The predator-sensitive foraging behaviour of free-living Verreaux's sifaka (*Propithecus verreauxi verreauxi*) at Berenty Reserve, Madagascar

by

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B.A., University of Victoria, 2005

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ABSTRACT

I studied the influence of microhabitat on the predator-sensitive foraging (PSF) of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) at Berenty Reserve, Madagascar from June 11, 2007 to August 10, 2007. Three groups of sifaka from a gallery, closed-canopy forest, a riverine forest, and the spiny/scrub forest were observed. PSF was assessed by measuring the spatial location, spatial cohesiveness, and rate of vigilance, vocal, and non-vocal alarm behaviour of foraging sifaka. While there were statistically significant between-group differences in the spatial location (i.e., terrestrial, low-, mid- and high-canopy) used while foraging, there were no statistically significant inter-group differences in spatial cohesiveness, terrestrial or aerial vigilance, or in the frequency of vocal (i.e., terrestrial and aerial calls) or non-vocal (i.e., gestural) alarms. Thus, it appears that the PSF of free-living Verreaux's sifaka is largely uninfluenced by variation in microhabitat.

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DEDICATED WITH LOVE
TO THE MEMORY OF
JAMES ALLANACH

CHAPTER ONE: INTRODUCTION

1.0 OVERVIEW OF PREDATOR SENSITIVE FORAGING

Regardless of the dietary, social, or environmental variation present amongst the order Primates, all members, irrespective of body size, are alike in their vulnerability as prey (Hart, 2007). On-going predator-prey relationships can exert a selective pressure on a primate species' morphological, social, and ecological adaptations (Fichtel, 2004; Goodman, 2003; Gursky and Nekaris, 2007; Miller and Treves, 2007; Zuberbühler, 2007). Nevertheless, due to not only the opportunistic nature of predation (Stone, 2007), but also the struggle that researchers have in habituating feral predator species (Stanford, 1998), attempting to directly document the predation of free-ranging primates is simply not a pragmatic point of investigatory departure (Miller, 2002; Sauther, 2002). However, primates possess a suite of anti-predator behavioural strategies that, when assessed, proffer insight into the predatory challenges faced by a particular species within a given habitat. Thus, the use of vigilance, the size and cohesiveness of primate social groups, and the employment of auditory, olfactory and visual communication are all anti-predator techniques that can be observed and compared. In this respect, one approach to determining the influence that predation assumes on a population, or even an entire species of primates, is to examine predator-sensitive foraging.

If they are to survive and become reproductively successful, free-living primates must satisfactorily meet a myriad of challenges, especially the threat of predation and the procurement of food resources (Miller, 2002). Each species must be able to mitigate their vulnerability to predators while simultaneously meeting, at a minimum, the nutritional baseline required for growth, physiological maintenance, and reproduction (Miller, 2002). Predator-sensitive foraging (PSF) or threat-sensitive foraging (Helfman, 1989), examines the extent to which vulnerability to predation determines where a prey species forages within the environment, and whether nutritional demands outweigh possible predation risks. In short, are animals sacrificing nutritional gain by feeding on low-quality resources to mitigate susceptibility to predation (Banks, 2001; Wirsing *et al.*, 2007), or conversely, are they choosing to feed on high-quality food items despite an elevated predation risk? Further, PSF investigates what other preventative (i.e., group cohesiveness, vigilance and niche exploitation) and response-based (i.e., alarm call vocalizations and gestural alarms) anti-predation strategies are employed while animals feed and forage (Fichtel, 2007). In my study I focused on both the preventative and response-based predation strategies utilized by three groups of Verreaux's sifaka from dissimilar microhabitats.

1.1 SIGNIFICANCE OF STUDY

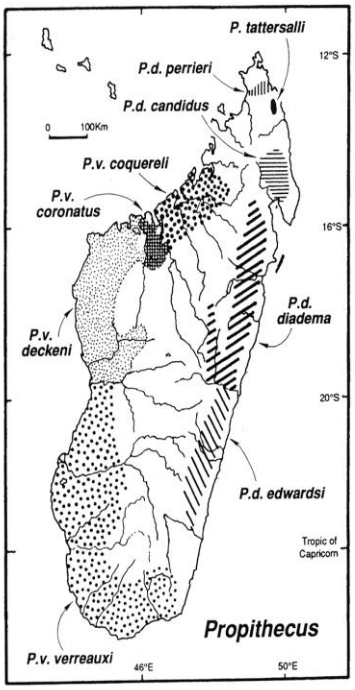
It is useful to address the three central reasons that this particular study holds value. First, research focused on the PSF of free-living primates is significant in both proximate and ultimate terms; however, Hart (2007) draws attention to the fact that until quite recently many primatologists have neglected to view primates as prey. By recognizing Verreaux's sifaka at Berenty, regardless of age, as potential items within the dietary repertoires of diurnal birds-of-prey, reptiles, and feral dogs and cats, my research seeks to rectify the past trend of disregarding primates as prey. Second, my study is significant as it seeks to elucidate similarities or differences with respect to the predation risk faced between groups of sifaka residing in dissimilar microhabitats. The ways in which predation risk influences the foraging decisions of members within the three study groups can be compared to provide information on how predation affects a number of variables for sifaka including diet, health, and demography. Observations focused on intra-specific diversity are important in the study of animal behaviour since one particular species may inhabit several microhabitats and is therefore vulnerable to distinct predatory challenges as a result of such ecological variation. An appreciation for the influence that predation has on these proximate factors can provide researchers with a better understanding of how such pressures in turn influence a species' adaptive responses, and ultimately, its evolution and success. Furthermore, at present the PSF behaviour of Verreaux's sifaka from Berenty Reserve has not been investigated. Finally, with respect to the behavioural and feeding ecology data that have been collected and published on the Berenty Reserve sifaka, few studies have focused on those sifaka inhabiting the gallery forest region of Ankoba, and even less is known about either the spiny forest sifaka or the riverine-forest sifaka that reside on the outskirts of the village of Berenty itself. My study will provide insight into the range of PSF behaviours present among free-living *Propithecus verreauxi verreauxi*.

1.2 BACKGROUND OF *P. V. VERREAUXI*

1.2.1 Geographical Distribution

Verreaux's sifaka (*P. v. verreauxi*), also referred to as the white sifaka (Strier, 2006), is found exclusively on the island of Madagascar (Gould and Sauther, 2007; Jolly, 1966; Petter, 1972; Richard, 1976; Sussman, 1999; Tattersall an Sussman, 1975) and inhabits

Fig. 1.1 – *Propithecus* distribution (Nash, 2007).



the spiny and dry deciduous forests (Carrai *et al.*, 2003; Gould and Sauther, 2007; Richard, 1976) of the island's south and west occidental zones (Carrai, 2000; Fichtel, 2004; Gould and Sauther, 2007; Petter, 1972; Richard, 1976; Tattersall and Sussman, 1975) (Fig. 1.1). Verreaux's sifaka is unique as it is the only non-nocturnal lemur species commonly found in many of Madagascar's spiny forest regions (Richard, 1976; Sussman, 1999). The fact that free- living *P. v. verreauxi* occupy a range of habitat types within Madagascar provides researchers with the opportunity to conduct numerous comparative ecological and behavioural studies. Currently, the conservation status of *P. v. verreauxi* is listed as Vulnerable (Baillie, 1996, IUCN, 1994 v. 2.3).

1.2.2 General Ecology

The genus *Propithecus* belongs to the Indriidae family of lemurs (Jolly, 1966; Petter, 1972). There are three sifaka species (Gould and Sauther, 2007): Verreaux's sifaka (*Propithecus verreauxi*), Tattersall's sifaka (*Propithecus tattersalli*) and the diademed sifaka (*Propithecus diadema*) (Sussman, 1999). Additionally, there are four separate subspecies of Verreaux's sifaka: *P. v. verreauxi, P. v. coquereli, P. v. coronatus,* and *P. v. deckeni* (Gould and Sauther, 2007; Jolly 1966). *P. v. coquereli* and *P. v. coronatus* are both found in the northwest region of Madagascar (Gould and Sauther, 2007; Sussman, 1999), and *P. v. deckeni* inhabits the western portion of Madagascar (Gould and Sauther, 2007; Sussman, 1999).

Adult male and female Verreaux's sifaka are monomorphic and weigh approximately 2.8 kg (Gould and Sauther, 2007; Lewis *et al.*., 2003; Simmen *et al.*., 2003). Sifaka body weight varies between the species, with *P. v. verreauxi* exhibiting the lowest mean body weight among *Propithecus* and *P. diadema edwardsi* having the highest mean weight at approximately 6.5 kg (Gould and Sauther, 2007; Powzyk and Mowry, 2003). In addition, unlike some other strepsirhines, *P. v. verreauxi* is also sexually monochromatic (Jolly, 1966).

Verreaux's sifaka is arboreal and spends the majority of its time in the lower and middle canopy (Petter, 1972). Howarth *et al.* (1986) found that the free-living sifakas observed at Berenty Reserve were terrestrial only 2.5% of the time. Because the locomotion style of *P. v. verreauxi* is vertical clinging and leaping (Sussman, 1999), Verreaux's sifaka do not move with as much facility while on the ground as when in trees, resulting in an increased vulnerability to predatory attacks initiated by both terrestrial and aerial species alike when moving terrestrially. Sifaka are highly susceptible to predation by the harrier hawk (*Polyboroides radiatus*) not only while on the terminal branches and in the upper canopy of trees, but also when terrestrial, as Sauther (2002) observed that the ground is actually a preferred striking location for this diurnal raptor. Thus, my study pays considerable attention to the spatial location of feeding and foraging sifaka so that any between-group discrepancies in terms of niche partitioning can be detected.

1.2.3 Group Structure and Social Interactions

Verreaux's sifaka form multi-male, multi-female social units that are slightly biased in favour of males (Jolly, 1966; Richard *et al.*, 2002; Richard *et al.*, 1991). Sifaka groups contain, at a minimum, between two and three adults, and do not generally exceed fourteen animals (Lewis *et al.*, 2003; Richard, 1976; Richard *et al.*, 2002). Carrai (2000) indicated that there are generally 1 to 2 adult males, 1 to 2 adult females and their non-adult offspring in a group; however, because Verreaux's sifaka are female philopatric (Richard *et al.*, 1991) the inter-group transfer of males is not uncommon (Sussman, 1999).

Adult female sifaka are dominant to males (Carrai, 2000; Jolly, 1966; Kappeler and Schäffler, 2008; Richard, 2003; Richard, 1976); however, social interactions, whether they are of an affiliative or agonistic nature, are minimal in this species relative to the amount of interactions documented among other primates (Jolly, 1966). This may reflect the fact that sifaka are predominantly folivorous (Sussman, 1999), as other behavioural folivores such as the Neotropical *Alouatta* (howler monkey sp.) also do not engage in many overt social interactions. A folivorous diet is energetically taxing and demands that animals devote a considerable portion of their activity budget to rest, and not sociality, in order to facilitate digestion (Strier, 2006). Nevertheless, although sociality may be reduced among sifaka species, it is not completely absent. Adults may sleep and rest in proximity of one another (Jolly, 1966; Wright, 1999), participate in play behaviour with infants (Bastian and Brockman, 2007; Grieser, 1992; Jolly, 1966), and also engage in allogrooming (Jolly, 1966; Richard, 1985). Richard (1985) observed that adult females receive the most allogrooming attention, yet they are not as likely to reciprocate and take part in grooming conspecifics. Finally, agonistic interactions also occur among sifaka, and may be negatively correlated with food availability or male mating competition (Brockman, 1999; Jolly, 1966; Richard and Heimbuch, 1975).

1.3 DIET AND FEEDING ECOLOGY

P. v. verreauxi is primarily folivorous (Howarth *et al.*, 1986; Petter, 1972; Wright, 1998). Similar to other folivorous primates, members of the genus *Propithecus* have low basal metabolic rates (Goodman, 2003), and possess morphological specializations to aid in digestion, such as a large (although not sacculated) stomach and an elongated and complex caecum (Sussman, 1999). In addition to leaves, sifaka also consume fruit and flowers when these items are available (Carrai, 2000); however, *P. v. verreauxi* at Berenty Reserve is thought to assume a dietary niche separate from that of both sympatric ring-tailed lemurs (*L. catta*) and the introduced red-fronted brown lemurs (*Eulemur fulvus rufus*). Verreaux's sifaka at Berenty are generally more folivorous than *E. f. rufus* and *L. catta* (Gould and Sauther, 2007; Simmen *et al.*, 2003b; Sussman, 1999).

Even during the dry season months, Verreaux's sifaka obtain sufficient water from the food resources they ingest; they have not been observed drinking water (Jolly, 1966; Simmen *et al.*, 2003). Indeed, descending to watering holes can be risky for primates, so the ability for sifaka to remain hydrated solely from flowers and leaves may be considered an adaptation to mitigate their susceptibility to predation. Such behaviour has also been observed in another behavioural folivore, the mantled howler monkey (*Alouatta palliata),* which only occasionally descends to the forest floor in search of water (Fedigan and Jack, 2001; Strier, 2006).

In *Propithecus* species, adult females exhibit feeding dominance over males (Kappeler and Schäffler, 2008; Wright, 1998). Periodic resource scarcity as a result of Madagascar's climactic unpredictability coupled with the high energetic needs of seasonally reproductive female lemurs have favoured female feeding dominance (Wright, 1999). Although common in lemurs, female feeding dominance is highly atypical in other primates (Kappeler and Schäffler, 2008). Nevertheless, despite female dominance in relation to access to food resources, Simmen *et al.* (2003b) observed that both males and females experience a drop in body mass during the austral winter season because of food scarcity. During the dry season, animals may resort to eating bark due to a lack of other more nutritious food items (Carrai, 2000). Although Carrai (2000) conducted her study in a dry deciduous gallery forest, her data highlighted the extent to which the sifaka diet varies according to seasonal climatic and precipitation variability.

1.4 THEORETICAL CONSIDERATIONS

1.4.1 Predation and Group Living

Social-living affords primates a number of advantages, especially the opportunity to learn skills from group members that are critical for survival. In particular, a primate can acquire from conspecifics, especially one's mother, vital predator avoidance strategies (Fichtel and van Schaik, 2006). Observing how group members respond to threatening stimuli is one way that an infant learns to recognize danger and respond accordingly (MacKinnon, 2007; McCarthy, 2004). In addition, group living also affords non-adult sifaka the opportunity to engage in social play with a number of different group members. Social play, not only with one's mother but also with other adults and immatures can assist in the development of motor skills that an infant primate can employ should they need to respond to predators (Gould, 1990; MacKinnon, 2007), and is thus another benefit of group living. The anti-predator techniques that an animal acquires as a result of group living can be transmitted horizontally between age-mates or in a vertical, trans-generational manner to one's offspring (McCarthy, 2004). Since Verreaux's sifaka form social units, it is assumed that *P. v. verreauxi* infants have an advantage over less gregarious animals in that they can learn anti-predator behaviours from a young age, thereby enhancing their ability to survive and become reproductively successful.

Second, it is predicted that the degree to which a primate is susceptible to predation is related to both the size and cohesive nature of the group to which an animal belongs (Miller and Treves, 2007). It is often assumed that group-living primates should be somewhat less vulnerable to predation due to the dilution effect (Miller and Treves, 2007). That is, animals that form larger, more cohesive groups should be at a lower risk of predation than animals in smaller units (Overdorff *et al.*, 2002), especially if members of the former are not spatially located on the outside or periphery of the group (Miller, 2002). However, research into predation among haplorhine primates has revealed that group size might not always reduce a primate's predation risk. For example, it was observed that belonging to a larger group did not afford Thomas langurs (*Presbytis thomasi*) increased predator protection (Sterck, 2002), and Stanford (1998) found that among red colobus (*Colobus badius*) at Gombe, smaller groups were less likely to fall victim to predation than were larger groups, despite the fact that members in large groups were able to detect predators sooner (Stanford, 1998). Indeed, Miller and Treves (2007) suggest that predators might be able to detect large groups with more facility.

Nevertheless, Sauther (2002) compared rates of social cohesion, foraging location and the frequency of mixed species association between 2 groups of free-living ring-tailed lemurs (*L. catta*), and concluded that animals belonging to larger groups were less susceptible to predation than those that formed smaller social units. Additionally, cohesion can exist in groups of various sizes, and animals should be more cohesive with conspecifics when foraging in hazardous locales (Sterck, 2002). The predation hypothesis as outlined by Isbell and Enstam (2002) assumes that animals, particularly adult females that are more threatened by predation than males, will be more likely to form cohesive social units even though this may result in a reduction in their overall foraging efficiency. Since females should be more threatened by predation when caring for infants due to reduced mobility, cohesion rates should be stronger when females have young offspring. In sum, spatial cohesion fluctuates according to changes in both social and environmental variables.

Third, group-living animals are often thought to be more vigilant towards predators than are solitary animals (Miller and Treves, 2007). Lewis (2005) did not find that male Verreaux's sifaka were more vigilant towards predators than females. This suggests that in Verreaux's sifaka male vigilance behaviour might be more related to monitoring the actions of conspecifics than it is to predator detection (Lewis, 2005). Also, Lewis (2005) did not conclude that group size and vigilance rates were related in *P. v. verreauxi*, nor did Stanford (1998) in his study on red colobus monkeys (*Colobus badius*). Therefore, the role of vigilance among Verreaux's sifaka, especially as it relates to predation, requires further investigation. Nevertheless, despite the advantages of living in social units (social learning, dilution via group cohesion and vigilance), the sum total of the costs that an individual experiences (i.e., food resource competition or competition over access to mates) must be less than or equal to the benefits gained (Miller, 2002).

1.4.2 Predation and Spatial Location

Where an animal feeds spatially should change according to the extent to which it deems itself susceptible to predation (Miller, 2002), yet animals are constantly forced to strike a balance between meeting their energetic requirements and reducing their predation vulnerability. In times of food limitation, animals may forage in higher risk locations in order to meet their daily nutritional demands (Sterck, 2002). Adult females might be willing to take more foraging risks when they do not have dependent offspring, as observed in Thomas langurs (*Presbytis thomasi*) (Sterck, 2002), and also when they are a part of a large social unit (Sauther, 2002). For Verreaux's sifaka, potentially risky foraging areas include both the ground, since these primates experience difficulties with locomotion while terrestrial (Howarth *et al.*, 1986), and the terminal branches of trees (Wright, 1998), as these limbs provide less protective cover from aerial predators. Conversely, safety from predation should increase as an animal ascends arboreally from the ground towards the mid-canopy, and also the closer an animal feeds near the trunk of a tree (Brockman, 2003).

1.5 PREDATION AND *P. V. VERREAUXI*

At present, the predator species that prey upon sifaka vary between sites, and therefore *Propithecus* species do not face a homogeneous set of predatory challenges. Environmental alterations due to deforestation (Wright *et al.*, 1997), for instance, have and will continue to have an impact on the success of many predator species. This is especially true if the predatory animals in question require fairly large home-ranges for survival. Nevertheless, *Propithecus* are still currently preyed upon by various carnivores, including reptiles such as crocodiles and snakes (Goodman, 2003). At Berenty Reserve, Verreaux's sifaka are susceptible to predation by Dumeril's ground boa, *Acrantophis dumereli* (Jolly *et al.*, 2006; O'Shea, 2007). In addition, Hart (2007) reported that both birds-of-prey and small-bodied carnivorous animals, such as endemic viverrids unique to Madagascar, account for the vast majority of primate predation events that occur in Madagascar. Comparing primate predation in Madagascar with South America, Asia and Africa, Hart (2007) stated that it is only within Madagascar that small carnivores are able to subsist by consuming primates as their key prey items.

At many research sites in Madagascar, the large viverrid, *Cryptoprocta ferox*, presents a serious risk to lemur survival (Fichtel and van Schaik, 2006; Patel, 2005; Wright *et al.*, 1997). Patel (2005) estimated that *C. ferox* may indeed pose the greatest predatory threat to sifaka species, and Wright *et al.* (1997), postulated that during the dry season, this carnivore might subsist almost exclusively on lemurs. Given the fact that predation-related deaths can account for nearly one quarter of the annual deaths within a particular community without the primate group in question experiencing any serious demographic consequences (Stanford 1998), then the above might hold true. Yet *C. ferox* is not the sole predator of large-bodied prosimians (Wright *et al.*, 1997), and is absent at Berenty reserve (Gould, 2007, pers. comm.). Domestic canids and felids are introduced predators in Madagascar (Goodman, 2003), and since they may successfully prey upon sifaka at Berenty Reserve and elsewhere (Fichtel and van Schaik, 2006; Goodman, 2003), should be considered potential predators. The extent to which dogs rely on sifaka and other lemurs might be inferred by conducting fecal analyses on recovered canid scat, or by studying the behavioural patterns of these predators themselves. Indeed, Cuozzo and Sauther (in prep.) are currently studying the impact of feral dog predation on *P. v. verreauxi* at Beza Mahafaly Special Reserve.

For many years, large-bodied strepsirhines including *Propithecus* were not considered to be at risk of predation by diurnal Malagasy raptors (Wright *et al.*, 1997), and any reaction lemurs displayed to raptors was considered to be a type of residual behaviour to the now extinct Holocene birds-of-prey, particularly the Malagasy crowned eagle, *Stephanoaetus coronatus* (Goodman, 2003). However, a number of researchers (Fichtel and van Schaik, 2006; Goodman 2003; Karpanty and Grella, 2001; Patel, 2005) have recently altered their position and have accepted that raptors might potentially prey upon larger-bodied adult strepsirhines. Despite the fact that most extant raptors in Madagascar are smaller in body size than sifaka (Hart, 2007), they still pose a serious threat to sifaka at Berenty Reserve (Goodman, 2003; Sauther, 2002). Two raptors in particular prey upon *P. v. verreauxi*: the harrier hawk (*P. radiatus*) (Fichtel and van Schaik, 2006; Goodman, 2003; Jolly, 1966) and the Madagascar buzzard (*Buteo brachypterus*) (Sauther, 2002). Other birds-of-prey such as owls may only consume lemurs weighing less than 2 kg (Wright, 1998). While body size may prevent adults from being preyed upon by owls, it is feasible that infant and juvenile sifaka may be at risk (Overdorff *et al.*, 2002).

Wright (1998) suggested that lemurs might be at the highest risk of predation between June and September when there is considerable food resource stress for predator and prey species alike. Additionally, unlike during the wet season when leaves are abundant, lemurs might not be able to hide in dense foliage in the winter months, making them more apparent to predators as a result (Wright, 1998). Brockman (2003) speculated that during the August mating season of *P. radiatus*, this raptor consumes a diet almost solely composed of sifaka. Nevertheless, it is likely that the harrier hawk preys upon sifaka in other months as well, although perhaps with not such marked acuity. Since my study took place during the peak harrier hawk predation season, the anti-predatory behaviour exhibited between study groups while foraging, especially in response to aerial predators, was of particular interest.

1.6 *P. V. VERREAUXI* ANTI-PREDATOR RESPONSES

1.6.1 Overview of Sifaka Anti-Predator Behaviour

The anti-predatory behaviour of sifaka has been studied since the early 1970s (Petter, 1972). Sifaka, like all primates, have a number of anti-predatory behaviours at their disposal that can be utilized in an effort to reduce successful predation events. These behaviours, however, differ in the extent to which they can be considered directly intentional. Fichtel and van Schaik (2006) suggested that anti-predator behaviours form part of the collective knowledge of a given primate group, which are not innate, but learned over time and then transmitted in a trans-generational manner. I will briefly review two broad anti-predatory categories based on visual and auditory cues and how these function as components of predator-sensitive foraging.

1.6.2 Visual Cues as a Component of PSF Behaviour

Propithecus use visual cues in response to the presence of predatory species to alert conspecifics to danger. These visual signals can include the posture an animal assumes after detecting danger (Fichtel, 2004), and also physical gestures such as 'head-tossing' (Brockman, 2003). Head-tossing is where one or more sifaka, upon becoming alarmed, may indicate their agitation by throwing their head backward swiftly one or more times. Conspecifics within visual range of the head-tossing animal are thus alerted to the potential threat, yet the absence of vocalizations allows sifaka to maintain a degree of crypsis. Additionally, other sifaka in a group might simply become aware that one or more group members are vigilant, and then note the direction of their gaze (Fichtel, 2004). Borrowing from Gould e*t al*'s (1997) definition, vigilance is defined as an intense visual attentiveness (i.e., staring), which immediately follows the abrupt cessation of an animal's current activity (Sauther, 2002). This may be a beneficial strategy in animals that are somewhat more cryptic. Since it has been suggested that as a species, Verreaux's sifaka tend to be far-sighted (Wright, 1998), they may be able to detect predators at a distance as a result of such scanning behaviour. This could prove useful especially if the predatory animal relies on an ambush attack strategy and is deterred by premature detection (Miller and Treves, 2007). Gould (2006a) observed that ring-tailed lemur vigilance increased upon descent from the canopy level to the ground, and also when infant group members were of weaning age and exploring the environment independently. Indeed, Godfrey *et al.* (2004) observed that immature primates tend to be less vigilant while feeding and foraging. Therefore, heightened adult vigilance when there are immature animals within a group may reduce the likelihood that the latter fall victim to predation. Once a predator is spotted, group members may join together in ‘mobbing’ the animal, as was observed in a predation attempt on an adult female Coquerel’s sifaka (*P. v. coquereli*) by a boa constrictor (*Acrantophis madagascariensis*) (Burney, 2002). In sum, the frequency that the study animals used the above-mentioned visual cues (i.e., body posture, head-tossing and vigilance) while feeding and foraging compared to times when animals are engaged in other activities might prove indicative not only the predation risk of a given microhabitat, but also the extent to which sifaka rely on PSF behaviours.

1.6.3 Auditory Cues as a Component of PSF Behaviour

Visual signals are not the only means, however, by which an animal can respond to and become aware of predation threats. Auditory cues also deserve consideration and are too often neglected despite the importance they could potentially assume as an anti-predatory behavioural category for lemuriformes (Miller and Treves, 2007). Indeed, Karpanty and Grella (2001) postulated that many primates might actually prefer to use auditory cues over visual cues. Sifaka, for instance, have both referential and general alarm call vocalizations that are emitted in response to threatening stimuli (Fichtel, 2004; Fichtel and van Schaik, 2006). While the former are used to alert group members to the presence of an avian predator, the latter are utilized in response to a number of potential hazards, including terrestrial predators (Fichtel, 2004; Fichtel and van Schaik, 2006). The use of and reaction to auditory cues while feeding and foraging, as with the use of visual cues above, may provide an indication of how threatened an individual or group perceives itself to be while foraging in a given spatial stratum. Moreover, because Verreaux’s sifaka differentiate between terrestrial and aerial predators, comparing the rates that the study animals use these two calls may suggest whether sifaka at Berenty are more at risk of predation by terrestrial species such as feral dogs, for instance, than by diurnal birds-of-prey. Therefore, these two types of vocalizations will be reviewed in turn.

1.6.4 Alarm Call Vocalizations

Sifaka have an alarm call vocalization that is produced in response to aerial predators (Fichtel, 2004; Fichtel and van Schaik, 2006). When a bird-of-prey is detected, Verreaux's sifaka produce a roar-like vocalization (Jolly, 1966). This serves to warn others within the vicinity of the presence of an aerial predator. An appropriate response to an aerial call would be to rapidly drop to a lower level within the canopy (Karpanty and Grella, 2001), where animals might be somewhat protected from predation. Afterwards, group members may remain alert and the roaring bark bout may, after some time, gradually transition to growling (Fichtel and van Schaik, 2006). In addition to aerial alarm calls, sifaka also produce their namesake vocalization, the 'tchifak', a general alarm call for a multitude of threats, including terrestrial predators (Fichtel and van Schaik, 2006). Unlike for the aerial alarm call vocalization where an appropriate response would be to descend from the upper canopy level, the general alarm call should prompt sifaka to ascend up into the canopy.

1.7 RESEARCH OBJECTIVES AND HYPOTHESES

1.7.1 Research Objectives

I conducted a comparative study on predator-sensitive foraging among three habituated groups of free-ranging Verreaux's sifaka (*P. v. verreauxi*) residing in different microhabitats at Berenty Reserve in southern Madagascar. The primary objective of my study was to determine whether sifaka predation risk while feeding and foraging is reduced or enhanced according to differences in microhabitat. My intent was to determine whether variation in microhabitat in turn influenced: 1. spatial location; 2. spatial cohesiveness; 3. the time spent engaged in vigilant behaviour; 4. the frequency of use of alarm call vocalizations; and 5. the use of gestural alarm (i.e., head-tossing) behaviours while members of the three study groups were feeding and foraging.

Although all three focal groups of sifaka inhabited the same reserve, due to the ecological variation present at this reserve, it was possible to select groups from dissimilar microhabitats. The first group was from Ankoba, a closed-canopy gallery forest microhabitat dominated by tamarind (*Tamarindus indica*) and monkey pod (*Pithecellobium dulce*) trees (Jolly *et al.*, 2006). The home-range of the second study group included both the deciduous-dry spiny forest (Jolly *et al.*, 2006), which is characterized by the Euphorbiaceae, Didiereaceae and Ascleopiadaceae vegetation families (Budnitz and Dainis, 1975), and the scrub forest, which features short succulent flora species (Jolly *et al.*, 2006), and lacked the continuous canopy found in Ankoba (Budnitz and Dainis, 1975). Lastly, the third study group, the Mandrare group, was from a riverine habitat slightly north of Ankoba. Since the Mandrare group was located on the outskirts of the village of Berenty, these animals utilized not only *Tamarindus indica* and

Celtis gomophophylla (Budnitz and Dainis, 1975), but also introduced tree species planted on residential and commercial properties, including baobab (*Adansonia* sp.). Because there was sufficient microhabitat variation at Berenty Reserve, a meaningful comparison in terms of PSF behaviour could be made.

Fig. 1.2 - Satellite photograph of Berenty Reserve
(Google Earth, 2007. Accessed February 21, 2008).

1.7.2 Research Hypotheses

Hypothesis One – Spatial Cohesion (NN Distance) while Feeding and Foraging

Sifaka in the Mandrare riverine forest, due to the elevated number of potential terrestrial predators (i.e., feral canids and felids) found within their home-range, exhibit the highest amount of spatial cohesiveness while feeding and foraging. The spiny forest sifaka show intermediate results, and the focal animals within the relatively protected closed-canopy Ankoba group maintain the greatest amount of distance from their nearest neighbours (NN) while foraging.

Due to dissimilar predation risks and differences in food resource availability between the three study microhabitats, the degree to which the sifaka expressed cohesive behaviour while feeding and foraging is expected to differ between the riverine, gallery and spiny forest groups. Sifaka in the Mandrare group must contend with a higher relative number of terrestrial predators than the other two study populations, especially feral canids (personal observation). Moreover, vegetation within the riverine sifakas' home-range is the most interrupted by numerous anthropogenic influences such as roadways and buildings; therefore, these animals must descend to the ground more often than sifaka in the other two groups. Thus, the riverine Mandrare group sifaka are expected to be more spatially cohesive as a result of the features of their home-range. The spiny forest group is predicted to show less group cohesion than the riverine sifaka, but due to less leaf cover to offer protection for the animals from predators, the spiny forest sifaka are predicted to be more spatially cohesive than the Ankoba sifaka. The Ankoba sifaka are predicted to be the least spatially cohesive study group because 1) they have the greatest amount of canopy cover to offer protection from aerial predators, and 2) they have fewer terrestrial predators than sifaka from the riverine group. Therefore, because foraging Ankoba sifaka do not have to rely on the dilution effect as an anti-predation strategy as much as sifaka from the other two groups, the Ankoba sifaka are expected to be less spatially cohesive.

Hypothesis Two – Spatial Position while Feeding and Foraging

The Mandrare riverine forest sifaka spend the greatest amount of time exploiting high-risk niches (i.e., the ground and upper-canopy) compared to the sifaka in the Ankoba or spiny forest groups. Of the three groups, the sifaka residing in the Ankoba gallery, closed-canopy forest spend the least amount of time feeding and foraging in hazardous locations, and the most amount of time in the safer middle canopy range.

Given that the gallery forest of Ankoba is characterized by a fairly continuous closed canopy (Jolly *et al.*, 2006), the sifaka group in this microhabitat is expected to spend less time in high-risk areas such as the ground while feeding and foraging, unlike members of the other two groups. The spiny forest sifaka, however, forage not only in parcel one of the spiny forest, but also in the scrub forest of Malaza, both of which lack a continuous closed canopy. Due to differences in vegetation cover, the spiny forest sifaka are predicted to 1) spend less time than the Ankoba group foraging in the safe mid-canopy zone, and 2) spend less time than the Mandrare forest sifaka feeding in high-risk areas. Finally, the Mandrare group is expected to spend the most time feeding and foraging in potentially dangerous zones.

Hypothesis Three – Frequency of Alarm Call Vocalizations

Out of the three study groups, sifaka in the Mandrare riverine forest produce alarm call vocalizations the most while feeding and foraging, and sifaka in the Ankoba gallery forest are expected to use such calls the least.

Since the Mandrare sifaka are thought to have a greater number of terrestrial predators within their home-range than sifaka in the spiny and Ankoba forests, the frequency of alarm call vocalizations produced by animals in this group are expected to be greater than in the other two groups. The spiny forest sifaka are predicted to use and respond to alarm calls less than the riverine group and more than the gallery forest Ankoba group. This is due to the fact that the habitat found within the spiny/scrub forest offers less protection, such as canopy cover, from aerial predators, therefore placing the spiny forest animals at a potentially greater risk of predation by birds-of-prey. Additionally, the vegetation within the scrub forest is considerably lower (to the ground) and far patchier than the trees found in the Ankoba and Mandrare home-ranges. To determine whether the null hypothesis is true, the mean number of times that sifaka in each microhabitat produce general and referential alarm call vocalizations while feeding and foraging per hour will be determined and then compared.

Hypothesis Four – Levels of Terrestrial and Aerial Vigilance

In all three study habitats, sifaka are more vigilant terrestrially than they are vigilant aerially. The Mandrare group exhibits the highest rates of terrestrial vigilance per hour, and the Ankoba group, the least.

Since all three study groups are more threatened by terrestrial predators such as reptiles and feral dogs and cats than by diurnal birds-of-prey, it is anticipated that all sifaka will show a tendency towards the use of the terrestrial over aerial vigilance. Furthermore, because the Mandrare group had a higher number of terrestrial predators relative to the other two groups (pers. obs.), I predict they will have a correspondingly high frequency of terrestrial vigilance per hour spent feeding and foraging. The members of the gallery forest group of Ankoba are expected to be at the least risk of predation, and therefore I predict them to be less vigilant than either the riverine or the spiny/scrub groups.

Hypothesis Five – Frequency of Head-Tossing Behaviour per Hour

Because Verreaux's sifaka in the Mandrare riverine forest have the highest number of terrestrial predators in their home-range, I predict them to utilize gestural communication (head-tossing behaviour) the most while feeding and foraging. I predict that the sifaka in Ankoba, which have the lowest terrestrial predator risk, will use head-tossing behaviours the least.

The members of the gallery forest group of Ankoba are expected to be at the least risk of predation, and therefore are predicted to display head-tossing behaviour less often than either the Mandrare or the spiny forest groups. Conversely, the sifaka in the riverine habitat are expected to show the most head-tossing behaviour while feeding and foraging, again due to the high-risk features of their home-range.

CHAPTER TWO: RESEARCH METHODS

2.0 STUDY SITE

In 1936, a French colonial sisal plantation owner, A. H. De Heaulme, founded Berenty Reserve (Budnitz and Dainis, 1975; Howarth *et al.*, 1986; Jolly and Pride, 1999; Jolly *et al.*, 2006; Jolly *et al.*, 2002; Oda, 1998) (Fig 2.1). Biologists have been conducting research at Berenty since 1963 (Budnitz and Dainis, 1975; Jolly, 1966; Jolly *et al.*, 1982). For instance, Budnitz and Dainis (1975), Gould (1990, 1992), Jolly (1966), Jolly and Pride (1999), Jolly *et al.* (2006, 2002), Koyama *et al.* (2002) and Takahata *et al.* (2001) have conducted research on Berenty's ring-tailed lemurs (*Lemur catta*). Additionally, Howarth *et al.* (1986), Jolly (1966), Jolly *et al.* (1982) and Simmen *et al.* (2003a, 2003b) have conducted research on Verreaux's sifaka (*Propithecus verreauxi verreauxi*) at this site. The 200-ha reserve was opened to tourists in 1983 (Simmen *et al.*, 2003b; Jolly and Pride, 1999; Gould, pers. comm).

Annually, this region, with an elevation of approximately 50 meters above sea level (Garbutt, 1999), experiences both a wet and a dry season (Simmen *et al.*, 2003a, 2003b). My research took place from June 11, 2007 to August 10, 2007, during Madagascar's austral winter. During the dry season months between May and October there is a reduction in both temperature and precipitation (Tattersall and Sussman, 1975; Simmen *et al.*, 2003), whereas the opposite holds true for the wet season, which experiences greater rainfall and higher temperatures (Richard, 1976). Precipitation tends to fluctuate annually in this region (Jolly *et al.*, 2006; Gould, 1992). Mean rainfall is 500 mm per year (Koyama *et al.*, 2002; Budnitz and Dainis, 1975), although some years might experience little to no precipitation at all due to drought (Jolly *et al.*, 2006).

Temperature at Berenty ranges between ≤ 4ºC at night during the dry season and up to 40ºC during the day in the wet season (Gould, pers. comm.; Jolly *et al.*, 2006).

2.0.1 Flora

There has been a paucity of research conducted on the flora in the extreme south of Madagascar (Sussman and Rakotozafy, 1994), which is largely comprised of xerophytic plants, especially those species belonging to the *Euphorbiaceae* and *Didiereaceae* families (Haevermans, 2003). These and other plant families feature adaptations such as succulent leaves and stems (Heavermans, 2003) that allow them to withstand the drought-like conditions characteristic of this area (Chauvet, 1972; Budnitz and Dainis, 1975). Moreover, much of the flora in the south reproduce via biotic pollination (Bodin *et al.*, 2006). Consequently, increased conservation efforts are essential for the continued success of both the flora and fauna in this ecoregion (Sussman and Rakotozafy, 1994).

The soils in the Mandrare River area are basaltic in nature (Du Poy and Moat, 2003), and support various types of vegetation. Specifically, Berenty features closed-canopy forests, open-canopy forests, a brush and scrub forest, and spiny (subdesert) forests (Gould, 1990; Gould, 1992; Budnitz and Dainis, 1975; Howarth *et al.*, 1986; Simmen *et al.*, 2003a, 2003b; Jolly, 1966), each of which will be considered in turn. The diversity present at Berenty is advantageous in that numerous endemic floral and faunal species are permitted to thrive in this protected reserve despite the excessive habitat loss that plagues much of Madagascar. Indeed, even small forest patches such as those found at Berenty, are of critical importance for the continued success of a wide range of species in the south of Madagascar (Bodin *et al.*, 2006).

Jolly *et al.* (2006) defined a forest in which ≤ 50% of the sky is visible as a gallery or closed-canopy forest (Fig. 2.1). The gallery forest, which characterizes most of the 100-ha of land within Berenty known as Malaza, contains mostly tamarind (*Tamarinus indica*) (Budnitz and Dainis, 1975; Simmen *et al.*, 2003a; Blumenfeld-Jones *et al.*, 2006), monkey pod (*Pithecellobium dulce*) (Binggeli, 2003; Jolly *et al.*, 2006), *Neotina isoneura* (Blumenfeld-Jones *et al.*, 2006; Howarth *et al.*, 1986) and *Celtis gomphophylla* trees (Budnitz and Dainis, 1975; Blumenfeld-Jones *et al.*, 2006). The trees in the closed-canopy forest depend not so much on rainfall as they do on ground water for survival (Budnitz and Dainis, 1975). Thus, canopy height in the gallery forest, which can reach up to 20 meters, exhibits a degree of variation depending on the distance that trees are situated from the Mandrare River and the amount of ground water available (Budnitz and Dainis, 1975; Blumenfeld-Jones *et al.*, 2006).

By and large the forest of Ankoba belongs to the second class of vegetation: open-canopy forest (Fig. 2.2). Similar to the first vegetation zone, the tamarind tree (*Tamarindus indica*) is also present in the open-canopy forests of Berenty (Budnitz and Dainis, 1975). In this second region, trees typically only reach 16 meters in height, although the occasional emergent may exceed 20 meters (Jolly *et al.*, 2006; Budnitz and Dainis, 1975). In addition, the open-canopy forest is further set apart from the closed-canopy forest in that it experiences relatively more undergrowth activity (Howarth *et al.*, 1986).

The third type of vegetation zone found at Berenty Reserve is known as the brush and scrub forest (Fig. 2.3). In this forest ≥ 50% of the sky is visible (Koyama *et al.*, 2002; Jolly *et al.*, 2006), and in places there is little or no canopy cover (Budnitz and Dainis, 1975). Trees are not entirely absent from the scrub forest, however. Trees belonging to the genus *Acacia* are the most common species (Howarth *et al.*, 1986). Other notable plants in this region include *Salvadora angustifolia, Azima tetracantha,* and *Guisivianthe papionaea* (Budnitz and Dainis, 1975).

Subdesert or spiny forest is the fourth forest zone found at Berenty Reserve (Fig. 2.4). There is very little canopy cover in this habitat. Plant species in the spiny forest belong largely to the Didiereaceae, Asclepiadaceae, Euphorbiaceae families (Budnitz and Dainis, 1975; Gould, 1992), many genera and subgenera of which are endemic to Madagascar (Haevermans, 2003; Hoffmann and McPherson, 2003). Regrettably, despite the high level of endemism present in the spiny forests of Berenty and in southern Madagascar generally, this particular forest type is listed as one of the most critically endangered ecoregions on the planet (Olson and Dinerstein, 1998; Rioux Paquette *et al.*, 2007).

Fig. 2.1- Closed-canopy forest

Fig. 2.2- Open-canopy forest

Fig. 2.3 – Scrub forest

Fig. 2.4 – Spiny forest

2.0.2 Fauna

Berenty Reserve is home to a number of endemic and introduced mammalian species, including six lemur species. There are two diurnal lemurs: Verreaux's sifaka (*P. v. verreauxi*), and the ring-tailed lemur (*L. catta*) (Simmen *et al.*, 2003b; Oda, 1998). The introduced red-fronted brown lemur hybrid (*Eulemur fulvus rufus* X *E. fulvus collaris*), present since 1975, is cathemeral (Jolly *et al.*, 2002). Additionally, Berenty Reserve is home to four nocturnal lemurs: the fat-tailed dwarf lemur (*Cheirogaleus medius*), the grey mouse lemur (*Microcebus murinus*), the white-footed sportive lemur (*Lepilemur leucopus*) and the grey-and-red mouse lemur (*Microcebus griseorufus*) (Jolly *et al.*, 2006; Garbutt, 1999). Other mammalian species present include rats (*Rattus* sp.), bats, especially *Pteropus rufus*, and three species of tenrec, small shrew-like insectivores endemic to Madagascar (Garbutt, 1999; Jolly *et al.*, 2006; MacKinnon *et al.*, 2003).

There are only a limited number of terrestrial and aerial predators at Berenty Reserve; however, the mammalian predators with which Verreaux's sifaka must contend include introduced semi-feral dogs (*Canis lupus familiaris*) and cats (*Felis silvestris*) (Takahata *et al.*, 2001). Avian predators of Verreaux's sifaka include the harrier hawk

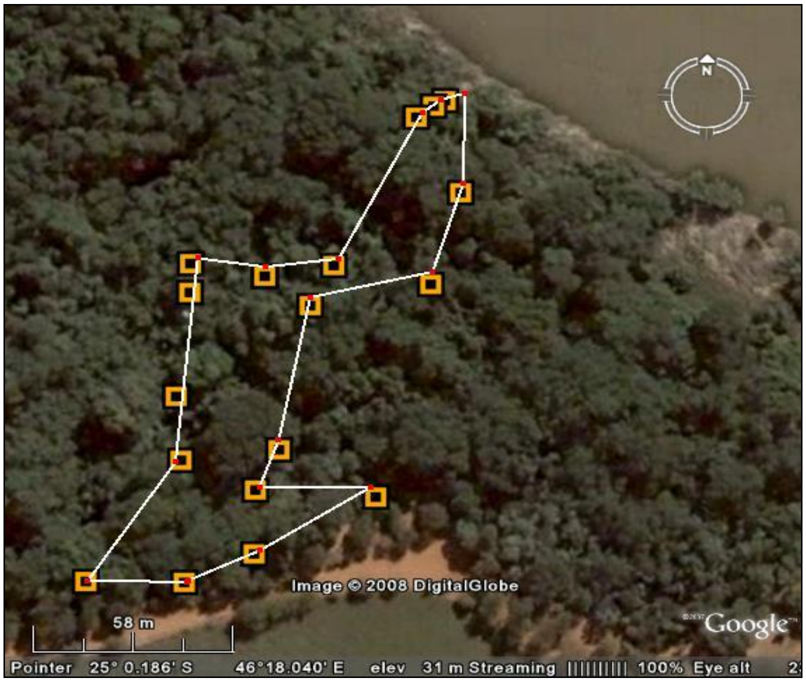
(*Polyboroides radiatus*) (Takahata *et al.*, 2001; Jolly *et al.*, 2006) and the Malagasy buzzard (*Buteo brachypterus*) (Jolly *et al.*, 2006). Finally, reptilian predators such as Dumeril's ground boa, *Acrantophis dumereli*, are also potentially threatening to *P. v. verreauxi* at this site (Jolly *et al.*, 2006).

2.1 STUDY SUBJECTS

2.1.1 Ankoba Group

A 40 hectare second-growth forest (Jolly *et al.*, 2006; Howarth *et al.*, 1986), Ankoba is home to *P. v. verreauxi*, *L. catta* and *E. f. rufus*, and features both endemic and introduced flora (Jolly *et al.*, 2002; Koyama *et al.*, 2002), including tamarind (*Tamarindus indica)*, monkey pod (*Pithecellobium dulce*) and *Neotina isoneura* trees (Howarth *et al.*, 1986; Jolly *et al.*, 2006). Classified as an open-canopy forest, in Ankoba, tree height ranges between 10 and 15 meters (Howarth *et al.*, 1986). Similar to the closed-canopy forest of Malaza to the southeast, Ankoba contains both interior and exterior trails (Rasamimanana *et al.*, 2000). In total, a group of five adult sifaka from the Ankoba gallery forest were observed for 19 days between June 13, 2007 and August 8, 2007. Ankoba group’s home-range was 0.93 hectares in size (Fig. 2.5). The number of focal animal sessions are found in Table 2.1.

Fig. 2.5 - Satellite photograph showing the home-range of the Ankoba group (Google Earth, 2007. Accessed May 18, 2008).



2.1.2 Spiny Group

The five sifaka from the spiny group foraged in both the spiny and scrub forests (Fig. 2.6). Table 2.1 lists group composition and the number of focal animal sessions collected on each group. The spiny forest is comprised of 4 parcels that are raised in elevation from the scrub forest (pers. obs.). This group fed exclusively in parcel one of the spiny forest, which contained dry-adapted, thorny plants, especially *Alluaudia procera* (Jolly *et al.*, 2006). The scrub forest also contained a number of xerophytic plant species including species from the genus *Euphorbia*, although a few tamarind (*Tamarindus indica*) were also present (Jolly *et al.*, 2006; Blumendfeld-Jones *et al.*, 2006), providing the sifaka with relatively more canopy cover than is found in the spiny forest. Generally, the troop would spend the morning sunning, grooming and feeding in the forest in which they had slept the previous night (i.e., the scrub forest), and then would gradually make their way to the second forest type (i.e., the spiny forest) by early afternoon. The troop would then forage in this second part of their home-range until sunset, at which time they would select and settle in an appropriate sleeping tree. This group had a home-range of 2.08-ha.

Fig. 2.6 - Satellite photograph highlighting the home-range of the spiny forest (Google Earth, 2007. Accessed May 18, 2008).

2.1.3 Mandrare Group

The Mandrare riverine sifaka were my third study group. Located northwest of Ankoba forest, the Mandrare sifaka foraged in riverine microhabitat found along the banks of the Mandrare, and in the trees located on the outskirts of the village of Berenty

(Fig. 2.7). This group's home-range measured approximately 1.62 hectares. The Mandrare group's home-range contained a few tamarind trees (*Tamarindus indica*), which they regularly exploited as well as introduced species of trees, such as the baobab (*Adansonia* sp.), planted around commercial and residential properties. The predation threat for this group is considered higher than that of the other two study groups, as over the study period a number of terrestrial predators, including semi-feral dog and cat species, were observed within this home-range. The study of the Mandrare sifaka is novel since these sifaka have never been studied. See Table 2.1 for group composition and number of hours observed.

Fig. 2.7 - Satellite photograph showing the home-range of the Mandrare group (Google Earth, 2007. Accessed May 18, 2008).

Table 2.1 Focal sessions

INDIVIDUALS	GROUP	SEX	Reproductive Status	Total Sessions
NINA	SF	F	Reproductive	64
DINAH	SF	F	Reproductive	64
DJANGO	SF	M	NA	58
OSCAR	SF	M	NA	68
LOUIS	SF	M	NA	54
CHENCHA	AF	F	Reproductive	80
FRIDA	AF	F	Non-reproductive	56
DIEGO	AF	M	NA	51
AGUSTIN	AF	M	NA	76
SALVADOR	AF	M	NA	54
MISS CELIE	MF	F	Reproductive	64
SHUG	MF	F	Non-reproductive	40
HARPO	MF	M	NA	55
ALBERT	MF	M	NA	56
MISTER	MF	M	NA	58
ADAM	MF	M	NA	44

Spiny Forest (SF), Ankoba Forest (AF), Mandrare Forest (MF).
(Reproductive Females n=4, Non-reproductive females: n=2. Males: n=10).

2.2 DATA COLLECTION

Data were collected using fifteen-minute continuous time focal animal sampling (Altmann, 1974). An ethogram, or description of each possible sifaka activity, was determined prior to commencing research (Appendix A). At the start of each session the time, the spatial location of the focal animal, and the identity and approximate distance in meters of its nearest neighbour (NN), if present, were noted. The focal animal was then observed for the duration of the session, and all behaviours (Appendix A) were recorded along with the time at which they occurred. Adult sifaka were individually recognized based on features such as facial markings, the presence or absence of freckles, eye colour, cap colour, cap shape, and overall pelage colour and condition. Each sifaka was also assigned a name in order to facilitate ease of recognition. Sessions were terminated if the focal animal was lost or went out of visual range for more than two minutes during the observation period. If less than half of the time of the focal session had elapsed prior to losing sight of the focal animal, the entry was discarded.

Binoculars were used to aid in the observation of sifaka. Additionally, using a WAAS-enabled, hand-held Garmin Geko 201 GPS navigating device, an attempt was made to determine the boundaries of each sifaka group's dry season home-range. On August 6, 2007, all sleeping and foraging sites in which members of each group had been observed over the study period were visited, and waypoints were entered. The geographic coordinates were recorded using the degree:minute (DM) format. These measurements were then entered into Google Earth 4.3 (beta) satellite imaging software. Google Earth's 'path' tool was used to distinguish group boundaries. Google Earth's 'ruler' tool was used when calculating the approximate total area of each group's home-range.

Data on the sifaka were collected six days a week and each group was observed twice weekly on a rotating basis. Group members were selected in a rotational manner in order to collect a proportionate amount of data on each individual. No attempt was made to gather equal amounts of data between the sexes, since the size of each group was too small to conduct meaningful intra-group sex-based analyses.

Groups were typically found in the early morning hours and, on average, focal sampling began by 07:46 HRS. A group was followed throughout the course of the day until the sifaka retired to a sleeping tree around sunset. No data were collected while sifaka were sleeping. Focal animal data collection sessions were rotated throughout the day so that all focal animals were observed at different times.

2.2.1 Collection of Predator Sensitive Foraging Behaviour Data

Because predation risk was assumed not to be homogeneous across the various microhabitats, and furthermore, since each microhabitat featured differing forms of vegetation, the frequency of predator-sensitive foraging behaviour of the three sifaka study groups was predicted to differ. In order to ascertain whether there were inter-group differences in *P. v. verreauxi* predator-sensitive foraging behaviour, data were collected on five different variables: 1) spatial position, 2) spatial cohesion, 3) vigilance, 4) frequency of alarm call vocalizations, and 5) frequency of gestures (head-tossing) used to convey alarm.

Spatial position was collected by recording where a focal animal was situated spatially during the focal session. The ground, low-canopy, mid-canopy and upper-canopy were assigned numerical values from 0 to 3, respectively. The initial spatial position of the study subject was recorded at the start of the session, and any vertical movement was noted throughout. Only spatial position exploited while feeding and/or foraging was later analyzed.

Approximate distance in meters of the focal animal to its NN was recorded so that spatial cohesion could be assessed. The distance between the focal animal and its closest conspecific was measured visually using six categories: 0.0-0.9 m, 1.0-1.9m, 2.0-2.9 m, 3.0-3.9 m, 4.0-4.9 m and no NN. Any changes with respect to a focal animal's NN, in terms of either distance or identity, were noted. Again, only data recorded while the focal animal was foraging were analyzed.

The frequency of the remaining three variables - vigilance, alarm call vocalizations and head-tossing behaviour- were recorded *ad libitum*. When an animal was vigilant while foraging, an attempt was made to determine whether the stimulus occurred terrestrially or aerially (Appendix A). Similarly, the type of alarm call vocalization (i.e., a 'tchifak' to indicate a general or terrestrial threat, or a 'roaring-bark' in response to an aerial stimulus), was also recorded.

2.3 DATA ANALYSIS

2.3.1 Storage of Data

Focal sessions were recorded by hand into notebooks, and were later entered into Microsoft Excel 2003. Excel spreadsheets were created for each group and each group member. In order to determine the frequency with which a given variable occurred, pivot tables concerning the five research foci: spatial position, NN distance, vigilance rates, vocalization rates, and occurrences of head-tossing behaviour while feeding and foraging were produced. Finally, data were entered into SPSS v. 15.0 and analyzed.

2.3.2 Statistical Analyses

Data were analyzed statistically using SPSS 15.0 software for Windows. The α-level of significance for each hypothesis was set at 0.05. In order to determine whether there were any statistically significant differences between the three groups with respect to the variables, the non-parametric Kruskal-Wallis one-way ANOVA analysis of variance test was used due to the small sample size (n= 16) and nature of the research hypotheses. The Kruskal-Wallace one-way ANOVA analysis of variance test is useful when analyzing the results of three or more non-related variables to determine the extent to which data are similar or dissimilar (Martin and Bateson, 1993). When analyzing the results between two groups only, the non-parametric Mann-Whitney *U* test of significance was used and a Bonferroni correction was used to correct for multiple tests.

CHAPTER THREE: RESULTS

3.0 RESULTS INTRODUCTION

My study compared the predator-sensitive foraging (PSF) behaviour of three groups of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) from dissimilar microhabitats at Berenty Reserve. Specifically, my research objectives were to determine whether:

1. Verreaux's sifaka prefer a particular spatial niche (i.e., the ground, low-, mid-or high-canopy) while foraging, and to ascertain to what extent spatial positioning was determined by microhabitat;
2. the distance sifaka maintained from their nearest neighbour (NN) differed according to microhabitat;
3. sifaka groups expressed differing rates of vigilance behaviour while foraging, and whether the study groups were equally vigilant towards terrestrial and aerial stimuli alike;
4. the frequency that sifaka produced both general and aerial alarm call vocalizations while foraging varied according to microhabitat; and
5. there were statistically significant inter-group differences regarding the frequency in which sifaka engaged in gestural communication while foraging to convey alarm.

3.1 SPATIAL POSITION OF *P. V. VERREAUXI* WHILE FORAGING

Differences in sifaka foraging location may affect their level of predation risk. Due to the dissimilar flora found within the home-ranges of the three study groups, a consistent measure for determining spatial position across each microhabitat was required. Thus, borrowing from Sauther's (2002) tree quadrant method, the canopy and ground were divided into four sections (Fig. 3.1, Fig. 3.2).

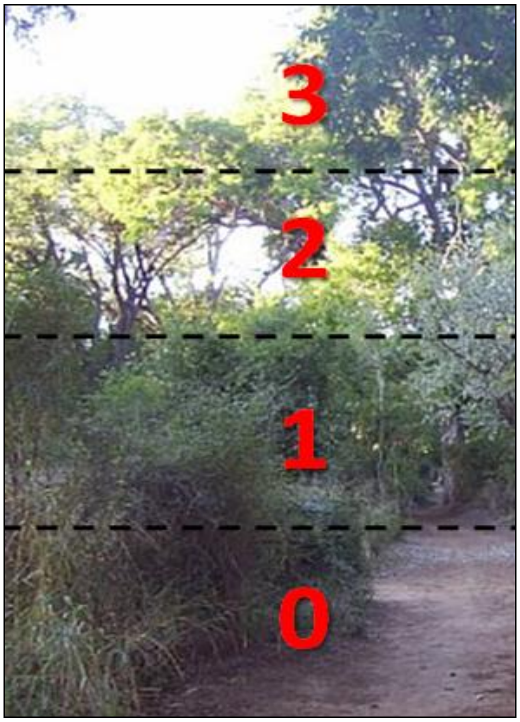


Fig. 3.1- Measuring spatial position in a closed-canopy forest.

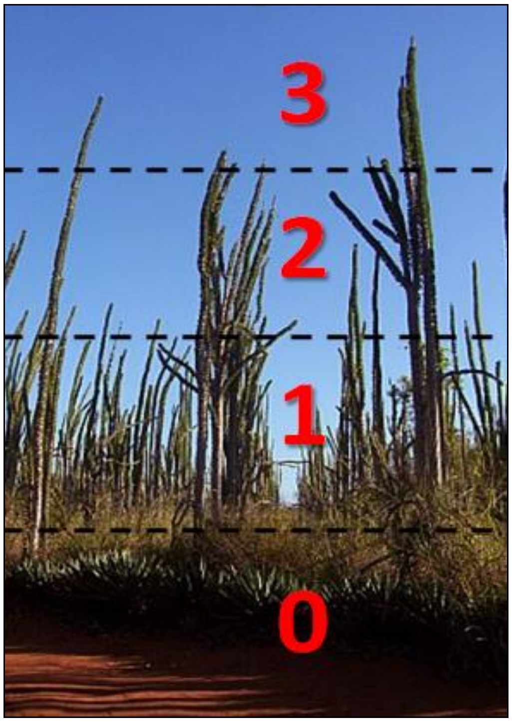


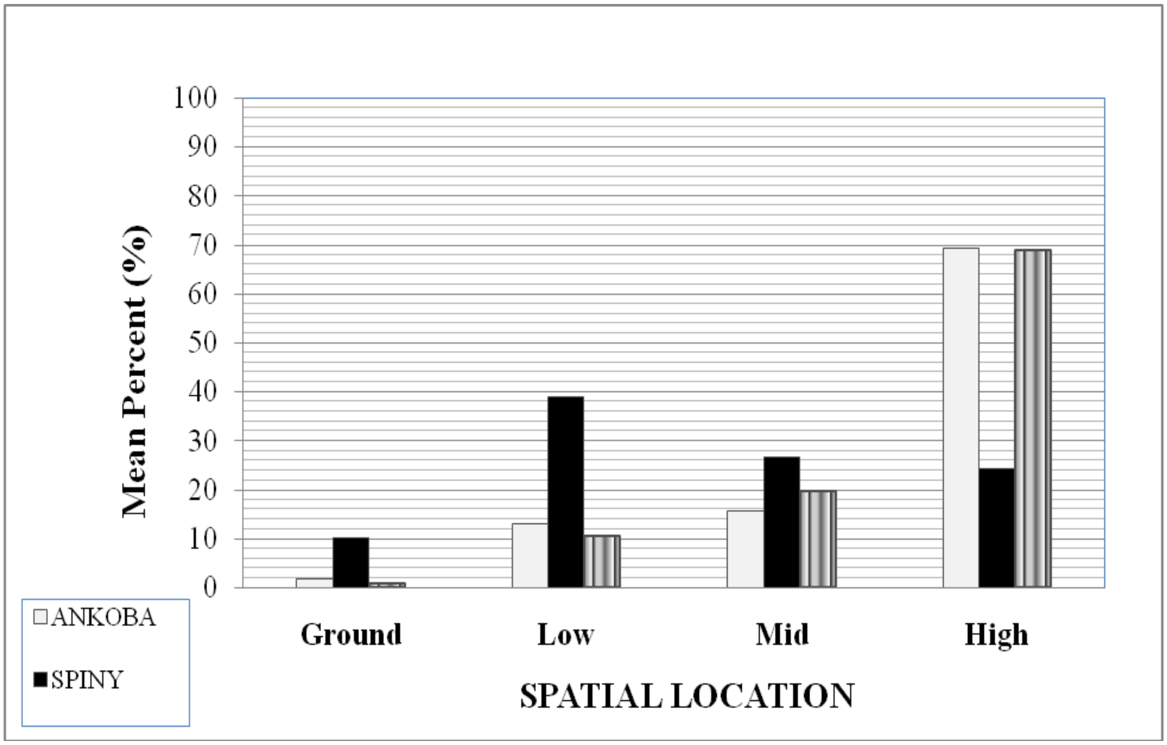
Fig. 3.2- Measuring spatial position in the spiny forest.

HYPOTHESIS: *I predicted that the spiny group would spend the greatest amount of time exploiting high-risk niches (i.e., the ground and upper-canopy) compared to the Mandrare or Ankoba groups. I hypothesized that the sifaka in the Ankoba gallery, closed-canopy forest would spend the least amount of time foraging in high-risk niches, and the most amount of time in the safer mid-canopy because of a reduced potential predation threat.*

3.1.1 Spatial Position Results

Fig. 3.3 shows the percentage of time each group foraged in the four spatial strata. There were statistically significant differences regarding the amount of time sifaka foraged terrestrially (Kruskal-Wallis non-parametric one-way ANOVA test of significance: n=16, $\chi^2 = 9.72$, $df= 2$, $p= 0.008$) and in the low- ($\chi^2 = 9.72$, $df= 2$, $p= 0.008$), mid- ($\chi^2 = 10.0$, $df= 2$, $p= 0.007$), and high-canopy ($\chi^2 = 11.17$, $df= 2$, $p= 0.004$). The first part of the null hypothesis predicting that the spiny group would exploit high-risk niches at a greater frequency than the Mandrare or Ankoba groups cannot be supported. Although the spiny sifaka spent relatively more time foraging terrestrially than the Ankoba or Mandrare sifaka, the other two groups foraged most often in the upper-canopy, which is also a dangerous spatial location. The prediction that the Ankoba sifaka would forage most often in the least dangerous strata (i.e., the mid-canopy) was also not supported. Sifaka from both the Mandrare and spiny groups spent more time foraging in the mid-canopy per hour than did the Ankoba sifaka.

Fig. 3.3 - Percent of time per hour foraging at each spatial location



3.2 SPATIAL COHESIVENESS WHILE FORAGING

HYPOTHESIS: *Due to the high number of terrestrial predators (i.e., semi-feral canids and felids) found within their home-range, I predicted that the Mandrare group would exhibit the highest amount of spatial cohesiveness while foraging. Foraging members of the spiny group were expected to have intermediate results because of an intermediate potential predation threat. Foraging Ankoba sifaka were predicted to maintain the greatest distances from their NN because they were predicted to have the least potential predation threat.*

Second, sifaka were expected to express increased spatial cohesiveness while foraging in dangerous niches. Sifaka were expected to be the most spatially cohesive while foraging terrestrially and in the upper-canopy because of the high potential predator risk in these niches. Sifaka were expected to be the least spatially cohesive while in the mid–canopy because this was considered the spatial niche with the lowest potential predation risk.

3.2.1 Spatial Cohesiveness Results

Overall spatial cohesion results are presented in Table 3.1. Regardless of microhabitat, Verreaux's sifaka from all three study groups had low rates of spatial cohesiveness and were most likely to forage without a NN. However, when a NN was present, focal animals from each group were mostly likely to maintain a distance of 1.0-1.9 m from their closest conspecific. The distances focal animals were least likely to keep from their NN differed between the three groups. The Mandrare group was least likely to forage 0.0-0.9 m from their NN, the Ankoba group was least likely to forage 3.0-3.9 m from their NN, and the spiny group was least likely to forage 4.0-4.9 m from their NN.

There were no statistically significant between-group differences when NN were between 0.0-0.9 m (Kruskal-Wallis non-parametric one-way ANOVA test of significance: $\chi^2 = 2.15$, $df = 2$, $p = 0.342$), 2.0-2.9 m ($\chi^2 = 0.58$, $df = 2$, $p = 0.748$), or between 3.0-3.9 m ($\chi^2 = 2.55$, $df = 2$, $p = 0.279$). Results were statistically significant when the distance that sifaka foraged from their NN was between 1.0-1.9 m, ($\chi^2 = 5.83$, $df = 2$, $p = 0.054$), 4.0-4.9 m ($\chi^2 = 6.10$, $df = 2$, $p = 0.047$), and when no NN was present ($\chi^2 = 7.84$, $df = 2$, $p = 0.02$).

Table 3.1 - Overall spatial cohesiveness by group

Distance of NN in meters	**Percentage (%) of Time per Hour Spent Feeding/Foraging from NN**		
	Ankoba Forest (AF)	Spiny Forest (SF)	Mandrare Forest (MF)
0.0 m - 0.9 m	8.0 %	2.0 %	3.6 %
1.0 m – 1.9 m	13.9 %	20.2 %	19.6 %
2.0 m – 2.9 m	11.4 %	10.3 %	12.1 %
3.0 m – 3.9 m	5.6 %	8.1 %	7.2 %
4.0 m - 4.9 m	12.1 %	0.9 %	6.9 %
No NN	49.0 %	58.5 %	50.6 %

Spatial cohesiveness was also analyzed in relation to spatial position (Fig. 3.4, 3.5, 3.6 and 3.7). All study groups expressed a preference for solitary feeding, regardless of the spatial position occupied. There were no statistically significant between-group differences in terms of spatial cohesion when animals foraged in the low-, mid- or high-canopy levels. Results were statistically significant when terrestrially foraging sifaka were between 0.0-0.9 m from their NN ($\chi^2 = 7.52$, $df= 2$, $p= 0.023$), 2.0-2.9 m ($\chi^2 =13.35$, $df= 2$, $p= 0.001$), and 3.0-3.9 m ($\chi^2 =7.52$, $df= 2$, $p= 0.023$) from their NN.

Fig. 3.4 - Spatial cohesion per group while terrestrial

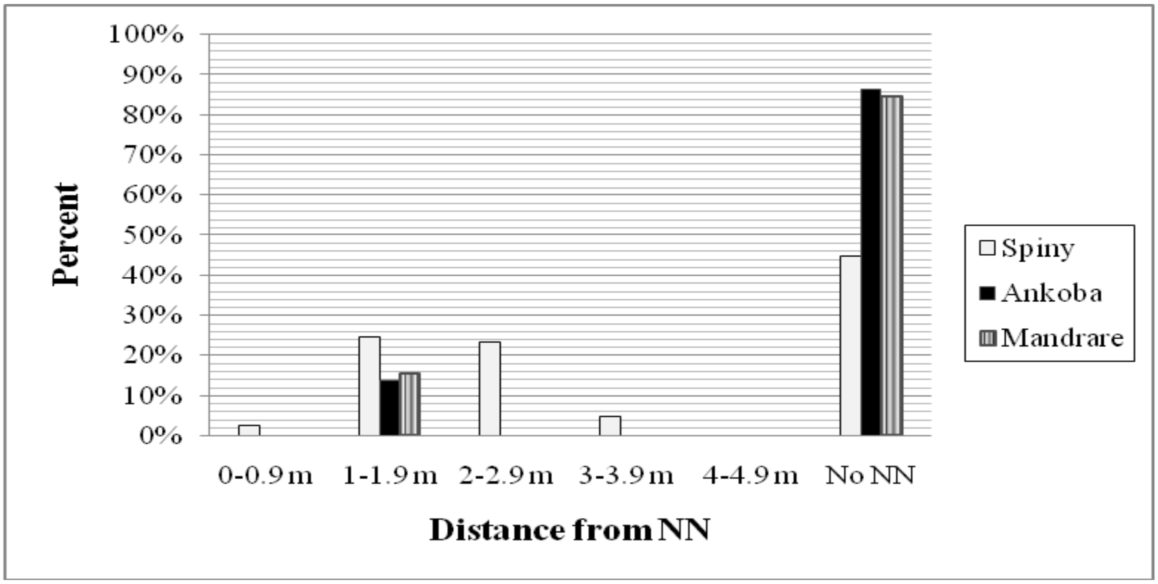


Fig. 3.5 - Spatial cohesion per group in the low-canopy

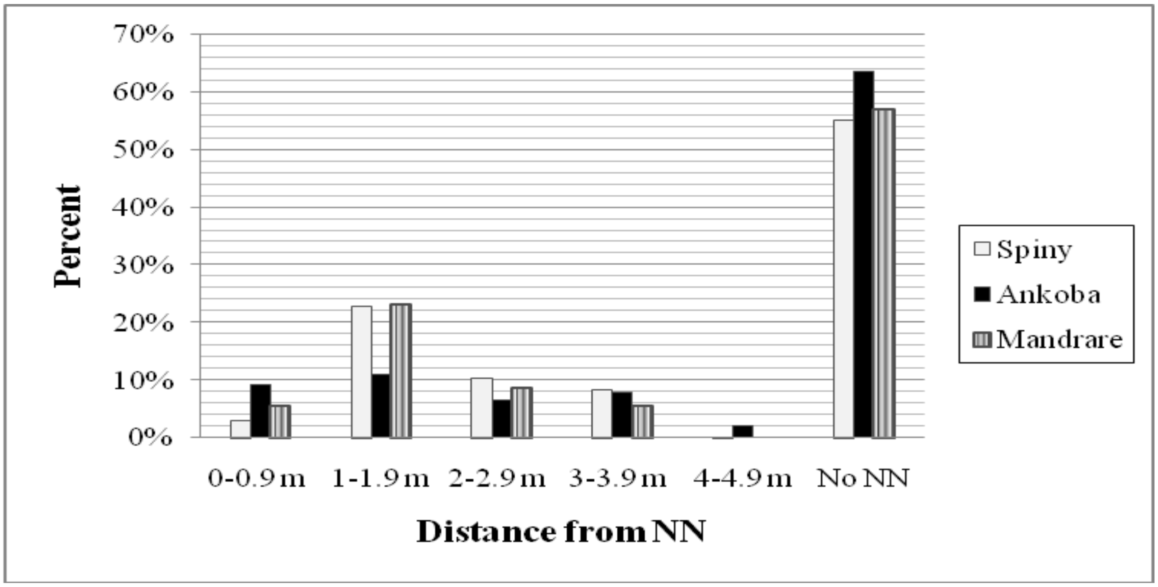


Fig. 3.6 - Spatial cohesion per group in the mid-canopy

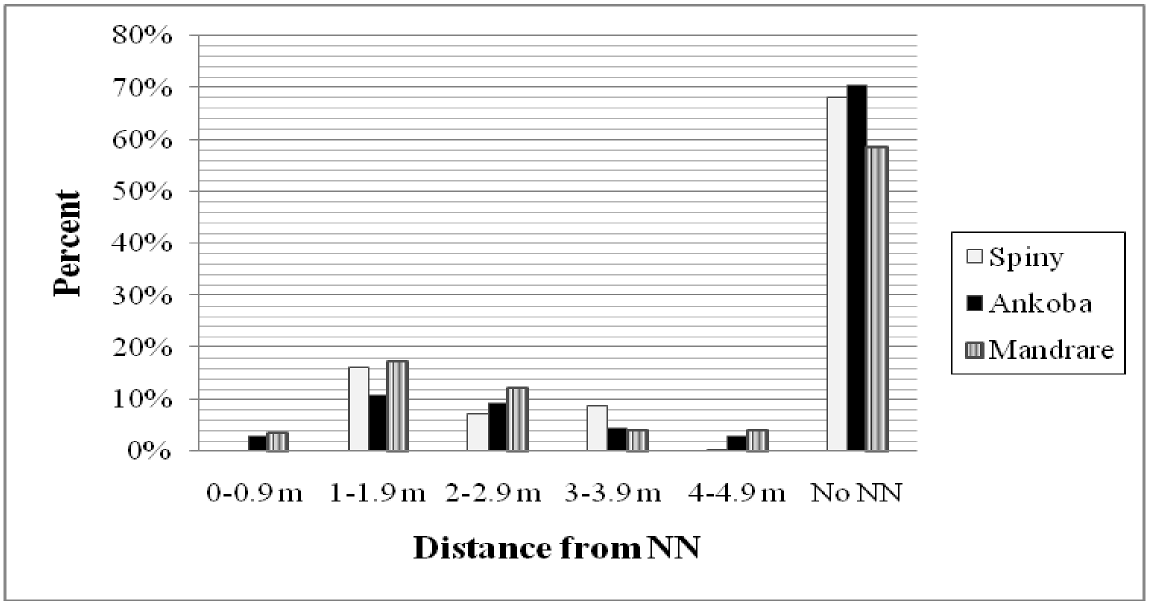
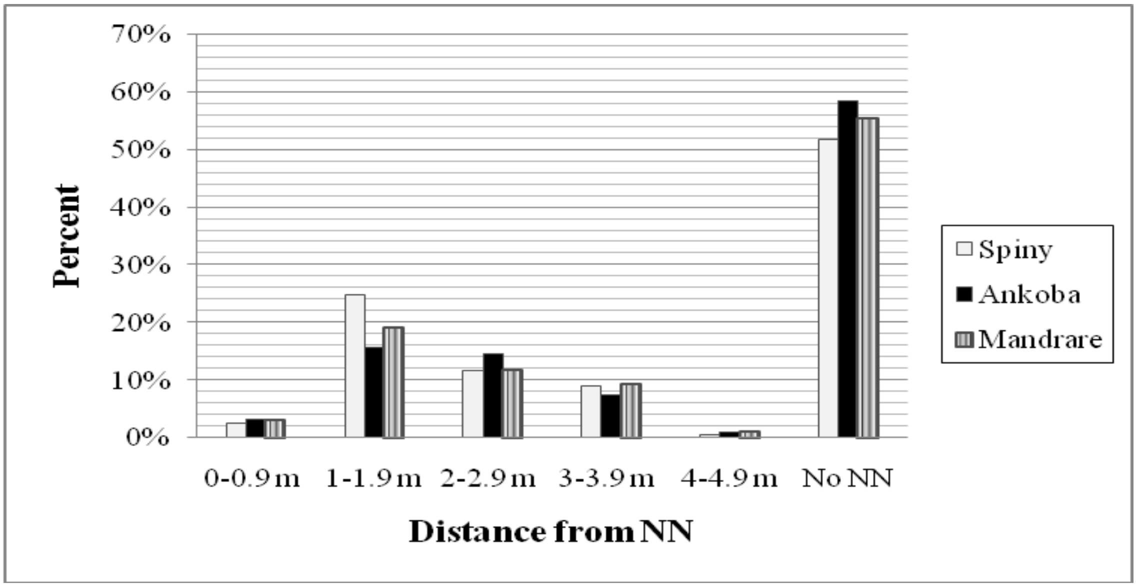


Fig. 3.7 - Spatial cohesion per group in the high-canopy



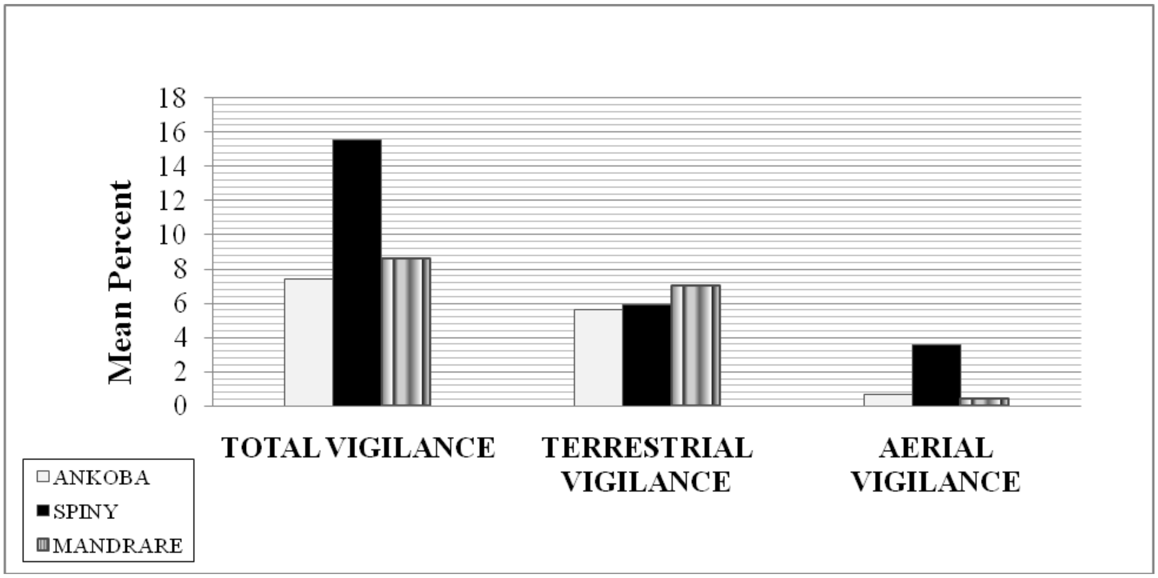
3.3 VIGILANCE BEHAVIOUR WHILE FEEDING AND FORAGING

HYPOTHESIS: *First, I predicted that the Mandrare group would express the highest rate of vigilance behaviour while foraging because of a high potential predation risk, and that the Ankoba group would express the least vigilance because of a lower potential predation risk. Second, I hypothesized that the Mandrare group would use terrestrial vigilance the most while foraging because of a high potential terrestrial predator risk. I predicted that the Ankoba group would use terrestrial vigilance the least because of a lower potential terrestrial predator risk. Third, I predicted that the spiny forest group would use aerial vigilance the most while foraging because of a high potential aerial predator risk and reduced canopy cover. The Ankoba group was predicted to use aerial vigilance the least because of a lower potential aerial predator risk. Fourth, I expected there to be inter-group differences in terms of terrestrial and aerial vigilance levels and a sifaka's spatial location because predation risk was hypothesized to differ according to foraging location. I predicted sifaka to be most terrestrially vigilant while foraging on the ground and in the low-canopy, and most aerially vigilant while foraging in the mid- and high-canopy.*

3.3.1 Overall Vigilance Rates

It was not always possible to determine a sifaka's direction of gaze while vigilant. All occurrences of vigilance behaviour (i.e., unknown, terrestrial and aerial) while sifaka were feeding were combined. Figure 3.8 displays the mean percentage of vigilance behaviour per group while sifaka were foraging. Overall, the spiny group was the most vigilant group (15.5 % of their observation time while foraging), the Mandrare group had intermediate results (8.6 %), and the Ankoba group was the least vigilant (7.4 %). These results approached statistical significance (Kruskal-Wallis non-parametric one-way ANOVA test of significance: $\chi^2 = 5.00$, *df* = 2, *p*= 0.082).

Fig. 3.8 – Mean percentage of time sifaka groups expressed general, terrestrial- and aerial vigilance while foraging



3.3.2 Terrestrially-Centred Vigilance

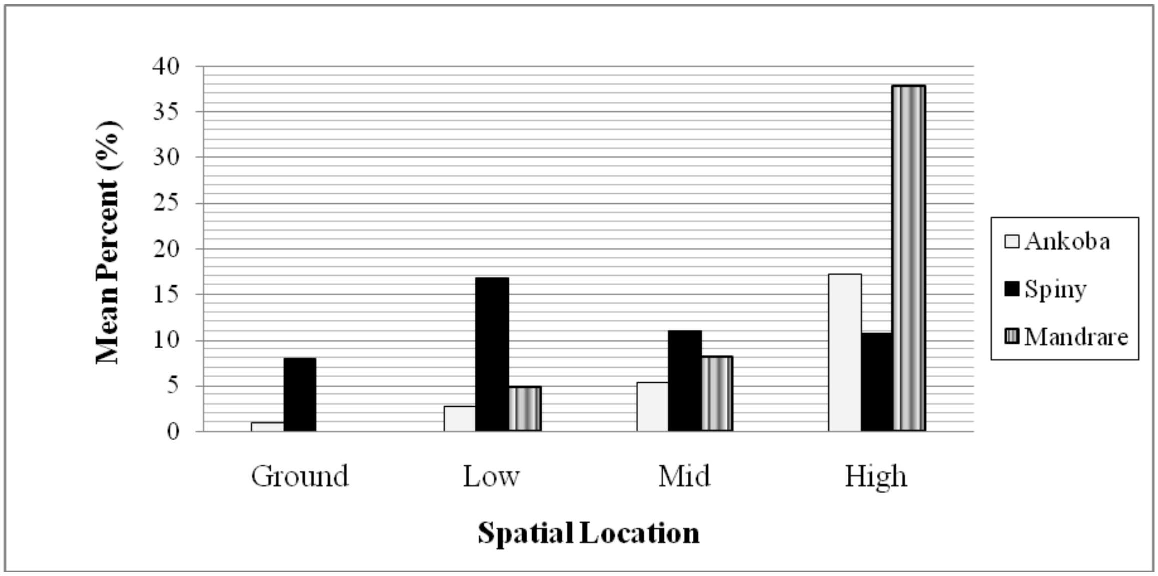
As predicted, the Mandrare group spent the most time terrestrially vigilant (7.0% of the observed foraging time), and the Ankoba group spent the least time terrestrially vigilant (5.6% of the observed foraging time). The spiny forest group expressed only slightly more terrestrial vigilance (5.9% of the observed foraging time) than the Ankoba sifaka. However, there were no statistically significant between-group differences regarding the amount of time sifaka were vigilant to terrestrial stimuli (Kruskal-Wallis non-parametric one-way ANOVA test of significance: χ^2=1.13, *df* = 2, *p*= 0.569).

When terrestrial vigilance levels were analyzed in relation to spatial location it was determined that there were significant between-group differences regarding the amount of time sifaka engaged in terrestrial vigilance behaviour while terrestrial (χ^2= 12.17, *df*= 2, *p*= 0.002). Using a Bonferroni correction to correct for multiple tests (α-level of significance was 0.016) there were no significant differences between Ankoba and Mandrare sifaka (Mann-Whitney *U* test: n_1= 5, n_3= 6, *z* =-1.09, *p*= 0.273). Results were statistically significant between terrestrially foraging spiny forest and Ankoba sifaka (n_2= 5, n_1= 5, *z* =-2.48, *p*= 0.013), and between spiny forest and Mandrare sifaka (n_2= 5, n_3= 6, *z* =-2.99, *p*= 0.003) (Fig. 3.9).

There were statistically significant between-group differences in terrestrial vigilance when sifaka foraged in the low-canopy (χ^2= 7.09, *df*= 2, *p*= 0.029). Using a Bonferroni correction to correct for multiple tests (α-level of significance was 0.016), there were statistically significant differences between spiny forest and Ankoba sifaka (n_2= 5, n_1= 5, *z* =-2.52, *p*=0.012), but no statistically significant differences between spiny forest and Mandrare sifaka (n_2= 5, n_3= 6, *z* =-1.97, *p*=0.049) or between Ankoba and Mandrare sifaka foraging in the low-canopy (n_1= 5, n_3= 6, *z* =-0.20, *p*=0.842).

There were no statistically significant differences in the amount of time sifaka spent terrestrially-vigilant while in the mid-canopy (χ^2= 0.65, *df*= 2, *p*= 0.724). There were statistically significant inter-group differences in terrestrial vigilance when sifaka foraged in the high-canopy (χ^2= 9.99, *df*= 2, *p*= 0.007). A Bonferroni correction was used to correct for multiple tests and the α-level of significance was 0.016. There were no statistically significant differences in terrestrial vigilance between spiny forest and Ankoba sifaka (n_1= 5, n_2= 5, *z* =-1.36, *p*= 0.175) or between Ankoba and Mandrare sifaka (n_1= 5, n_3= 6, *z* =-2.191, *p*=0.028) when foraging in the high-canopy. There were statistically significant differences between spiny forest and Mandrare sifaka (n_2= 5, n_3= 6, z =-2.47, p=0.013).

Fig. 3.9– Mean percentage of terrestrial vigilance per group while foraging

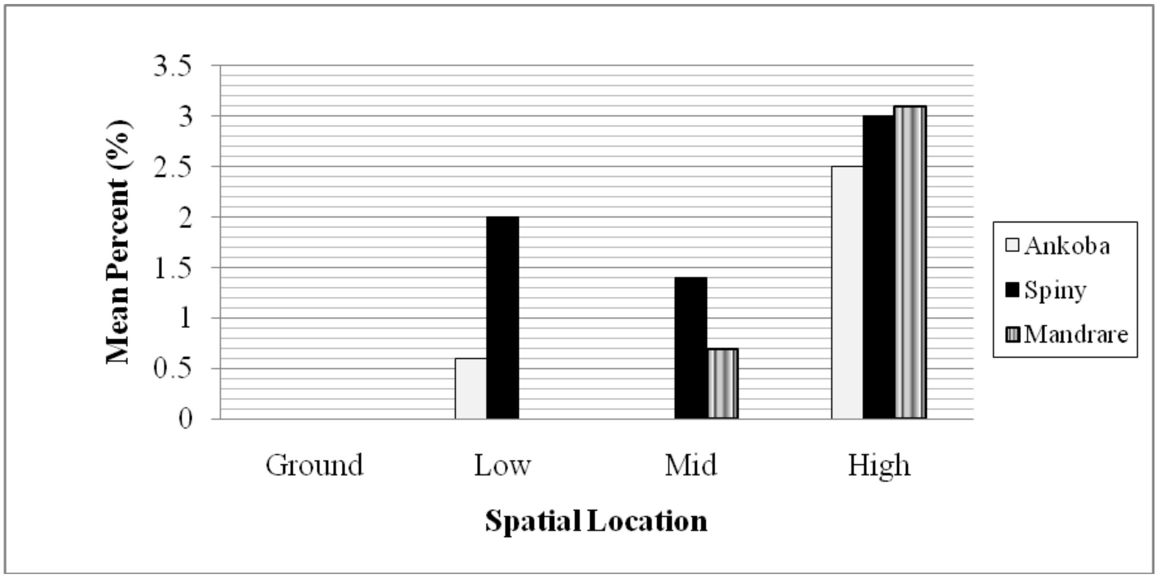


3.3.3 Aerially-Centred Vigilance

Regardless of microhabitat, sifaka in each of the three groups had fewer incidents of aerially-centred vigilance than terrestrially-centred vigilance per hour spent foraging. Figure 3.10 displays aerial vigilance rates per group according to spatial location. As predicted, foraging spiny forest sifaka were the most vigilant to aerial predators (3.6% of observed foraging time). The Mandrare and Ankoba groups had similar rates of aerial vigilance; however, it was the Mandrare and not the Ankoba sifaka that were the least aerially vigilant (0.4 % and 0.7 % of observed foraging time). The overall between-group aerial vigilance results were not statistically significant (Kruskal-Wallis non-parametric one-way ANOVA test of significance: $\chi^2 = 4.03$, *df* = 2, *p*= 0.133), thus the null hypothesis was rejected.

There were only statistically significant differences between-group levels of aerial vigilance when sifaka foraged in the low-canopy ($\chi^2 = 8.01$, *df* = 2, *p*= 0.018). There were no statistically significant inter-group differences in aerial vigilance when sifaka foraged terrestrially ($\chi^2 = 0.00$, *df* = 2, *p*= 1.00), or in the mid- ($\chi^2 = 3.52$, *df* = 2, *p*= 0.172) or high-canopy ($\chi^2 = 0.15$, *df* = 2, *p*= 0.929). Hence, the results suggest that spatial position exerts little influence on the frequency that foraging Verreaux's sifaka at Berenty Reserve are vigilant to aerial predators.

Fig. 3.10– Mean percentage of aerial vigilance per group while foraging



3.4 ALARM CALL VOCALIZATIONS WHILE FORAGING

HYPOTHESIS: *First, I predicted that foraging Mandrare group sifaka would produce terrestrial alarm call vocalizations the most because of a high potential terrestrial predation risk. The Ankoba group was predicted to use terrestrial alarm calls the least* *because of a reduced potential terrestrial predation risk. Second, I predicted that of the three groups, the spiny forest sifaka would use aerial alarm calls the most while foraging because of a high potential aerial predation risk. The Ankoba group was predicted to use aerial alarm calls the least while foraging because of a lower potential aerial predation risk.*

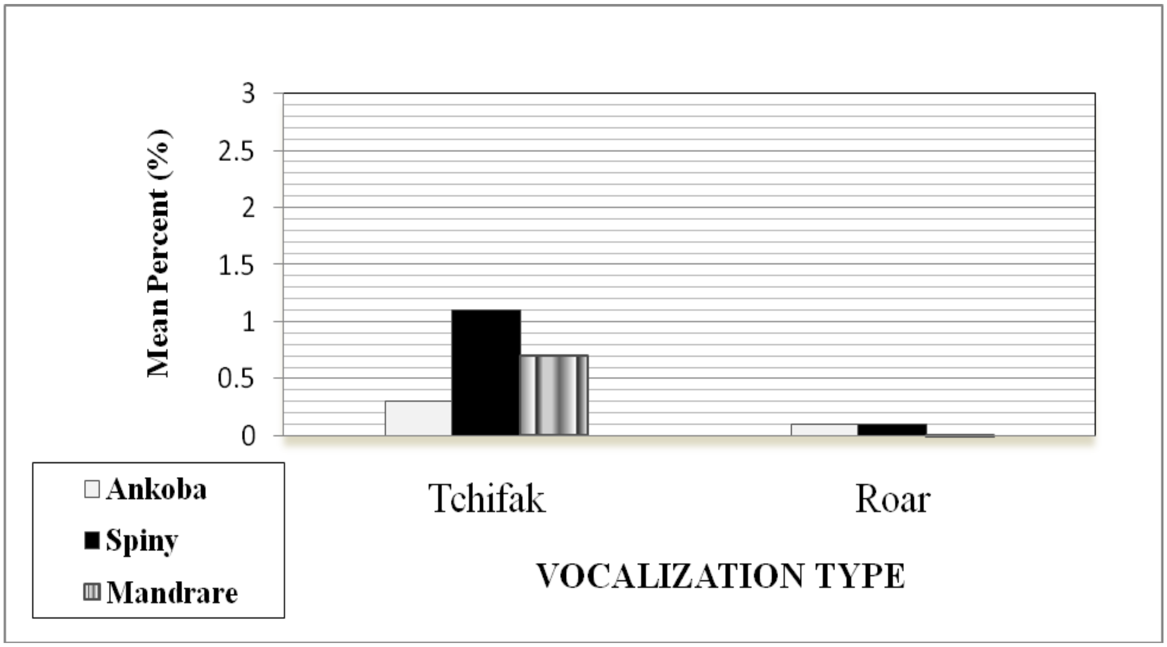
3.4.1 Terrestrial Alarm Calls

Figure 3.11 displays the mean percentage of terrestrial alarm call vocalizations produced per study group while foraging. The results indicated that the spiny forest sifaka, and not the Mandrare sifaka, produced the most terrestrial alarm call vocalizations while foraging. The spiny group used the 'tchifak' vocalization while foraging 1.1%, the Mandrare group 0.7%, and the Ankoba group 0.3%. There was no significant between-group difference (Kruskal-Wallis non-parametric one-way ANOVA test of significance: χ^2=3.43, *df*= 2, *p*= 0.180).

3.4.2 Aerial Alarm Calls

There were no significant inter-group differences in terms of the use of aerial alarm call vocalizations (χ^2=0.10, *df* = 2, *p*= 0.950). Figure 3.11 displays the mean percentage of time sifaka from each group produced aerial 'roar' alarm calls. Both the spiny and Ankoba sifaka had identical rates of aerial alarm call use (0.1% of the total time spent foraging) and the Mandrare group used the aerial alarm call 0.01% of the time spent foraging.

Fig. 3.11 – Mean percentage of alarm call vocalizations per group while foraging

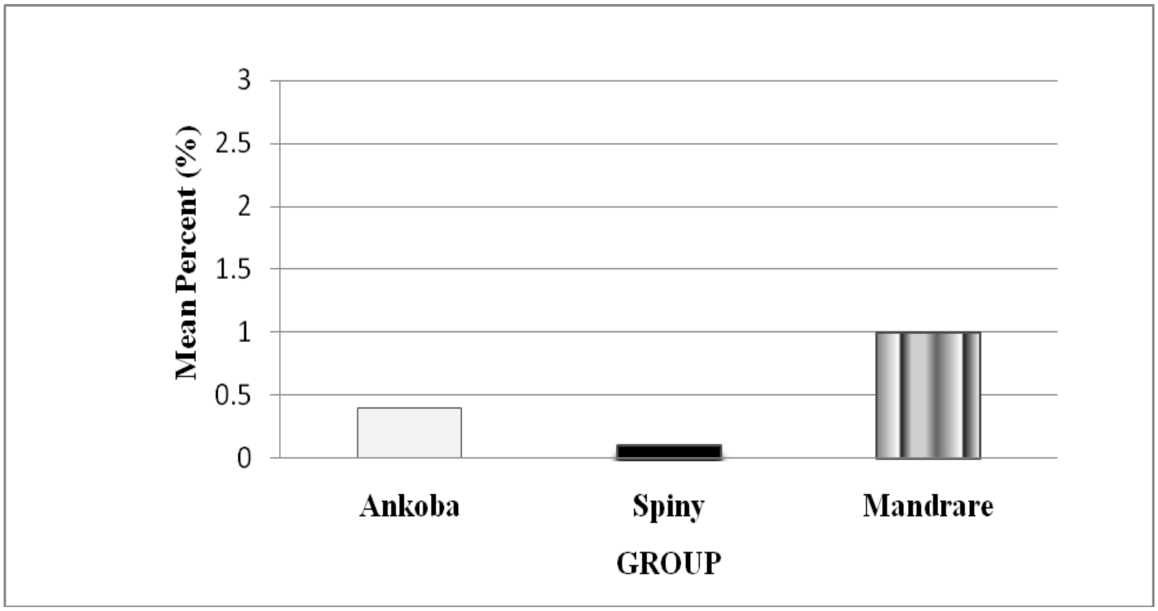


3.5 GESTURAL ALARMS WHILE FEEDING AND FORAGING

HYPOTHESIS: *I predicted that the Mandrare group would use head-tossing behaviour more often than the other two groups because they had a high terrestrial predator risk. Because the Ankoba group has a lower terrestrial predator risk, I predicted they would use head-tossing behaviours the least.*

Figure 3.12 illustrates the mean percentage of head-tossing behaviours observed while sifaka from each group foraged. The Mandrare sifaka used the head-toss alarm 1% of the observed time foraging, the Ankoba group 0.4%, and the spiny forest group 0.1%. Since there were no statistically significant between-group differences (Kruskal-Wallis non-parametric one-way ANOVA test of significance: χ^2=2.00, *df*= 2, *p*= 0.368) the null hypothesis was not rejected.

Fig. 3.12 - Mean percentage of head-tossing behaviour per group while foraging



CHAPTER FOUR: DISCUSSION

4.0 SPATIAL POSITION AS A COMPONENT OF PSF

To determine whether microhabitat influences the predator-sensitive foraging (PSF) behaviour of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) the spatial position used while foraging was analyzed. Sifaka should favour foraging in strata that maximize energetic returns and minimize predation vulnerability. Sifaka from each group were assumed to have similar energetic needs, but differed in terms of potential predation risk and food resource availability. Thus, the study groups were predicted to exhibit differences in the spatial stratum used most often while foraging. In general, the Ankoba and Mandrare groups consistently ranged in each spatial strata (i.e., ground, low-canopy *etc*.) with comparable frequencies. The spiny forest group, however, exhibited more deviation regarding the spatial location used while foraging than did sifaka in the Ankoba gallery or Mandrare riverine microhabitats. First, the spiny forest group was farther removed in distance from the Ankoba and Mandrare groups, whereas the latter were closer in geographic proximity to one another. Second, the Ankoba and Mandrare groups both resided near human habitations whereas the spiny group did not. As a result, the predation vulnerability could have been greater for the Mandrare and Ankoba groups than for the spiny group, thereby accounting for the observed differences in foraging patterns. Finally, variation in vegetation may have been more pronounced between the spiny forest, and the Mandrare and Ankoba forests than between the Mandrare and the Ankoba forests.

4.0.1 Terrestrial Foraging

Verreaux's sifaka from all study groups devoted the least amount of time to terrestrial foraging. The availability of terrestrial food resources was assumed to differ between the three groups. The Mandrare and Ankoba groups exploited terrestrial food resources very infrequently compared to the spiny forest group (that fed terrestrially more often). For the Mandrare sifaka, the ground was assumed to contain the least amount of edible food items and provide minimal energetic returns relative to the food resources found in the low-, mid- and high-canopy. Further, the Mandrare group's home-range had the most anthropogenic disturbances. Conversely, the spiny forest group had the least amount of anthropogenic interference and was assumed to have the most edible terrestrial food items in its home-range.

Additionally, predator pressure was considered most acute for terrestrially foraging Verreaux's sifaka. At Berenty Reserve at least four predators hunt terrestrial prey. Two introduced mammalian carnivores, felids (*Felis silvestris*) and canids (*Canis familiaris*) pose a threat to Verreaux's sifaka foraging on the ground (Brockman *et al.*, 2008; Fichtel, 2004; Fichtel and van Schaik, 2006; Goodman *et al.*, 2003; Kleiman and Eisenberg, 1973). The cathemeral Dumeril's ground boa (*Acrantophis dumerili*) (O'Shea, 2007; Raxworthy, 2003) and the diurnal harrier hawk (*Polyboroides radiatus*) are also capable of preying upon terrestrially-situated sifaka of any size (Fichtel, 2004; Crompton and Sellers, 2007; Sauther, 2002). Although some predators (i.e., Dumeril's ground boa) were thought to pose an equal threat to each study group (Raxworthy, 2003), other terrestrial predators (i.e., feral canids and felids) were observed be more concentrated in the Mandrare group's home-range than in the Ankoba or spiny forests (pers. obs.). Dogs and cats were frequently spotted in the Mandrare group's home-range. During my study, however, only one canid and no felids were seen in the Ankoba forest. No mammalian carnivores were spotted in the spiny forest during my study.

Finally, the vertical-clinging-and-leaping (VCL) locomotion used by the genus *Propithecus* may reduce the ability for Verreaux's sifaka to successfully evade predators while terrestrial (Crompton and Sellers, 2007). This could prove especially true as the distance between a terrestrially foraging sifaka and the closest tree (in to which that sifaka could ascend) increases. Although Crompton and Sellers (2007) noted that the erratic way in which sifaka locomote while terrestrial could potentially confuse predators, sifaka are primarily adapted to arboreal locomotion. Thus, sifaka are expected to move most efficiently in trees than terrestrially to escape potential predators.

4.0.2 Foraging in the Low-Canopy

Sifaka foraging in the low-canopy are assumed to be safer than those foraging terrestrially. First, sifaka in the low-canopy can effectively utilize their vertical-and-clinging leaping ability to evade predators should a predation attempt occur. Second, sifaka that forage in the low-canopy may not be at risk of predation by canids (Kleiman and Eisenberg, 1973), although Dumeril's ground boa and felids still pose a threat (Kleiman and Eisenberg, 1973; Garbutt, 1999). The Mandrare and Ankoba groups were less likely to exploit the low-canopy than were the spiny forest sifaka. This could suggest that the former experience a higher potential predator risk while in the low-canopy than the latter. The spiny forest sifaka, however, preferred to forage most often in the low-canopy. The spiny and scrub forests lacked the protective canopy cover present in both the Mandrare and Ankoba home-ranges. Thus, foraging in the low-canopy may have offered spiny forest sifaka overhead protection, albeit minimal, from avian predators. While terrestrial predators were assumed to pose less of a risk for the spiny forest group, diurnal birds-of-prey were frequently spotted in this home-range. By foraging most often in the low-canopy the spiny forest sifaka appear to be negotiating both their perceived predation risk with their nutritional requirements given the characteristics of their microhabitat. Furthermore, this deviation indicates that the gallery and riverine microhabitats are more similar to one another than they are to the spiny forest microhabitat. Future studies would do well to compare the dietary quality of the food resources found in each spatial stratum per microhabitat.

4.0.3 Foraging in the Mid-Canopy

The mid-canopy is assumed to be the safest spatial stratum for foraging sifaka. First, the primarily terrestrial predators (i.e., canids and Dumeril's ground boa) that threatened sifaka in the first two strata are unlikely to successfully prey upon individuals in the mid-canopy. In addition, although while arboreal Verreaux's sifaka are most preyed upon by the Madagascar buzzard (*Buteo brachypterus*) (Karpanty and Grella, 2001), Henst's goshawk (*Accipiter henstii*) (Karpanty and Grella, 2001), and the harrier hawk (*P. radiatus*) (Crompton and Sellers, 2007; Fichtel, 2004; Fichtel and van Schaik, 2006; Karpanty and Grella, 2001; Oda, 1998; Sauther, 2002), sifaka in the mid-canopy can use their vertical-clinging-and-leaping abilities to escape raptor attacks (Crompton and Sellers, 2007). In addition, the wing-span of some diurnal birds-of-prey may prohibit successful predation attempts in the mid-canopy (Crompton and Sellers, 2007). Thus, given the advantages of foraging in this third stratum in terms of reduced predation vulnerability, the fact that no group preferred to forage most often in the mid-canopy is noteworthy. The mid-canopy was, however, the second-most preferred feeding stratum for all groups.

4.0.4 Foraging in the Upper-Canopy

Sifaka that forage in the upper-canopy are at risk of predation by diurnal birds-of-prey (Brockman, 2003; Crompton and Sellers, 2007; Karpanty and Goodman, 1999; Karpanty and Wright, 2007; Langrand, 1990; Miller, 2002; Sauther, 1989). Despite such risks, however, the Mandrare and Ankoba groups ranged in the upper-canopy most often. Since my study took place in the dry season when food scarcity is most pronounced, the Mandrare and Ankoba sifaka might have exploited the food resources in the upper-canopy to meet their dietary requirements despite potential avian predation risks. Indeed, primates may often exploit different canopy levels according to season and fluctuations in resource availability (Kingdon, 1974). By contrast, the spiny forest sifaka preferred to feed in the low- and mid- canopy over the upper-canopy. This suggests that: 1) the spiny forest group perceived their avian predation risk to be greater in the upper-canopy than did sifaka in the other two groups, or 2) unlike the Mandrare or Ankoba groups, the spiny forest group could adequately meet their nutritional demands without ranging in the upper-canopy level. Thus, it appears that free-living Verreaux's sifaka are able to adjust their foraging behaviours according to fluctuations in microhabitat, such as food resource availability and quality, and predator pressure.

4.1 SPATIAL COHESIVENESS WHILE FORAGING

In general, animals are broadly categorized as being either cohesive or dispersed depending on the extent of their sociality (Schulke and Kappeler, 2003; Miller, 2002).

Cohesion is typically viewed as advantageous for most non-human primates since cohesive, gregarious animals may defend food patches with more facility than non-gregarious individuals (Terborgh and Janson, 1986; van Schaik, 1983). Moreover, members of social units may detect potential predators sooner than solitary/dispersed animals (Burger and Gochfeld, 1992; Cords, 1990; Cresswell *et al.*, 2003; Quinn and Cresswell, 2004; Schulke and Kappeler, 2003), so they may also experience a decrease in predation risk (Schulke and Kappeler, 2003). Cohesion, however, can be detrimental in terms of intra-group feeding competition (Sauther, 2002; Miller, 2002; Isbell and Enstam, 2002). For some individuals, this could result in diminished rates of foraging efficiency (Miller, 2002). Nevertheless, Holt (1984) maintains that the predation-related benefits gained by animals residing in cohesive units typically compensate for any feeding costs incurred.

Given the benefits that increased spatial cohesiveness entails, the high incidence of Verreaux's sifaka in all three study habitats foraging without a NN regardless of the spatial stratum exploited requires explanation. Since neither predation risk or resource distribution expressed inter-group constancy, the highly uniform results are particularly interesting. Moreover, the fact that members of all groups were second-most likely to maintain a high degree of spatial cohesiveness from their NN, when one was present, instead of gradually reducing the distance between conspecifics, also merits consideration. Indeed, the only time that spatial location influenced NN distance was when sifaka foraged in risky spatial locales. Thus, to understand the results obtained, spatial cohesiveness will be examined in terms of: 1) environmental and 2) biological variables.

Cohesion between group members is not static (van Schaik, 1983), but rather, may fluctuate in response to resource abundance (Miller and Enstam, 2002; Irwin, 2007) and predator pressure (Miller, 2002; Sterck, 2002). Animals that forage in closer proximity to a nearest neighbour (NN), for instance, are considered less at risk of predation relative to conspecifics that exhibit greater group spread (Miller, 2002). Thus primates should maintain higher rates of spatial cohesiveness when ranging in potentially dangerous spatial strata (Sterck, 2002). Lima (2002) maintained that prey species should forage in food patches that have the lowest risk of predation. However, animals might occasionally sacrifice safety from predators in order to fulfill their energetic requirements (Miller, 2002). During the dry season months in Madagascar when there is food scarcity sifaka may spend less time actively engaged in PSF behaviours (i.e., low rates of spatial cohesion) to meet their basic nutritional demands (Miller, 2002; Quinn and Cresswell, 2004). Indeed, resource distribution appeared to dictate the spatial cohesion observed in two groups of Diademed sifaka (*Propithecus diadema*) from dissimilar forests at Tsinjoarivo, Madagascar (Irwin, 2007). Irwin (2007) found that a similar pattern of spatial cohesion (i.e., no NN within at least 10 meters while foraging) was preferred among foraging Diademed sifaka inhabiting a highly fragmented forest (Irwin, 2007), while the group residing in a continuous canopy forest exhibited higher rates of group cohesion. These results were attributed to discrepancies in food resource distribution between the two populations (Irwin, 2007). Thus, food scarcity could account for the low rates of spatial cohesion observed in each of the study groups. However, while some researchers posit that lower rates of spatial cohesion are more the result of resource distribution than they are of predator pressure (Isbell and Enstam, 2002), this answer does not explain why Berenty sifaka inhabiting three separate microhabitats with dissimilar vegetation preferred to maintain enhanced social cohesion, irrespective of their spatial location, when a NN was present. Indeed, if resource distribution alone influenced the rates of spatial cohesion observed among Verreaux's sifaka, then at least some inter-group differences in spatial cohesion should be expected due to discrepancies in microhabitat (Isbell and Enstam, 2002), but this was not the case. Thus, the rates of spatial cohesion observed when a NN was present appear to be not solely the result of between-group similarities in resource distribution, but also predator pressure.

Since predation risk can affect the majority of a prey species's behaviours (Lima, 2002), it is probable that predation also partly determines the foraging patterns observed among free-ranging primates. Contrary to the resource distribution hypothesis (Isbell and Enstam, 2002), the predation hypothesis predicts that an animal's foraging decisions are governed more by its perceived predation vulnerability than by the location and quality of food resource items (Isbell and Enstam, 2002). Verreaux's sifaka form multi-male/multi-female social units (Jolly, 1966) that are too small in number for this species to rely on group size as a type of anti-predator behaviour. Since aggregations of animals might actually attract predators (Stanford, 1998), it seems that while feeding at least, Verreaux's sifaka might attempt to minimize their detection by predators by increasing the distance maintained between group members in favour of a more cryptic foraging strategy (Wright, 1998), which also functions to reduce the rates of within-group feeding competition (Quinn and Cresswell, 2004). Crypsis is arguably utilized in other sifaka species, including Milne-Edwards' sifaka (*P. diadema edwardsi*) (Karpanty, 2006; Karpanty and Wright, 2007; Scheumann *et al.*, 2007; Wright, 1998; but see Overdorff *et* *al.*, 2002), and may have evolved as a way for sifaka to minimize their predation vulnerability while foraging. Although the focal animals in each group preferentially maintained distances of > 5 m from conspecifics, group members were still within the auditory, and in most cases, visual range of one another. Thus, group members could still use and react to any vocal or non-vocal alarms produced in response to potential predators.

Finally, it should be noted that biological variables may also influence the spatial cohesiveness observed among foraging Verreaux's sifaka. Lehmann *et al.,* (2007) hypothesized that a positive relationship usually exists between the size of a given species' neocortex and its mean group size. Arguably, the larger one's neocortex, the more cohesive, social relationships one is able to maintain (Lehmann *et al.*, 2007). However, Lehmann *et al.* (2007) suggested that Verreaux's sifaka forms bigger social groups than anticipated based on neocortex size, which can result in lower rates of social cohesion between members. Hence, it is probable that the rates of spatial cohesion maintained between free-living Verreaux's sifaka while foraging were determined by the concurrent interplay of several environmental (i.e., the availability and spread of resources across seasons, and fluctuations in predator pressure) and biological (i.e., neocortex size) variables (Lehmann *et al.*, 2007). In sum, by avoiding reliance on simple 'either/or' dichotomies in lieu of an appreciation for the complexity of factors that influence anti-predator behaviour, it is anticipated that a more realistic explanation for the PSF observed among Verreaux's sifaka can be achieved.

4.2 VIGILANCE BEHAVIOUR WHILE FORAGING

Vigilance was defined as ‘intently staring beyond the immediate vegetation with a stationary, alert posture’ (Gould *et al.*, 1997, p. 405; Gould, 1996). In my study, vigilance was further demarcated into three separate categories: terrestrial, aerial and unknown, which were each assumed as accurately as possible based on the focal individual’s direction of gaze (Appendix A). The vigilance levels observed in free-living animals are thought to correspond to their perceived level of predation risk (Bednekoff and Lima, 1998). For this reason, the first two vigilance categories (i.e., terrestrial and aerial) were given particular attention to determine whether Verreaux’s sifaka at Berenty Reserve perceived themselves to be more at risk of predation by terrestrial or avian predators. Further, whether this perceived risk varied according to microhabitat was also of interest. Finally, since animals should show higher rates of vigilance while occupying dangerous spatial locations such as the ground than when in relatively safer areas, for example the mid-canopy (Gould, 1996; Gould *et al.*, 1997; Gould and Sauther, 2007), the frequency that sifaka were vigilant both terrestrially and aerially while occupying the four spatial strata were also analyzed. Nevertheless, vigilance may be used not only to detect predators (Gould, 1996; Gould *et al.*, 1997; Treves, 2000; Cresswell *et al.*, 2003; Beauchamp, 2003) but also to survey the actions of heterospecifics (Gould, 1996; Gould *et al.*, 1997) and intra- and inter-group conspecifics (Gould, 1996; Gould *et al.*, 1997; Treves, 2000). Thus, it is reasonable to expect vigilance events to occur at any spatial strata, leaving researchers with the responsibility of determining the stimulus to which a vigilant animal is reacting.

Vigilance is costly since it interrupts the time a focal animal could otherwise spend feeding (Cords, 1990; Miller, 2002; Treves, 2000). Consequently, an animal should adjust its vigilance to maximize predator detection while minimizing any foraging disruptions (Brown *et al.*, 1999). Gregarious animals are considered to be at an advantage over solitary animals since the former may rely on vigilant conspecifics to detect and alert group members to danger, thereby reducing the amount of time group-living primates devote to vigilance behaviour (Beauchamp, 2003; Burger and Gochfeld, 1992; Catterall *et al.*, 1992; Clark and Mangel, 1986; Cords, 1990; Li and Jiang, 2008; Bednekoff and Lima, 1999; Terborgh and Janson, 1986). This is referred to as the 'predator-detection hypothesis' (Alexander, 1974; Gould *et al.*, 1997; van Schaik, 1983). Thus, in some avifaunal and faunal taxa, individual vigilance levels are inversely related to group size (Beauchamp, 2003; Burger and Gochfeld, 1992; Cresswell *et al.*, 2003). Nevertheless, Treves (2000) and Stanford (1998) do not concur with the notion that group size decreases the amount of time primates spend engaged in vigilance. Additionally, female primates may tolerate male group members in spite of the higher intra-group feeding costs that social living entails because males often provide both detection of and protection from predators (Baldallou and Henzi, 1992; Gould, 1996; Gould *et al.*, 1997; Rose and Fedigan, 1995; Terborgh and Janson, 1986; Treves, 2000). However, this was not the case among ring-tailed lemurs (*Lemur catta*) (Gould, 1996; Gould *et al.*, 1997), and may not hold true for Verreaux's sifaka either. Indeed, during a 16-month study concerning vigilance among Verreaux's sifaka at Kirindy Forest, Lewis (2005) found that male *P. v. verreauxi* had comparatively higher rates of vigilance than females, yet the conclusion that male vigilance was concerned solely with predator detection could not be supported.

4.2.1 Terrestrially-Centred Vigilance

Foraging sifaka at Berenty Reserve were predicted to spend more time terrestrially vigilant than aerially vigilant. At this site, terrestrial predators were thought to pose a greater risk to sifaka than aerial predators. The fact that Verreaux's sifaka in all three groups used terrestrial vigilance more often than aerial vigilance supports this assumption. Nevertheless, the density of potential terrestrial predators appeared to differ according to microhabitat. Therefore, the frequency that foraging sifaka were vigilant to terrestrial stimuli was expected to express between-group variation. The Mandrare sifaka were predicted to be the most terrestrially vigilant group. As hypothesized, the Mandrare group had the overall highest rates of terrestrial vigilance while foraging. First, the Mandrare sifaka inhabit an area in which both feral canids and felids were frequently spotted. Second, the Mandrare group had to contend with a substantial amount of anthropogenic disturbances including human traffic. At Berenty Reserve humans do not prey on sifaka; however, the relatively higher levels of terrestrial vigilance displayed by the Mandrare group suggests that humans are still considered potentially threatening.

That the Ankoba sifaka had higher rates of terrestrial vigilance than the spiny forest sifaka was unexpected. This suggests that the Ankoba group experiences a slightly higher rate of potential terrestrial predators than the spiny forest group. First, it is possible that the Ankoba sifaka experience more canids, felids and human traffic in their home-range than do the spiny forest sifaka due to the geographic proximity of the former to Berenty village and the tourist complex. Many Malagasy workers and villagers, as well as students and researchers frequently travel through Ankoba forest. Second, while tourists rarely frequent the spiny forest during the day, tourists often visit Ankoba to observe Verreaux's sifaka, red-fronted brown lemurs, and ring-tailed lemurs. Tourist presence could also account for the higher rates of terrestrial vigilance observed among the foraging Ankoba sifaka compared to the spiny forest sifaka. Nevertheless, because the null hypothesis predicting significant between-group differences in terrestrial vigilance levels was rejected suggests that all groups face similar levels of potential terrestrial predation regardless of microhabitat.

The percentage of time sifaka devoted to terrestrial vigilance was further expected to differ between groups according to the spatial location occupied while foraging. Due to the elevated risk of predation faced by many primate species while terrestrial, the ground is often a locale in which prey exercise a number of anti-predator tactics, especially vigilance. Gould (2006a) noted that ring-tailed lemurs (*L. catta)* at Beza Mahafaly Special Reserve exhibited elevated levels of vigilance while terrestrial. Since ring-tailed lemurs occur sympatrically with Verreaux's sifaka and have the same predators, it was assumed the latter would also exhibit greater terrestrial vigilance when foraging on the ground. In addition, Verreaux's sifaka were expected to have high rates of terrestrial vigilance while in the low-canopy level, as sifaka were expected to face terrestrial predation while foraging within this stratum as well. However, since differences in microhabitat were thought to put some groups at a higher risk of terrestrial predation than others, the rates of vigilance each group expressed while in the four strata were anticipated to deviate.

Interestingly, although the spiny forest sifaka were the least terrestrially vigilant group overall, when vigilance was assessed in relation to spatial location, this group was significantly more vigilant than the Mandrare or Ankoba sifaka while terrestrial and in the low-canopy ranges. The spiny forest sifaka were least vigilant to terrestrial predators while in the upper-canopy. The Mandrare and the Ankoba sifaka, however, had similar rates of terrestrial vigilance while foraging on the ground or in the low- and mid-canopy, suggesting that spatial location had less of an influence on the rates of terrestrial vigilance observed among these two groups. The fact that Mandrare sifaka had significantly higher rates of terrestrially-centred vigilance while foraging in the upper-canopy than the other two groups warrants attention. Given that the Mandrare animals likely had the highest density of felids within their home-range, it could be that these sifaka had to maintain terrestrial vigilance even when foraging in upper-canopy layers. Unlike canids, which are both restricted to the ground and do not rely on an ambush attack strategy when hunting (Cresswell *et al.*, 2003; Treves, 2000; Miller and Treves, 2007), felids are not restricted to the ground and stalk non-vigilant prey (Uhde and Sommer, 2002). Therefore, terrestrial vigilance even while foraging in the upper-canopy might prove critical to survival for the Mandrare group sifaka. Since between-group differences in terrestrial vigilance did occur based on spatial location, it appears that Verreaux's sifaka are capable of adjusting their PSF behaviour according to fluctuations in microhabitat.

4.2.2 Aerially-Centred Vigilance

Karpanty and Goodman (1999) found that during the dry season months at Berenty Reserve Verreaux's sifaka, regardless of age, are preyed upon extensively by the Madagascar harrier hawk (*P. radiatus*), especially during the latter's mating period in

August (Brockman, 2003). Researchers typically consider increased rates of vigilance to be representative of predation threat in a particular locale. Nevertheless, although some avian predators such as *P. radiatus* favour an ambush attack strategy that could be deterred by increased aerial vigilance (Brockman, 2003), other raptors do not stalk their prey (Bednekoff and Lima, 1998), but rather hunt in an opportunistic fashion (Cresswell *et al.*, 2003; Miller and Treves, 2007). Therefore, increased rates of aerial vigilance might prove detrimental to the foraging success of Verreaux's sifaka while providing only minimal anti-predator benefits in return. These reasons may account for the lower overall rates of aerial vigilance observed. Furthermore, it is assumed that Verreaux's sifaka rely primarily on visual vigilance to detect aerial predators; however, little is known about the importance of using auditory and olfactory vigilance to detect predator species (Karpanty and Grella, 2001; Lima and Bednekoff, 1999; Miller and Treves, 2007). Sifaka, for instance, may detect an approaching harrier hawk acoustically rather than visually (Brockman, 2003). Thus, even though the three study groups expressed lower rates of aerially-centered vigilance while foraging relative to the frequency of terrestrially-centred vigilance bouts, more research is required before concluding that diurnal birds-of-prey pose less of a predation risk to Verreaux's sifaka at Berenty Reserve than terrestrial predators.

It was anticipated that aerial vigilance rates would differ between the three groups due to differences in microhabitat. The results obtained did not support this hypothesis. Although the spiny forest group did have the highest aerial vigilance while foraging, as expected, there were no statistically significant between-group differences. Therefore, it is likely that regardless of microhabitat, sifaka at Berenty Reserve are at an equal risk of predation by avian raptors. In addition, spatial location did not exert a strong influence on the aerially-centred vigilance behaviours of sifaka at Berenty. Only when sifaka foraged in the low-canopy level were there significant differences in the percentage of aerial vigilance recorded for each group. The spiny forest sifaka spent significantly more time vigilant to aerial predators while feeding in the low-canopy than did either the Mandrare or Ankoba sifaka. Since the spiny forest group had little overhead leaf cover to conceal them from diurnal birds-of-prey (unlike the other two study groups), it is probable that increased levels of aerial vigilance were required to successfully detect potential avian predators.

4.3 RESPONSE-BASED ANTI-PREDATION BEHAVIOURS

Whereas the preceding variables (i.e., spatial position, spatial cohesiveness and vigilance) were precautionary in nature, attention was also paid to two response-based anti-predation measures: vocal and non-vocal alarms (Fichtel, 2008). Foraging Verreaux’s sifaka employed and responded to both terrestrial and aerial alarm calls. Furthermore, in response to threatening stimuli sifaka also produced a gestural, non-vocal alarm: the ‘head-toss’. By alerting group members to potential predators, and by reacting appropriately to these cues when they are given by conspecifics, sifaka can reduce the likelihood that a successful predation attempt will occur (Miller and Treves, 2007; Fichtel, 2008). To understand the role that these alarms play in the PSF behaviours of Verreaux’s sifaka, the percentage of time used while sifaka were foraging was assessed. These results were compared to determine whether the use of response-based anti-predation behaviours varied between microhabitats.

4.3.1 Terrestrial Alarm Calls

Most non-human primates learn from infancy to associate particular vocalizations produced by both con- and heterospecifics with danger, and further, to develop appropriate reactions in response to such alarms (Fichtel, 2004; Fichtel and van Schaik, 2006; Fichtel, 2006; Fichtel, 2008). Fichtel (2008) determined that by six months of age infant Verreaux’s sifaka reacted appropriately to alarm call vocalizations. Similar to white-handed gibbons (*Hylobates lar*) (Uhde and Sommer, 2002), and tamarins (*Saguinus* spp.) (Kirchhof and Hammerschmidt, 2006), for example, Verreaux’s sifaka use referential and non-referential alarm calls in response to threatening stimuli (Fichtel, 2004; Fichtel, 2008). Among Verreaux’s sifaka, the ‘tchifak’, is used as a general alarm in response to a number of potentially threatening stimuli (Scheumann *et al.,* 2007; Fichtel and van Schaik, 2006), although a referential alarm call system also exists for certain aerial predators (Fichtel and van Schaik, 2006; Fichtel, 2006; Fichtel, 2008). For instance, a ‘tchifak’ may typically be used to indicate the presence of most terrestrial and some aerial predators (Fichtel and van Schaik, 2006; Fichtel, 2008), but it may also be produced in response to the lost calls of group members or during inter-group interactions (Fichtel and van Schaik, 2006; Fichtel, 2008). Moreover, Brockman *et al.* (2008) reported that Verreaux’s sifaka use a ‘roaring bark’, and not a 'tchifak', in response to canids. Nevertheless, in general the ‘tchifak’ alarm call refers to terrestrial predators and should prompt group members to ascend arboreally and maintain careful terrestrial vigilance (Scheumann *et al.,* 2007; Fichtel, 2007). Indeed, some predominantly terrestrial predators such as felids and snakes are capable of arboreal ascension and will preferentially attack unwary prey (Kleiman and Eisenberg, 1973; Scheumann *et al.*, 2007). However, no significant inter-group differences were found in rates of terrestrial alarm calls emitted while foraging. The minimal use of terrestrial alarm calls while foraging suggests that Verreaux's sifaka at Berenty, regardless of microhabitat, experience a low rate of terrestrial predation events.

4.3.2 Aerial Alarm Calls

Many lemurs, including the ring-tailed lemur (*L. catta*) (Gould, 1996; Gould and Sauther, 2007; Oda, 1998; Sauther, 1989) the red-fronted brown lemur (*E. f. rufus*) (Karpanty and Grella, 2001), and *Propithecus* species (Brockman *et al.*, 2008; Fichtel and van Schaik, 2006; Fichtel, 2006; Fichtel, 2008; Karpanty and Grella, 2001; Oda, 1998; Sauther, 1989; Wright, 1998) respond to the presence of some avian predators by giving alarm call vocalizations In addition to the general 'tchifak' alarm call, *P. v. verreauxi* use a 'roaring bark' vocalization as a type of referential alarm for some aerial predators (Brockman *et al.*, 2008; Fichtel and van Schaik, 2006; Fichtel, 2006; Fichtel, 2008). Verreaux's sifaka 'roar' especially in response to the harrier hawk (*P. radiatus*) (Brockman *et al.*, 2008; Fichtel and Kappeler, 2002). An aerial alarm call should incite individuals to drop lower into the canopy and maintain aerial vigilance (Brockman *et al.*, 2008; Fichtel, 2007; Karpanty and Grella, 2001; Scheumann *et al.*, 2007).

There were no significant inter-group differences regarding the percentage of aerial alarm call bouts produced while sifaka were foraging. In fact, the Ankoba and spiny forest groups had identical mean rates of alarm call vocalizations while foraging. Moreover, it is possible that in some instances the sifaka were responding vocally not to a diurnal raptor, but to aircraft passing overhead. Such low frequencies of aerial alarm calling suggest that Verreaux's sifaka at Berenty reserve, irrespective of microhabitat, have a low potential avian predator risk. This risk may fluctuate according to season, however. During their mating season in August, harrier hawks are reported to prey heavily on Verreaux's sifaka (Brockman, 2003; Karpanty and Goodman, 1999). While three active harrier hawk nests have been observed at Berenty in the past (Goodman *et al.*, 1999), continued monitoring could provide a better indication of the risk these birds-of-prey pose to sifaka at present.

4.3.3 Gestural Alarm Behaviour

Primates use non-vocal communication as a means of encoding messages related to conspecifics (Call and Tomasello, 2007a). For example, chimpanzees (*Pan troglodytes*) (Call and Tomasello, 2007a; Call and Tomasello, 2007b; Pika and Mitani, 2006), orang-utans (*Pongo* spp.) (Liebal, 2007), and Barbary macaques (*Macaca sylvanus*) (Hesler and Fischer, 2007) use physical signalling in a variety of affiliative (i.e., grooming, playing *etc*.) and agonistic social interactions (Call and Tomasello, 2007b; Liebal, 2007; Pika and Mitani, 2006). In addition, certain gestural signals and body postures may alert group members to possible predators (Call and Tomasello, 2007a; Fichtel, 2004; Miller and Treves, 2007; Treves, 2000). Among sifaka, an individual may throw its head back rapidly one or more times to indicate danger to nearby conspecifics, a gesture known as 'head-tossing' (Jolly, 1966). Group members may respond to the 'head-toss' by assuming a vigilant posture, engage in 'head-tossing' behaviour themselves, or by emitting a vocal alarm call (pers. obs.). Head-tossing is a non-referential visual cue that is advantageous because it allows individuals to maintain a degree of acoustical crypsis while still alerting others to potential dangers (Fichtel, 2004; Richard, 2003).

As predicted, the Mandrare group was most likely to engage in head-tossing while foraging, unlike the spiny forest group, which was least likely to head-toss while foraging. By comparison, while foraging the Ankoba group had intermediate rates of head-tossing behaviour. Nevertheless, these differences were not statistically significant. First, the lack of statistically significant between-group differences in head-tossing behaviour suggests that regardless of home-range, sifaka at this reserve experience a similar low level of potential predation pressure. Second, the low frequency of head-tossing used across the study groups indicates that sifaka may favour other forms of communication (i.e., vocal alarm calls) when alerting group members to possible predatory threats.

CHAPTER FIVE: CONCLUSION

5.0 SUMMARY

Microhabitat did not appear to influence the majority of the predator-sensitive foraging behaviours observed among Verreaux's sifaka (*Propithecus verreauxi verreauxi)* at Berenty Reserve. While there were statistically significant inter-group differences regarding the spatial location, the production of alarm call vocalizations, most vigilance behaviour, the distance sifaka were most likely to maintain from their nearest neighbour (NN), and the use of head-tossing while foraging was undetermined by fluctuations in microhabitat. Table 5.1 summarizes the influence that microhabitat had on the five predator-sensitive foraging (PSF) variables.

Table 5.1 – The influence of microhabitat on the PSF behaviour of Verreaux's sifaka

Influenced by Microhabitat	***Not Influenced by Microhabitat***
✓ Spatial location	✗ Alarm call vocalizations ✗ Vigilance rates ✗ Spatial cohesion ✗ Gestural Communication

5.1 DIRECTIONS FOR FUTURE RESEARCH

First, future studies conducted on Verreaux's sifaka (*Propithecus verreauxi verreauxi*) would benefit from inter-group nutritional analyses of the food resources consumed. Sampling plant parts ingested by sifaka collected from various spatial locations (i.e., ground, low-canopy) would provide insight into the nutritional costs or benefits that feeding in a particular niche entails. A marked avoidance by the Ankoba and Mandrare groups of terrestrial foraging, for instance, suggests three possibilities: 1) that the predation risk associated with this level is too costly to be considered worthwhile, 2) that the food resources found terrestrially in these groups is of too poor quality to be deemed energetically profitable, or 3) both, which could be determined by further analysis. Additionally, nutritional analyses could confirm whether the spiny forest group fed in the low-canopy to evade predation, and whether doing so is costly in terms of nutritional quality. Moreover, nutritional analyses could confirm whether the Ankoba and Mandrare groups fed most often in the upper-canopy because the dietary advantage gained outweighed the risk of predation by diurnal raptors.

Second, future PSF studies could examine the role of seasonality and the foraging behaviour of free-ranging Verreaux's sifaka. In times of resource scarcity, to what extent does social dominance determine spatial positioning while foraging (Janson, 1990)? Do subordinate sifaka occupy more hazardous positions (i.e., terminal branches vs. the mid-canopy) than dominant conspecifics while foraging, and does this fluctuate according to season? Further, future research could determine whether sifaka spatial cohesion varies seasonally (Irwin, 2007), and what consequences this has on an individual's vulnerability to predation. Finally, future studies could examine the use of alarm call vocalizations, gestural communication, and vigilance rates between the wet and the dry seasons.

Third, future research could examine the influence of sex on Verreaux's sifaka PSF behaviour at Berenty Reserve. Gould (1996), for instance, examined the vigilance behaviour of male and female ring-tailed lemurs (*Lemur catta*). Additionally, Lewis (2005) examined inter-sexual differences in vigilance among Verreaux's sifaka (*P. v. verreauxi*) in Kirindy forest, although there have been no such studies at Berenty Reserve. While research has been conducted on intra-sexual differences in the PSF behaviour of other free-living primates, such as Thomas langurs (*Presbytis thomasi*) (Sterck, 2002), research is needed on the PSF behaviour of reproductive and non-reproductive female Verreaux's sifaka.

Future studies could also compare Verreaux's sifaka from two or more research sites from Madagascar to see if there are any significant intra-specific differences in terms of PSF behaviour. Moreover, the PSF foraging behaviour of Verreaux's sifaka could be compared with that of other congeneric species such as the diademed sifaka (*Propithecus diadema* sp.) or Tattersall's sifaka (*Propithecus tattersalli*), or with that of other Indriidae (i.e., *Indri indri* or *Avahi* sp.). Finally, the PSF behaviour of Verreaux's sifaka could be compared with that of sympatric species, such as the ring-tailed lemur (*L. catta*), for example.

5.2 CONCLUSIONS

1. The spatial position Verreaux's sifaka use while foraging is determined by the features of a group's microhabitat. There were significant between-group differences in terms of the spatial position exploited while foraging.

2. The spatial cohesion maintained between foraging Verreaux's sifaka appears largely unaffected by microhabitat. Focal animals from all groups were most likely to feed alone, or between 1.0-1.9 m from their NN when one was present. However, microhabitat may have influenced the distances that sifaka from each group were least likely to maintain.

3. Microhabitat appeared to exert minimal influence on spatial cohesiveness when sifaka foraged in the four spatial niches (i.e., ground, low-canopy, *etc*.). There were no statistically significant inter-group differences when sifaka foraged in the low-, mid- and high-canopy. Spatial cohesion was only statistically significant when the amount of time sifaka foraged terrestrially was assessed. The spiny forest sifaka were the most spatially cohesive group while foraging terrestrially.

4. Overall, vigilance rates per group did not appear to be determined by microhabitat. There were no statistically significant inter-group differences in the amount of time sifaka were terrestrially or aerially vigilant while foraging.

5. Microhabitat may have influenced the amount of time sifaka were terrestrially vigilant while foraging in the four spatial strata. There were significant between-group differences in terrestrial vigilance when sifaka foraged terrestrially and in the low- and high-canopy.

6. Aerial vigilance appeared to be less influenced by microhabitat at Berenty than terrestrial vigilance. When the rates at which sifaka were aerially vigilant in each spatial location were assessed, it was revealed that there were only significant between-group differences in aerial vigilance when sifaka foraged in the low-canopy.

7. Microhabitat did not appear to influence the rate of terrestrial or aerial alarm call vocalizations sifaka produced while foraging.

8. The frequency that foraging sifaka use head-tossing behaviours is likely not influenced by microhabitat. There were no significant between-group differences regarding the use of this gestural alarm.

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APPENDIX A:

ETHOGRAM DEFINITION OF VERREAUX'S SIFAKA ACTIVITIES

ACTIVITY	DEFINITION
FEED (FE)	Ingestion and mastication of edible food resources.
FORAGE (FOR)	Procurement of edible food resources. Does not imply ingestion or mastication.
GROOM (ALGR, AUGR)	Behaviour whereby one individual inspects its own coat (auto-grooming) or that of another (allo-grooming) for ectoparasites (Gould, pers. comm., 2007).
HEAD-TOSS (HT)	Throwing the head back rapidly one or more times (Jolly, 1966).
LOCOMOTE (LOC)	Physical movement including vertical clinging and leaping.
PLAY: (ALPL, AUPL)	Non-agonistic activities such as jumping, swinging, wrestling, tumbling, and play-fighting may be accompanied by the 'play face'. Play may be solitary (auto-play) or with other individuals (allo-play) (Garber, pers. comm., 2006; Gould, pers. comm., 2007).
REST (RE)	Any period of inactivity including sleep.
VIGILANCE (VIGU, VIGT, VIGA)	'[I]ntently staring beyond the immediate vegetation with a stationary, alert posture' (Gould *et al.*, 1997, p. 405; Gould, 1996).
VOCALIZE (VOCT, VOCR)	Any communication via the vocal channel, including the 'tchi-fak' (VOCT), roaring bark (VOCR), grunts and growls (Fichtel *et al.*, 2006).