." Nature **363**(6426): 223-234.

Martin, R. D. (2000). "Origins, diversity and relationships of lemurs." International Journal of Primatology **21**(6): 1021-1049.

Martin, R. D., C. Soligo, et al. (2007). "Primate Origins: Implications of a Cretaceous Ancestry." Folia Primatologica **78**(5-6): 277-296.

Maruhashi, T. (1981). "Activity patterns of a troop of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan." Primates **22**(1): 1-14.

Masters, J. C., M. J. de Wit, et al. (2006). "Reconciling the Origins of Africa, India and Madagascar with Vertebrate Dispersal Scenarios." Folia Primatologica **77**(6): 399-418.

Mckey, D. and P. G. Waterman (1982). "Ranging Behavior of a Group of Black Colobus (Colobus-Satanas) in the Douala-Edea Reserve, Cameroon." Folia Primatologica **39**(3-4): 264-304.

Medicine, U. f. L. A. (2001). Guidelines for Anesthesia, Analgesia & Postanesthetic Care of Nonhuman Primates. Michigan, University of Michigan**:** 1-11.

Mellen, T. K., E. C. Meslow, et al. (1992). "Summertime Home Range and Habitat Use of Pileated Woodpeckers in Western Oregon." The Journal of Wildlife Management **56**(1): 96-103.

Mendel, F. (1976). "Postural and locomotor behavior of Atouatta pallata on various substrates." Folia Primatologica **26**: 36-53.

Mills, K. J., B. R. Patterson, et al. (2006). "Effects of Variable Sampling Frequencies on GPS Transmitter Efficiency and Estimated Wolf Home Range Size and Movement Distance." Wildlife Society Bulletin **34**(5): 1463-1469.

Milton, K. (1984). "Habitat, Diet, and Activity Patterns of Free-Ranging Woolly Spider Monkeys (Brachyteles-Arachnoides E-Geoffroy 1806)." International Journal of Primatology **5**(5): 491-514.

Milton, K. and M. L. May (1976). "Body-Weight, Diet and Home Range Area in Primates." Nature **259**(5543): 459-462.

Mittermeier, R., J. Ganzhorn, et al. (2008). "Lemur diversity in Madagascar." International Journal of Primatology **29**(6): 1607-1656.

Morland, H. S. (1991). "Preliminary report on the social organization of ruffed lemurs (Varecia variegata variegata) in a northeast Madagascar rain forest." Folia Primatologica.

Morris, J. R. W. (1973). "Accelerometry, A technique for the measurement of human body movements." Journal of Biomechanics **6**(6): 729-736.

Murphy, P. G. and A. E. Lugo (1986). "Ecology of Tropical Dry Forest." Annual Review of Ecology and Systematics **17**: 67-88.

Murray, C. M., L. E. Eberly, et al. (2006). "Foraging strategies as a function of season and rank among wild female chimpanzees (Pan troglodytes)." Behavioral Ecology **17**(6): 1020-1028.

Nagy, H. (2007). A Preliminary Analysis of Verreaux's Sifaka Habitat in Kirindy Mitea National Park, Madagascar. Nicholas School of the Environment and Earth Sciences, Duke. **MSc**.

Napier, J. R. (1967). "Evolutionary aspects of primate locomotion." American Journal of Physical Anthropology **27**(3): 333-341.

Napier, J. R. and A. C. Walker (1967). "Vertical clinging and leaping - a newly recognized category of locomotor behaviour of primates." Folia Primatologica **6**(3-4): 204-219.

Napier, J. R. and A. C. Walker (1967). "Vertical Clinging and Leaping - a Newly Recognized Category of Locomotor Behaviour of Primates." Folia Primatologica **6**(3-4): 204-&.

Nash, L. T. (1998). "Vertical clingers and sleepers: Seasonal influences on the activities and substrate use of Lepilemur leucopus at Beza Mahafaly Special Reserve, Madagascar." Folia Primatologica **69**: 204-217.

Norscia, I., V. Carrai, et al. (2006). "Influence of Dry Season and Food Quality and Quantity on Behavior and Feeding Strategy of Propithecus verreauxi in Kirindy, Madagascar." International Journal of Primatology **27**(4): 1001-1022.

Nunes, A. (1998). "Diet and feeding ecology of ateles belzebuth belzebuth at Maraca Ecological Station, Roraima, Brazil." Folia Primatologica **69**(2): 61-76.

Oates, J. F. (1977). "Social-Life of a Black-and-White Colobus Monkey, Colobus-Guereza." Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology **45**(1): 1-60.

Orsdol, K. G. V., J. P. Hanby, et al. (1985). "Ecological correlates of lion social organization (Panthers, leo)." Journal of Zoology **206**(1): 97-112.

Overdorff, D. (1988). "Preliminary report on the activity cycle and diet of the red-bellied Lemur (Lemur rubriventer) in Madagascar." American Journal of Primatology **16**(2): 143-153.

Overdorff, D. J. (1996). "Ecological correlates to social structure in two lemur species in Madagascar." American Journal of Physical Anthropology **100**(4): 487-506.

Oxnard, C. E. and R. H. Crompton (1990). Animal Lifestyles and Anatomies The Case of the Prosimian Primates. Seattle, University of Washington Press.

Oxnard, C. E., R. H. Crompton, et al. (1990). Animal Lifestyles and Anatomies The Case of the Prosimian Primates. Seattle, University of Washington Press.

Oxnard, C. E., R. German, et al. (1981). "The functional morphometrics of the hip and thigh in leaping prosimians." American Journal of Physical Anthropology **54**(4): 481-498.

Palombit, R. A. (1997). "Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*)." Folia Primatol (Basel) **68**(6): 321-37.

Pellis, S. M. and V. C. Pellis (2012). "Anatomy is important, but need not be destiny: Novel uses of the thumb in aye-ayes compared to other lemurs." Behavioural Brain Research **231**(2): 378-385.

Peplowski, M. M. and R. L. Marsh (1997). "Work and power output in the hindlimb muscles of Cuban tree frogs Osteopilus septentrionalis during jumping." J Exp Biol **200**(22): 2861-2870.

Pereira, M. and M. Weiss (1991). "Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs." Behavioral Ecology and Sociobiology **28**(2): 141-152.

Poux, C. l., O. Madsen, et al. (2005). "Asynchronous Colonization of Madagascar by the Four Endemic Clades of Primates, Tenrecs, Carnivores, and Rodents as Inferred from Nuclear Genes." Systematic Biology **54**(5): 719 - 730.

Powzyk, J. A. and C. B. Mowry (2003). "Dietary and feeding differences between sympatric Propithecus diadema diadema and Indri indri." International Journal of Primatology **24**(6): 1143-1162.

Preuschoft, H. (1985). "On the quality and magnitude of mechanical stresses in the locomotor system during rapid movements." Z. Morphol. Anthropol **75**: 245-262.

Preuschoft, H., M. M. Gunther, et al. (1998). "Size dependence in prosimian locomotion and its implications for the distribution of body mass." Folia Primatologica **69**(S1): 60-81.

Prost, J. H. (1965). "The methodology of gait analysis and gaits of monkeys." American Journal of Physical Anthropology **23**(3): 215-240.

Radespiel, U. and E. Zimmermann (2001). "Female dominance in captive gray mouse lemurs (Microcebus murinus)." American Journal of Primatology **54**(4): 181-192.

Rasmussen, D. T. (1985). "A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs (Lemur andVarecia)." International Journal of Primatology **6**(5): 501-517.

Rasmussen, D. T. (1990). "Primate origins: Lessons from a neotropical marsupial." American Journal of Primatology **22**(4): 263-277.

Ravosa, M. J., D. M. Meyers, et al. (1993). "Relative growth of the limbs and trunk in sifakas: Heterochronic, ecological, and functional considerations." American Journal of Physical Anthropology **92**(4): 499-520.

Reynolds, T. R. (1985). "Stresses on the limbs of quadrupedal primates." American Journal of Physical Anthropology **67**(4): 351-362.

Richard, A. (1985). "Social boundaries in a Malagasy Prosimian, the Sifaka (Propithecus verreauxi)." International Journal of Primatology **6**(6): 553-568.

Richard, A. F. and R. E. Dewar (1991). "Lemur Ecology." Annual Review of Ecology and Systematics **22**(1): 145-175.

Richard, A. F., R. E. Dewar, et al. (2000). "Mass change, environmental variability and female fertility in wild Propithecus verreauxi." Journal of Human Evolution **39**(4): 381-391.

Richard, A. F. and M. E. Nicoll (1987). "Female social dominance and basal metabolism in a malagasy primate, Propithecus verreauxi." American Journal of Primatology **12**(3): 309-314.

Richard, A. F., P. Rakotomanga, et al. (1993). "Dispersal by Propithecus-Verreauxi at Beza-Mahafaly, Madagascar - 1984-1991." American Journal of Primatology **30**(1): 1-20.

Rose, K. D. (1994). "The earliest primates." Evolutionary Anthropology: Issues, News, and Reviews **3**(5): 159-173.

Rose, K. D. and A. Walker (1985). "The skeleton of early Eocene *Cantius*, oldest lemuriform primate." American Journal of Physical Anthropology **66**(1): 73-89.

Ross, C. (2001). "Park or ride? Evolution of infant carrying in primates." International Journal of Primatology **22**(5): 749-771.

Schaik, C. P. v. and M. A. v. Noordwijk (1985). "Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (Macaca fascicularis)." Journal of Zoology **206**(4): 533-549.

Schatz, G. E., P. P. Lowry, et al. (1996). "Conspectus of the vascular plants of Madagascar: A taxonomic and conservation electronic database." Biodiversity of African Plants: 10-17.

Schmid, J. and J. U. Ganzhorn (1996). "Resting metabolic rates of Lepilemur ruficaudatus." American Journal of Primatology **38**(2): 169-174.

Schmitt, D. (1999). "Compliant walking in primates." Journal of Zoology **248**(02): 149-160.

Schmitt, D., M. Cartmill, et al. (2006). "Adaptive value of ambling gaits in primates and other mammals." Journal of Experimental Biology **209**(11): 2042-2049.

Schoeller, D. A., E. Ravussin, et al. (1986). "Energy expenditure by doubly labeled water: validation in humans and proposed calculation." American Journal of Physiology - Regulatory, Integrative and Comparative Physiology **250**(5): R823-R830.

Scholz, F. and P. Kappeler (2004). "Effects of Seasonal Water Scarcity on the Ranging Behavior of Eulemur fulvus rufus." International Journal of Primatology **25**(3): 599-613.

Scholz, F. and P. M. Kappeler (2004). "Effects of seasonal water scarcity on the ranging behavior of Eulemur fulvus rufus." International Journal of Primatology **25**(3): 599-613.

Schultz, A. H. (1936). "Characters Common to Higher Primates and Characters Specific for Man (Continued)." The Quarterly Review of Biology **11**(4): 425-455.

Sellers, W. I. and R. H. Crompton (2004). "Automatic monitoring of primate locomotor behaviour using accelerometers." Folia Primatol (Basel) **75**(4): 279-93.

Sellers, W. I. and R. H. Crompton (2004). "Automatic Monitoring of Primate Locomotor Behaviour Using Accelerometers." Folia Primatologica **75**(4): 279-293.

Sellers, W. I., J. S. Varley, et al. (1998). "Remote monitoring of locomotion using accelerometers: a pilot study." Folia Primatologica **69** (S1): 82-85.

Shekelle, M. (2005). "Tarsiers: Past, Present, and Future - future classic?" American Journal of Primatology **67**(2): 273-278.

Simmen, B., A. Hladik, et al. (2003). "Food intake and dietary overlap in native Lemur catta and Propithecus verreauxi and introduced Eulemur fulvus at Berenty, southern Madagascar." International Journal of Primatology **24**(5): 948-967.

Smith, A. P. and J. U. Ganzhorn (1996). "Convergence in community structure and dietary adaptation in Australian possums and gliders and Malagasy lemurs." Australian Journal of Ecology **21**(1): 31-46.

Soligo, C. and R. D. Martin (2006). "Adaptive origins of primates revisited." Journal of Human Evolution **50**: 414-430.

Sorg, J. P., Rohner, U. (1996). Climate and tree phenologyof the dry deciduous forest of the Kirindy Forest. Ecology and economy of a tropical dry forest in Madagascar. J. U. Ganzhorn, Sorg, J. P., Primate Rep Special Issue. **46(1):** 57-80.

Stanger-Hall, K. F. (1997). "Phylogenetic Affinities Among the Extant Malagasy Lemurs (Lemuriformes) Based on Morphology and Behavior." Journal of Mammalian Evolution **4**(3): 163-194.

Stankiewicz, J., C. Thiart, et al. (2006). "Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals." Journal of Biogeography **33**(2): 221-235.

Stevens, N. J. (2008). "The effect of branch diameter on primates gait sequence pattern." American Journal of Primatology **70**: 356-362.

Stone, A. I. (2007). "Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest." American Journal of Primatology **69**(2): 142-157.

Stoner, K. E. and R. M. Timm (2011). Seasonally Dry Tropical Forest Mammals: Adaptations and Seasonal Patterns Seasonally Dry Tropical Forests : Ecology and Conservation. R. Dirzo, H. S. Young, H. A. Mooney and G. Ceballos. Washington, Island Press**:** 85-106.

Storey, M., J. J. Mahoney, et al. (1995). "Timing of Hot Spot--Related Volcanism and the Breakup of Madagascar and India." Science **267**(5199): 852-855.

Strier, K. B. (1987). "Activity Budgets of Woolly Spider Monkeys, or Muriquis (Brachyteles-Arachnoides)." American Journal of Primatology **13**(4): 385-395.

Sussman, R. W. (1977). Feeding behaviour of *Lemur catta* and *Lemur fulvus* Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. T. H. Clutton-Brock. London, Academic Press. **1:** 1-36.

Sussman, R. W. (1991). "Demography and Social-Organization of Free-Ranging Lemur-Catta in the Beza-Mahafaly-Reserve, Madagascar." American Journal of Physical Anthropology **84**(1): 43-58.

Sussman, R. W. (1991). "Primate origins and the evolution of angiosperms." American Journal of Primatology **23**(4): 209-223.

Tattersall, I. (1982). The Primates of Madagascar. New York, Columbia University Press.

Tattersall, I. (2006). "The Concept of Cathemerality: History and Definition." Folia Primatologica **77**(1-2): 7-14.

Tattersall, I. (2007). "Madagascar's lemurs: cryptic diversity or taxonomic inflation?" Evolutionary Anthropology: Issues, News, and Reviews **16**(1): 12-23.

Terranova, C. J. (1996). "Variation in the leaping of lemurs." American Journal of Primatology **40**: 145-165.

Thorpe, S. K. S., R. H. Crompton, et al. (2007). "Orangutans use compliant branches to lower the energetic cost of locomotion." Biology Letters **3**(3): 253-256.

Tilden, C. D. (1990). "A study of locomotor behavior in a captive colony of red-bellied lemurs (*Eulemur rubriventer)*." American Journal of Primatology **22**(2): 87-100.

Tilden, C. D. (1990). "A Study of Locomotor Behavior in a Captive Colony of Red-Bellied Lemurs (Eulemur-Rubriventer)." American Journal of Primatology **22**(2): 87-100.

Tobler, M. W., S. E. Carrillo-Percastegui, et al. (2008). "An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals." Animal Conservation **11**(3): 169-178.

Torigoe, T. (1985). "Comparison of object manipulation among 74 species of non-human primates." Primates **26**(2): 182-194.

van Schaik, C. P. and P. M. Kappeler (1996). "The Social Systems of Gregarious Lemurs: Lack of Convergence with Anthropoids due to Evolutionary Disequilibrium?" Ethology **102**(7): 915-941.

Vasey, N. (2005). "Activity budgets and activity rhythms in red ruffed lemurs (Varecia rubra) on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. (vol 66, pg 23, 2005)." American Journal of Primatology **66**(4): 393-394.

Vick, L. and M. E. Pereira (1989). "Episodic targeting aggression and the histories of Lemur social groups." Behavioral Ecology and Sociobiology **25**(1): 3-12.

Vilensky, J. A. and S. G. Larson (1989). "Primate Locomotion: Utilization and Control of Symmetrical Gaits." Annual Review of Anthropology **18**(1): 17-35.

Ward, S. C. and R. W. Sussman (1979). "Correlates between locomotor anatomy and behavior in two sympatric species of *Lemur*." American Journal of Physical Anthropology **50**(4): 575-590.

Warren, R. D. and R. H. Crompton (1997). "A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar." Journal of Zoology **243**(2): 397-415.

Warren, R. D. and R. H. Crompton (1997). "A comparative study of the ranging behaviour, activity rhythms and sociality of Lepilemur edwardsi (Primates, Lepilemuridae) and Avahi occidentalis (Primates, Indriidae) at Ampijoroa, Madagascar." Journal of Zoology **243**: 397-415.

Warren, R. D. and R. H. Crompton (1997). "Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*." Am J Phys Anthropol **104**(4): 471-86.

Warren, R. D. and R. H. Crompton (1997). "Locomotor ecology of Lepilemur edwardsi and Avahi occidentalis." American Journal of Physical Anthropology **104**(4): 471-486.

Warren, R. D. and R. H. Crompton (1998). "Diet, body size and the energy costs of locomotion in saltatory primates." Folia Primatologica **69**: 86-100.

Weinert, D., D. Weinert, et al. (2001). "ACTIVITY RHYTHMS OF WILD AND LABORATORY GOLDEN HAMSTERS (MESOCRICETUS AURATUS) UNDER ENTRAINED AND FREE-RUNNING CONDITIONS." Chronobiology International **18**(6): 921-932.

Whitehurst, A. S., J. O. Sexton, et al. (2009). "Land cover change in western Madagascar's dry deciduous forests: a comparison of forest changes in and around Kirindy Mite National Park." Oryx **43**(2): 275-283.

Whitehurst, A. S., J. O. Sexton, et al. (2009). "Land cover change in western Madagascar's dry deciduous forests: a comparison of forest changes in and around Kirindy Mite National Park." Oryx **43**(02): 275-283.

Wright, P. (1995). "Demography and life history of free-ranging *Propithecus diadema edwardsi* in ranomafana national park, madagascar." International Journal of Primatology **16**(5): 835-854.

Wright, P. (1995). "Demography and life history of free-rangingPropithecus diadema edwardsi in ranomafana national park, madagascar." International Journal of Primatology **16**(5): 835-854.

Wright, P. (1999). "Lemur traits and Madagascar ecology: Coping with an island environment." Yearbook of Physical Anthropology 1999 **42**(42): 31-72.

Wright, P. C. (1999). "Lemur traits and Madagascar ecology: Coping with an island environment." American Journal of Physical Anthropology **110**(S29): 31-72.

Wunderlich, R. E. and J. C. Schaum (2007). "Kinematics of bipedalism in *Propithecus verreauxi*." Journal of Zoology **272**(2): 165-175.

Yamashita, N. (2002). "Diet of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar." International Journal of Primatology **23**(5): 1025-1051.

Yoder, A. D. (2007). "Lemurs: a Quick Guide." Current Biology **17**(20): 866-868.

Yoder, A. D., M. Cartmill, et al. (1996). "Ancient single origin for Malagasy primates." Proceedings of the National Academy of Science USA **93**(10): 5122-5126.

Yoder, A. D., R. M. Rasoloarison, et al. (2000). "Remarkable species diversity in Malagasy mouse lemurs (primates, Microcebus)." Proceedings of the National Academy of Sciences **97**(21): 11325-11330.

Youlatos, D. (1998). "Seasonal variation in the positional behavior of red howling monkeys (Alouatta seniculus)." Primates **39**(4): 449-457.