

UNIVERSITY OF CALGARY

Adult Male Orangutan Ranging Behaviours

In Gunung Palung National Park, West Kalimantan, Indonesia.

by

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Abstract

To investigate the ranging behaviour of adult male orangutans, three males were observed for a combined total of 68 full days between February and August 1998, in the Cabang Panti study site. The amount of fruit in the diet, the presence of bark in the diet, the amount of rainfall, and the presence of other orangutans were tested to investigate their effect on ranging behaviour. When fruit was prevalent in the male's diet or other orangutans were present, they tended to move slower, and for shorter distances. Long call frequency, intensity and duration were also tested for two of these adult males to investigate any association with their ranging behaviour. For one male, the emission of a long call was associated with shorter travel bouts and longer day lengths.

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Chapter One: Introduction

There are many factors that influence primate ranging behaviour. The distribution and abundance of prime food items are of primary importance (Clutton-Brock, 1977; Raemakers, 1980; Isbell, 1983; Bennett, 1986; Oates, 1987; Yamagiwa and Mwanza, 1994). The variations in habitat and food extraction techniques are both associated with patterns of animal movements (McKey and Waterman, 1982). Social factors such as group size (Waser, 1977), inter-group interactions (Struhsaker, 1974; 1975; Rasmussen, 1979; Isbell, 1983; Bennett, 1986; Yamagiwa and Mwanza, 1994), and the number of impregnable females available to males (Rasmussen, 1979), also influence primate ranging behaviours. Climatic factors such as weather patterns have also been noted to affect primate movements (Chivers, 1969; Clutton-Brock, 1977; Raemakers, 1980; Curtin, 1982; Isbell, 1983; Bennett, 1986).

Food availability and access to food resources are considered the most consistent influences on ranging behaviours in primates (Chivers, 1969). The distribution of food resources will affect the distribution of females in the environment, which in turn will determine the distribution of males (Wrangham, 1979; van Hooft and van Schaik, 1994).

Males and females in species, which exploit clumped food resources, tend to range independently. In these species, males are often found to range further than females (Galdikas, 1979; Newton, 1992). This pattern is most common in species where food availability is unreliable, it requires females to range independently of the males in order to acquire adequate food. When the females are dispersed to best access food, the males have to compete for access to these

females, and this leads to sexual dimorphism. When males are larger than females, they require larger amounts of food in absolute terms, which further increases the distance that males have to travel to access food resources. Males may also have to range further in their attempt to interact with receptive females.

The orangutans (*Pongo pygmaeus*) is one of the species that exploits clumped food resources, and in which males and females range independently (Galdikas, 1985a). Adult males are unable to monopolize either prime food sources or females; their ranging behaviours probably reflect the optimum way to access these limited resources.

Despite the fact that orangutans have been studied in the wild for over 30 years, little is known about adult male orangutans' ranging behaviours and the factors that influence them. This is likely due to the fact that males are difficult to follow and have much larger ranges than females, which results in few precise measurements (Galdikas, 1979).

Research Objectives

Male orangutans travel farther than females (Galdikas, 1985b; 1988) and, at least some males do not seem to re-use an area very often. These two factors make male home ranges notoriously difficult to measure. This project looks at possible ecological, social, and climatic influences on adult male orangutan ranging behaviours.

More specifically, adult male orangutan ranging behaviours are investigated around the Cabang Panti research site in Gunung Palung National Park, West Kalimantan, Indonesia, and the factors that potentially influence male movements. Six measures of male movements were used, including the male's daily range, the distance between consecutive nests, the speed of travel, the pattern of travel, the directness of travel, and the day length. These measures are defined in the Methods chapter. How these measures of male ranging behaviour were influenced by ecological (the amount of fruit in the diet and the presence of bark in the diet), social (the presence of other orangutans), and climatic (rainfall patterns) factors was then tested.

Also under consideration is the association between long calling behaviour and ranging behaviour of adult male orangutans. Long calling is a spacing mechanism between adult males and may be used to announce the presence of a dominant male in an area. In particular, the frequency, duration and intensity of long calls were compared for two study subjects. A home range was estimated for two of the focal animals for the duration of their observation.

One of the original objectives of this study involved the construction of temporary satellite camps at the edges of the study site to accommodate searching and following male orangutans outside the study site trail-system. I had hoped to study the ranging behaviours of adult male orangutans that rarely come to the study area and to try to assess if some males did show a "nomadic" pattern of ranging behaviour (transient males), as opposed to males who show a tendency to re-use the same area (resident males) (Rodman, 1984; Galdikas, 1985b). I requested permission to build satellite camps, but this permission was denied because of a difficult security situation. Indeed, illegal loggers were taking guns into the forest and even the edges of the study site were considered

dangerous. I thus focussed my data collection on the males that ranged within the study area.

The primary goal of this research is to contribute to the understanding of adult male orangutan ranging behaviour. This information will help researchers gain a better understanding of orangutan habitat-use and social organisation. It is also useful for the assessment of population density and of carrying capacity in the rapidly declining sections of natural habitat left for wild orangutans.

Chapter Two: Investigating Adult Male Orangutan Ranging Behaviours

In this chapter, I describe the factors that contribute to the solitary social organisation of orangutans, and how these factors may also influence their ranging behaviours. I discuss ecological (access to food), social (access to mates), and climatic (rainfall patterns) factors that influence ranging behaviours across various taxa and that may also be applied to orangutans. I describe how orangutan diet and habitat influence their sociality and movements. I also briefly discuss, in relation to orangutans, two other factors that have been seen to influence the grouping patterns of other diurnal primates: predation and infanticide. I describe the social structure and ranging behaviours of adult orangutans and the factors that make estrus females a limiting resource for males. Finally, I look at the adult male orangutan long call as a potential factor influencing ranging behaviours.

Ecological, Social, and Climatic Factors that Influence Animal Ranging Behaviours

Ranging decisions are made to increase an individual's daily survival and, ultimately, their reproductive success (Rasmussen, 1979). It is thus necessary to understand the resources that limit the reproductive success of individuals to understand what resources influence their movements. The distribution of females in a given environment is a response to the distribution of risks and food resources in that specific environment, while the distribution of males is a

response to the spatio-temporal distribution of mating opportunities and food resources (van Schaik and van Hooff, 1996). Male reproductive success is limited by access to estrus females (Trivers, 1972). Male-male competition for access to females may be direct, in the form of aggressive fighting, or indirect, where a male has to maintain proximity to a female and exclude rival males (Smuts, 1987). This competition imposes time and energy expenditures on adult males, who have to search for females, defend their mate from rival males, and secure female cooperation in the sexual association (Smuts, 1987). Therefore, on a daily basis, males need reliable access to food resources to be able to compete with other males for access to females.

Access to Food

The distribution and abundance of food resources play an important role in the pattern of habitat use in animals. Animals that are omnivorous can exploit a broader range of food resources, whereas frugivorous animals may face more challenges in acquiring adequate food resources in some environments. Folivorous primates typically travel shorter daily distances to feed than do frugivorous primates. Frugivorous animals may have to travel long distances between highly dispersed food sources, and this consumes time and energy (Strier, 1987). Nevertheless, even folivorous animals may exploit prime foods that are sometimes dispersed in a clumped fashion (Koenig *et al.*, 1998). Therefore, food distribution and abundance may also affect their ranging behaviours.

In times of fruit scarcity, frugivorous animals use two strategies to obtain adequate food. They may increase their daily range distance to search further for fruit sources, which increases the energetic costs associated with obtaining food (Curtin, 1982; Rogers, 1987; Lovari *et al.*, 1994), or they may decrease their daily range and broaden their diet to include foods that are easier to find, such as bark and leaves (Clutton-Brock, 1977; Raemaekers, 1980; Curtin, 1982; Bennett, 1986). This minimizes the energy spent searching for food, and has been seen in gibbons (*Hylobates lar*: Raemakers, 1980), banded langurs (*Presbytis melalophos*: Bennett, 1986), and red colobus (*Colobus badius tephrosceles*: Struhsaker, 1981; Isbell, 1983). Because the quality of the food they ingest decreases, frugivorous animals often have to eat larger quantities to meet their nutritional needs (Clutton-Brock, 1977).

Folivorous, and omnivorous animals such as red deer (*Cervus elaphus*: Emlen, 1973), banded langurs (*Presbytis melalophos*: Curtin, 1982) and foxes (*Vulpes vulpes*: Lovari *et al.*, 1994) who exploit clumped resources, also increase their daily ranging when food availability is reduced. Foxes exploit clumped resources such as juniper berries and carrion. When these resources are available, they tend to use them until the source is finished, which reduces the number of feeding sites they use per day, and thus, reduces their daily range (Lovari *et al.*, 1994).

When the absolute size of an animal is large, this can further influence travel, as the absolute quantity of food needed is also large. Home range and day range size also increase with group size. Indeed, in most species, the time required to travel during foraging increases with the size of the group (van Schaik, 1989). When food is found in discrete clumps, larger groups will deplete the individual food patches more quickly, which will require them to travel further than small

groups to obtain the same amount of food per individual (Isbell, 1991). So, when food is limited, one strategy is to decrease the size of groups, the minimal size being of course single animals.

Access to Mates

Male competition for access to mates accounts for sexual dimorphism in many species (van Schaik and van Hooff, 1996). The frequency and intensity of male-male competition depends on the species' social organisation. Specifically, the number of males and females in a group and the availability of estrus females will influence the expression of male-male competition (Smuts, 1987). In groups with more than one adult male, dominance hierarchies are usually found, which influence males' access to females. In many cases, an increased rank leads to increased access to females (Harcourt, 1989). In species in which at least some males do not have a permanent association with females, these extra-group males may alter their daily range to get access to potential mates (Smuts, 1987). Indeed, solitary male mountain gorillas (*Gorilla gorilla beringei*) who follow groups to try and attract mates, increase their daily range compared to days when they are not in the vicinity of other groups. This shows that social factors can influence the ranging decisions of a solitary individual (Watts, 1991). In species in which females range solitarily, the distribution of mates and the distribution of other competitors that try to access the same mates are major determinants of habitat use in males (Rasmussen, 1979).

Large-bodied animals usually have long inter-birth intervals (Dunbar, 1987). If mates are rare due to long inter-birth intervals and because food can only

support one large frugivorous animal in an area, it would not make sense for a male to monitor a female too closely (Horr, 1975). Rather, a male should spend most of his time concentrating on finding adequate food resources and only occasionally monitor the females by moving through their ranges.

In orangutans, when a male is in consort with an estrus female, he puts a lot of his energy into guarding that female from rival males and can frequently neglect to feed (Galdikas, 1979; 1985a; 1985b). Males also increase the length of time they are out of their nests (day length) while in consort with a female (Galdikas, 1988; 1995). Therefore, males need to be able to reserve energy for times of consort.

Given these constraints, I would expect solitary male orangutans to spend most of their energy moving in ways to best acquire food resources. However, if a female is present in the course of a male's daily ranging, I would expect a male orangutan to alter his movements to inspect or temporarily guard the female. He may monitor the female more closely if another male was also present, so that he could potentially be the first male she considers mating with if she is receptive. This could dramatically change his daily movements, either by decreasing them to stay near the female, or by increasing them to chase away rival males.

Rainfall Patterns

Heavy or prolonged rainfall decreases or temporarily halts animal movements (Chivers, 1969; MacKinnon, 1971; Goodall, 1977; Isbell, 1983; Vedder, 1984). While some studies have found no significant correlation between rainfall

patterns and daily ranging behaviours (*Colobus badius tephrosceles*: Isbell, 1983; *Gorilla gorilla beringei*: Watts, 1991), some have found a marked reduction in travel on cloudy or wet days and a suppression of activity during the rain (*Alouatta palliata*: Chivers, 1969; *Gorilla gorilla beringei*: Goodall, 1977).

Isbell (1983) suggests that the lack of correlation between rainfall and daily ranging may be explained by the fact that authors generally use pooled rainfall data for a 24-hour period. This type of data does not allow the researcher to see if there is a close correspondence between bouts of rainfall and bouts of movement. Rainfall patterns may also indirectly influence ranging decisions, as rainfall can affect fruiting patterns in tropical forest (Bennett, 1986; Oates, 1987).

Orangutans in their Environment

There seems to be enormous individual variation in the ranging behaviour of adult male orangutans. Some males do not range very far, while others seem to cover vast distances (Galdikas, 1988). In the following section, I review how orangutans are distributed in their environment, and the factors that influence male orangutan ranging behaviours.

Diet and Use of Habitat:

Influence of Distribution of Food on Social Organisation

The distribution of orangutans in their habitat is influenced by their diet, their foraging and processing techniques, as well as by the availability and

distribution of food in the environment. It is important to investigate these variables to understand orangutan ranging behaviours and, ultimately, orangutan social organization.

Orangutans are highly frugivorous, and supplement their diet with young leaves, small vines, flowers, bark, fungus, ants, termites and honey (Harrison, 1960; MacKinnon, 1974; Rijksen, 1978; Galdikas, 1978; 1988; Leighton, 1993). They are opportunistic foragers, in that they use seasonal abundance of food resources (MacKinnon, 1971; 1974). Orangutans are the largest arboreal mammals and due to their size, they require large absolute amounts of food. Despite their extreme sexual dimorphism, male and female orangutans spend the same amount of time foraging, but they utilize different proportions of resources in their diet (Galdikas, 1988). Sexual dimorphism may indeed lead to different nutritional requirements and different abilities to process certain foods (Selander, 1972; Rodman and Mitani, 1987). For example, gut size is associated with the degree of digestibility of the food eaten (Aiello and Wheeler, 1995). Male orangutans have larger guts than females, which probably allows them to digest larger amounts of one type of food and also more fibrous material. Smaller gut size in females is more effective for a diverse diet of easily digestible foods such as ripe fruit (Selander, 1972; Rodman and Mitani, 1987; Aiello and Wheeler, 1995).

In terms of foraging technique, orangutans can consume most of the fruits in a particular tree at a single sitting (Horr, 1975; Galdikas, 1978). Furthermore, most of the common fruit-bearing trees that orangutans exploit have a small diameter at breast height, which is associated with a small crop of fruit (Leighton, 1993; Knott, 1998). These combinations of a large body size, small crop size of the trees

they exploit and exhaustive foraging techniques presumably force orangutans to forage in small groups or alone.

Male orangutans face inter-specific and intra-specific competition for fruit. Indeed, there are many other arboreal frugivores that share orangutan habitat, and therefore can be considered food competitors for orangutans. However, these competitors, such as birds, squirrels and monkeys are able to exploit fruit from all parts of a tree, including the thin branches that would not support male orangutans. Female orangutans are also much smaller than male orangutans, and may access fruits on much thinner branches. These inter and intra-specific competitors thus contribute to depleting fruit resources.

Today, wild orangutans are limited to pockets of primary tropical rain forests in Sumatra (*P. p. abelli*) and Borneo (*P. p. pygmaeus*), in Indonesia (Rodman, 1988). In these habitats, precipitation varies seasonally, while temperature is relatively constant year round (29-31°C: Sugardjito *et al.*, 1987). This lack of large-scale temperature variation produces unsynchronized fruiting patterns in the forests (Horr, 1977). As a result, fruit is irregularly distributed in space and time in the forest (te Boekhorst *et al.*, 1990). Presumably, these factors make effective fruit exploitation a complex strategy.

When fruit is abundant, orangutans do not travel far between feeding sites (Knott, 1998), this has been associated with small daily ranges in other apes (Wrangham *et al.*, 1996). Conversely, in times of fruit scarcity, orangutans have to travel more between feeding sites, which results in larger daily ranges for these periods and presumably is also associated with nutritional stress. Indeed, ketones in the urine of wild orangutans, which indicate that stored fat is being used, vary in concentration between periods of high and low fruit availability

(Knott, 1998). Orangutans may have evolved the ability to take advantage of periods of high fruit availability by storing excess energy as fat (Knott, 1998). This might be an essential adaptation for orangutans, enabling them to mobilize stored energy to survive periods of severe fruit shortage or allowing them to devote all their time to following and defending a mate when a female becomes available.

The various habitats in which orangutans are found differ in their phenological characteristics. One characteristic, which seems to influence orangutan ranging behaviour is the presence or absence of fig trees (Genus *Ficus*). Figs are non-seasonal, so they are available throughout the year (Rodman, 1988; Laman, 1997). Fig trees have a large fruit crops in relation to the other fruiting trees typically harvested by orangutans (Leighton, 1993). As a result, they are a valuable resource for orangutans to exploit during times of scarcity of other fruits (Laman, 1997). Some of the habitats characterized by the presence of figs also go through periods, called a “mast fruiting”, during which fruit availability increases dramatically. These happen every 4 to 7 years, when an unusually high number of trees fruit at the same time (Laman, 1997). This results in a period of fruit abundance, which results in certain areas of forest being able to support much larger concentrations of individuals than usual.

The presence of figs, whether during a mast fruiting period or not, leads to a reduction in feeding competition in orangutans (van Schaik, 1996), and consequently, a reduction in the distance traveled between feeding sites. Due to the patchy nature of the distribution of these fruiting trees, and their unusually large concentration of fruit, orangutans will tend to aggregate at these trees simply because many individuals can simultaneously use the same resources (Wrangham *et al.*, 1996). This is even more apparent during a mast fruiting,

when individuals are more gregarious. Even adult males may be seen foraging together, which is otherwise unlikely (Knott, pers. comm.).

The Influence of Predation and Male Infanticide on Social Organisation

Besides the distribution of food resources, the threats of predation and of male infanticide are often considered important pressures that influence gregariousness in animals (van Schaik, 1989; Sterk *et al.*, 1997). If a particular grouping pattern results in or is associated with the presence of these pressures on individual members of a species, then one might expect that an absence of gregariousness could be linked to an absence of these threats. Thus, because orangutans are solitary, it can be asked whether they do face an absence of threat from predators, or from infanticidal males.

Orangutan predators include tigers in Sumatra (van Schaik and van Hooff, 1996), clouded leopards in Borneo (Sugardjito, 1983), and wild forest pigs in both Sumatra and Borneo (Galdikas, 1978). Evolutionarily speaking, orangutans may have responded to the threats of predators by remaining highly arboreal and by outgrowing the size of their potential predators (Horr, 1975). Female orangutans are rarely observed on the forest floor, which may be a means by which they avoid terrestrial predators. Female orangutans' size and ability to move out onto and build nests on small branches could also provide adequate protection from arboreal leopards (Horr, 1977). The combination of size and habitat use, and the female's ability to defend herself and her offspring against predators, seems to render unnecessary the continued presence of an adult male or other adult females for protection (Horr, 1975).

The threat from potentially infanticidal conspecific males may explain female sociality in some species (Wrangham, 1979; Dunbar, 1988; Brereton, 1995). Female orangutans have long inter-birth intervals. As a result, males must typically wait long periods for females to come back into estrus. In theory, a male orangutan could easily overpower a female and kill her dependent offspring in an attempt to bring her back into estrus. He could shorten her inter-birth interval and, assuming that he successfully mates with her, he could increase his reproductive success. However, infanticide has never been reported in orangutans in the many sites where fieldwork has been done over the past 30 years. Infanticide thus apparently does not occur in orangutans. Two reasons could potentially explain why infanticide does not seem to occur. First, females may have evolved successful counter-strategies. For example, females could move away from the male if they hear them approaching, or move into the upper canopy where the branches will not support the larger males. Secondly, males may not gain reproductively by killing infants. Mating tends to be promiscuous (van Schaik and van Hooff, 1996), and males do not associate closely with females during pregnancy. Males also do not associate with their offspring during infancy, probably resulting in a low certainty of offspring paternity and low differential familiarity towards specific infants. Species with promiscuous mating patterns typically have low occurrences of infanticide (for example: multi-male multi-female groups of macaques and baboons; Struhsaker and Leland, 1997).

Infanticide has been associated with the concept of sexual coercion (Smuts, 1993). Sexual coercion is defined as those cases where a male uses force or the threat of force to increase the chances that a female will mate with him. Female orangutans do indeed experience sexual coercion in the form of forced copulation, primarily by subadult males (MacKinnon, 1971; Rodman, 1973;

Rijksen, 1978; Galdikas, 1985c; Mitani, 1985a) but also by adult males (Mitani, 1985a). Again, however, as in the case of infanticide, these forced copulations may not be a sufficient enough threat for females to force them into groups and to increase the level of food competition.

The absence of infanticide and low predation pressure may have contributed to the lack of sociality in orangutans. It remains, however, that the availability of food in their habitat seems to be of primary importance in the orangutan solitary social system.

Social Structure and Sociality

Orangutan social structure has been described as “dispersed polygyny”. Females are solitary and use a home range that sometimes overlaps with other females. Males are also solitary, but they have a larger home range that incorporates multiple female ranges (Rijksen, 1975; Galdikas, 1981; 1985a; 1988; Mitani, 1985). When males do interact socially, they spend most of that time in consortship with an adult female (Galdikas, 1985a). Males are in association with females only infrequently, however, which presumably allows them to maintain reproductive information on multiple females without compromising their nutritional intake (Mitani, 1985a).

The Availability of Females for Reproduction

Inter-birth interval in orangutans has been estimated between 3.5 to 8 years (Horr, 1975; 1977; Galdikas and Wood, 1990). These long inter-birth intervals result in male-biased operational sex ratios (Mitani, 1985a; Dunbar, 1988). But the inter-birth interval is not an accurate measure of the availability of females as mates because these calculations of inter-birth interval were done using only infants that reach weaning age. So if one were to include all births to estimate the frequency at which females become fertile, the value would probably be closer to 3.5 years. In any case, cycling adult females are rare spatially and temporally in the forest. This, combined with the female's lack of sexual interest in males between births (Wrangham, 1996), leads to a high degree of male-male competition for the small number of receptive females (Trivers, 1972; Mitani, 1985b), and may contribute to the dispersion of males (Horr, 1975).

Adult males are intolerant of each other (Galdikas, 1985b; Mitani, 1985b). All male-male interactions end in avoidance or aggression (Galdikas, 1985b): avoidance usually occurs in the absence of females, while aggression is seen more frequently when an adult female is present. This supports the hypothesis that sexual dimorphism in orangutans evolved as a result of intense male reproductive competition (Rodman and Mitani, 1987).

Male orangutans are not able to monopolize or coerce females to follow them (Mitani, 1985a). Therefore, if a male wants to access a female when in estrus, males have to guard and follow them, resulting in close temporary associations called "consortships" (Galdikas, 1985a; b). Female orangutans show no external signs of estrus (Galdikas, 1988; van Schaik and van Hooff, 1996), so the onset of

estrus must be assumed from the female's displays of proceptive behaviours ranging from approaching a male to assisting intromission (Nadler, 1977; Galdikas, 1981).

For a male orangutan to follow an estrus female over the several days of consortship is energetically expensive (Galdikas, 1985a; 1995). During these days of close association, the two orangutans share food resources, resulting in more rapid depletion of the food source. Males have been seen to almost stop eating during consortship (Galdikas, 1985b; 1995). Fully adult males require a high level of metabolic energy to maintain their size and strength (Maggioncalda, 1995). A male's neglect of food so as to follow females places a time limit on the duration of consorts (Rodman, 1979). Males who are in association with females would have to move more and therefore eat more (Rodman, 1979). Due to these large costs, males are probably highly selective about when and with whom they consort (Galdikas, 1985a). They seem more likely to engage in consortship with adult females without dependent offspring (Galdikas, 1985b).

Paternal investment in offspring is literally non-existent in orangutans because there are no permanent associations between orangutan males and females (Horr, 1977). This lack of paternal investment has, perhaps, an influence on the fact that males are not confined to an area, and have flexible home ranges (Horr, 1977). It has been suggested that if males do not locate cycling females within their normal range, they will extend their range to incorporate another female (Horr and Ester, 1976).

Orangutan Ranging Behaviours

Adult male and female orangutans have different ranging patterns. Female orangutans tend to have stable ranges (Galdikas, 1988), with size estimates from 0.7km² (Horr, 1972; Rodman, 1973) and 2.5km² (MacKinnon, 1974) to 5-6km² (Galdikas, 1988). This variation may reflect different sampling techniques, or may reflect different fruit availability due to different habitat types.

Male home ranges are larger and apparently more variable than those of the females (Rodman, 1973; Rijksen, 1975; Horr and Ester, 1976; Galdikas, 1988). As a result, a male's home range size is difficult to estimate (Horr, 1975; Horr and Ester, 1976; Mitani, 1985a; Rodman and Mitani, 1987). Precise data are difficult to obtain mainly because home ranges are frequently larger than a study area (Galdikas, 1985b; van Schaik and van Hooft, 1996). However, the consensus is that male orangutans seem to use two different ranging strategies: resident and transient (Rodman, 1973; 1979; 1988; Rijksen, 1975; Horr and Ester, 1976; Galdikas, 1981; 1985a; 1988; Mitani, 1985a; te Boekhorst *et al.*, 1990; van Schaik and van Hooft, 1996). A "resident" male's strategy is to maintain a stable home range encompassing multiple female home ranges (Galdikas, 1985b; Rodman and Mitani, 1987). Resident male home ranges have been estimated to be 5-6km² (Galdikas, 1979; 1981). Conversely, a "transient" male's strategy is to wander through the forest, not establishing a claim on any particular area for an extended amount of time. The size of a transient's home range cannot even be estimated due to the lack of field research and the lack of published data (Horr, 1972; Mitani, 1985; Rodman and Mitani, 1987).

Researchers believe that there are two significant factors influencing adult male orangutan ranging behaviours. The first is access to adequate amounts of appropriate food to satisfy energetic needs (Galdikas, 1979; 1988; te Boekhorst *et al.*, 1990; Kaplan and Rogers, 1994) without having to travel too far (Dunbar, 1988). The second is access to adult females for reproduction (Horr, 1975; 1977; Mitani, 1985a; Rodman, 1988). It is possible that a combination of both access to food and to females influences the ranging behaviours of adult male orangutans.

Male Orangutan Long Calls

When they are fully developed, male orangutans emit calls that can be heard from long distances. Only fully adult males, possessing cheek pads and a throat pouch, have the capability to long call (Rodman, 1973). Long calls are considered to have a spacing function between rival adult males (MacKinnon, 1971; Galdikas, 1981; 1983; Mitani, 1985b). High-ranking males long call more frequently and more spontaneously than subordinate males (Galdikas, 1978; Mitani, 1985b). By long calling, a male presumably informs other males in the area of his identity, and that he is actively defending the core area of his home range (Galdikas, 1981; 1983; Mitani, 1985b). It has been hypothesized that male orangutan long calls act as an announcement for males moving into an area (van't Land, 1990; van Schaik and van Hooff, 1996), and may help maintain exclusive access to the females in their home range. Long calls have also been observed to occur both spontaneously and in response to a stimulus, for example, falling trees (Rodman, 1988).

Playback experiments with male orangutan long calls have been done using male and female orangutans as recipients (Mitani, 1985b). The main results are that highest-ranking males approached the calls, presumably to contact or display to the other male, and subordinate males avoid the calls by moving away.

Interestingly, sexually active females do not move towards the calls, which led the author to conclude that long call behaviour do not attract females, but do act as a spacing mechanism between males, and as an announcement for their location.

Chapter Three: Methods

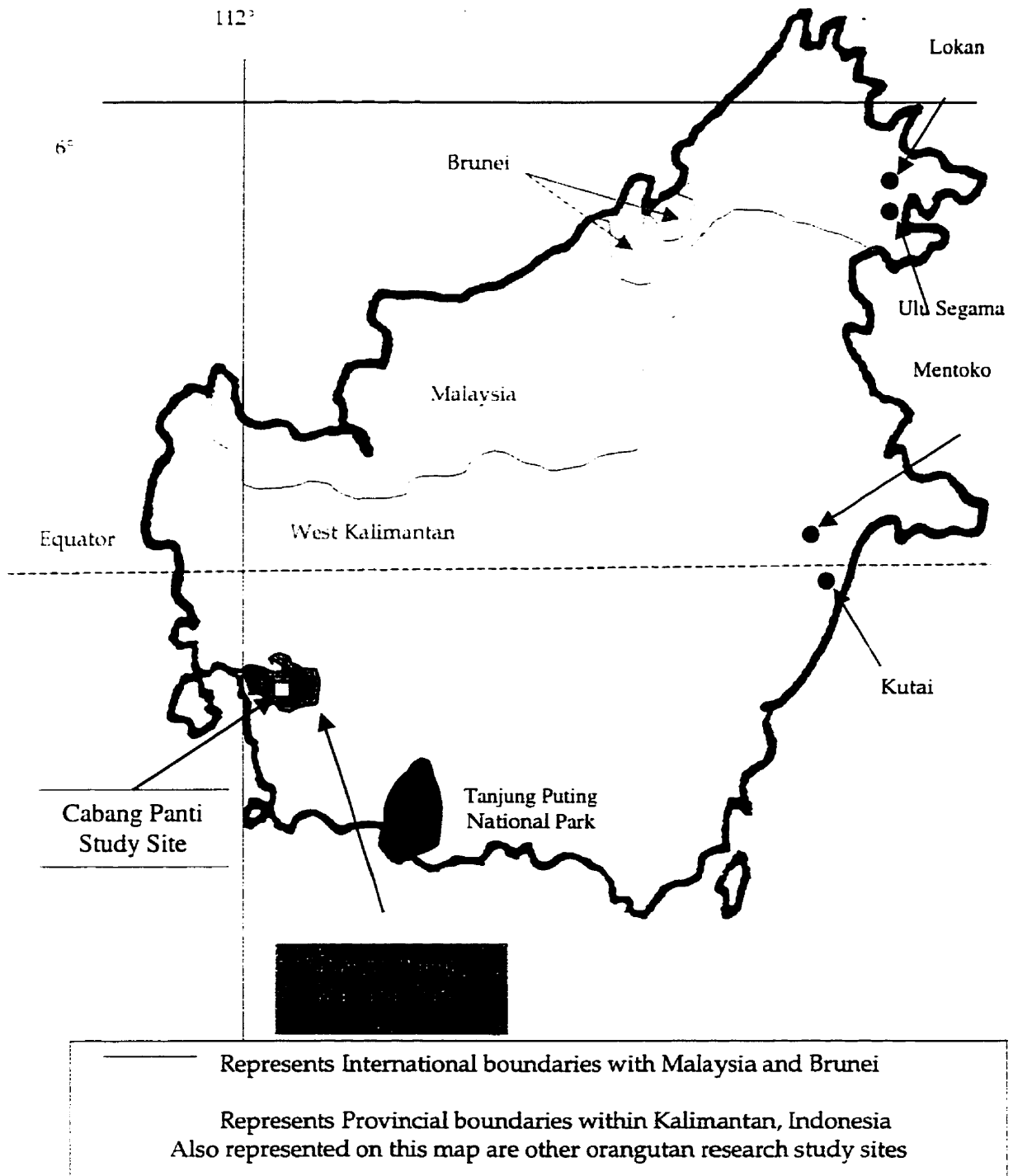
Study Site

The data analysed was collected between March and August 1998 around the Cabang Panti research station in Gunung Palung National Park, West Kalimantan, Indonesia (Figure 1). Dr. Mark Leighton of Harvard University established this research site in 1986 when his research focused on tropical rainforest ecology. Since 1994, Harvard Primatologist, Cheryl Knott, has been doing research on female orangutan reproductive ecology at this site. The research station is located in primary tropical rainforest and has seven distinct habitats, peat swamp, freshwater swamp, alluvial bench, lowland sandstone, lowland granite, sub-montane, and montane. For this study, orangutans were observed in all habitats except sub-montane or montane. The core study area covers 15km² inside the 900km² National Park. The density of orangutans in Gunung Palung is one of the highest in Borneo, estimated at 4 individuals per km² (Leighton and Darnaedi, 1996). In comparison, orangutans at other sites report a range of 1-3 individuals per km² on Borneo (MacKinnon *et al.*, 1996), and 1-5 individuals per km² on Sumatra (MacKinnon, 1973; Kaplan and Rogers, 1994).

Study Subjects

The orangutan (*Pongo pygmaeus*) is the only Asian great ape. There are two subspecies that are geographically isolated on the islands of Sumatra (*P. p. abelli*) and

Figure 1: Location of the Cabang Panti Study Site in Gunung Palung National Park, West Kalimantan, Indonesia.



Borneo (*P.p. pygmaeus*), Indonesia. The study population at Cabang Panti consists of approximately 20-30 individuals that have been followed relatively consistently over the past 11 years (Cheryl Knott, pers. comm.). The research conducted at this site is focussed on female orangutans. My study was the first specific attempt to systematically follow males at this site.

In this study, which was known as the “ male project”, only fully adult male orangutans were followed. Fully adult males were identified by their display of full secondary sexual characteristics: large cheek pads and throat pouch (Galdikas, 1983). It is notoriously difficult to find and to follow male orangutans (Mitani, 1985b) and, I was able to follow only three males: two well known individuals (Roman and Jari Manis) and one moderately known individual (Bones). Roman and Jari Manis have been identified and consistently seen by observers at the site for the past 4 years, and the study-site records contain photographic references for them. Bones has been seen occasionally in the study site over the past few years.

A total of 86 days of observations were collected on these three males (Table 1), with the majority of full follows being on Roman. Roman was the most habituated of the three males and seemed undisturbed by observers. Roman was identified by a hairless back and from photographic references. Jari Manis was consistently aggressive to observers: he regularly performed branch-throwing displays or charged, and eventually became too dangerous to follow. Jari Manis was identifiable by his missing finger on his left hand. Bones was the least habituated and therefore tended to avoid observers. Long-term field assistants identified Bones.

Table 1: Total Follows of Adult Male Orangutans.

Male Orangutans	Partial Day Follows	Full Day Follows	Total
Roman	11	47	58
Jari Manis	7	14	21
Bones	4	3	7
Total	22	64	86

The history of the relationship between Jari Manis and Roman is based on anecdotal information gathered over the years by researchers at the site and on photographic records also found at the research site. Four years ago, observers reported that Roman was dominant over Jari Manis. He was also more aggressive towards other orangutans and observers than Jari Manis. Researchers also reported that Roman was larger than Jari Manis and that he long called more frequently (Knott, pers. comm.). Pictures taken in 1993, showed Roman with large cheek-pads and very tight skin on his face as opposed to Jari Manis, who exhibited smaller cheek pads and relaxed skin. During my study, the opposite was true: Roman tended to be very quiet and to travel on the ground just 10-15m away from observers without seeming concerned, the skin on his face was more relaxed, and his cheek-pads were not as large. Jari Manis on the other hand, was larger in size, his cheek-pads were large, and his facial skin was tight. He frequently charged observers and long called more consistently than Roman. I only observed tight skin on the cheekpads of very large males. I associate this tight skin with males who are maintaining extremely large bodies,

which is only of benefit in competition with rival males over mates. This suggests that adult males who are in their prime can maintain an enhanced body size, but that it is only temporary. When males grow older or when mating potential decreases, it would not be profitable to try and maintain such a large body that requires high-energy input and maintenance. These changes and information gathered by researchers at the site suggest that there was a period of challenge between the two males during which Jari Manis became dominant over Roman, and Roman decreased his size probably to be able to decrease his required energy input and thus his activity levels.

Searching for Orangutans and Data Collection

Despite being large animals with noticeable red hair, orangutans are difficult to find in the forest canopy. I used a variety of techniques to search for focal animals. "Random" searching involved walking slowly and quietly along trails through the study site and trying to listen for orangutans in the trees. Orangutans were usually heard before they were seen. Occasionally, a short rest stop was used to listen quietly for orangutan activity. "Systematic" searches involved the same searching techniques as random searching but the daily search routes were done in a systematic sequence of habitats. For example, if searching in peat swamp one day yielded no orangutans, an alternate habitat would be chosen for searching the following day. The "wait and chase" technique involved walking to a point in the forest, resting in a hammock, and waiting to hear a long call. Upon hearing a long-call, the observers would travel rapidly in the direction of the sound. The "educated guess" technique was the

most successful. It involved searching for focal animals around an area where there were known females and/or fruiting trees.

Most searching days lasted from approximately 0700 to 1400 hours. Everyday between 1200 and 1400, rain would begin. Orangutans are very still in the rain, and this makes them increasingly more difficult to find. Searching was attempted most days when weather permitted and when there was not already a focal animal to follow.

The male project ran for 167 days at the Cabang Panti field site. During this time, there was a range of two to ten people working in the forest each day. On any of these days, they could have come into contact with adult male orangutans. These people included staff from Cheryl Knott's project, and from the male project. The success rate calculated here is conservative in the sense that no matter the number of independent teams in the forest on any given day, it is still only considered one day of searching. This is because information on the number of teams in the forest each day from the reproductive ecology project was not available. Male orangutans were seen on 86 of the 167 days of time in the forest, resulting in a 51% success rate in finding a male orangutan on any given day.

When a focal animal was found, data collection began (see below) and continued until the orangutan entered his night nest and was no longer visible to the observer. Then, the nest tree was tagged and numbered and a cotton string (in a hip-chain measuring device) was used to measure from the nest tree to the nearest trail. A piece of flagging tape identified the point of intersection with the nearest trail and was marked with pertinent information about the nest location (height of tree, height of nest, nest tree number, distance of nest tree from trail).

This assisted the observer in locating the nest early the next morning in order to continue following the focal animal. Orangutans usually leave their nests when the sun rises, around 0600hours. In order to ensure arrival at the nest before the orangutan left and began to travel, observers typically arrived at the nest by 0500hours.

During a “follow” day, data were collected continuously throughout the day using 5-minute interval scan sampling. Information was also recorded between scan intervals if the activity changed. For this study, information was recorded on the directions and distances of movement of the study subject. Also recorded was information about primary (feeding, eating, moving, sleeping) and secondary activities (long calling, urinating, aggressions towards the observer), weather conditions (rain and temperature), diet, and foraging techniques exhibited by the focal animal (see Appendix 1 for a detailed description of the data sheet). All data were collected on a comprehensive data sheet designed by Cheryl Knott. This data sheet is used for her reproductive ecology project at the Cabang Panti research site.

A map of the study site was used to chart a daily range map of the study subject, marking as accurately as possible the distances and direction of each bout of traveling (see Appendix 2 for a map of the study site). The combination of many trails within the study area and a large scale on the study area map (3.5mm on map was equal to 50m in the forest) made it relatively easy to report with accuracy the daily movements of the study subjects.

When study subjects were followed from the time they left their nest in the morning until they entered their new night nest, this was considered a *full day*

follow. If the study subject was already out of his nest and moving when found, or was lost during the day, it was considered a *partial day follow*.

In addition to myself, I had three assistants who were hired and trained to specifically search for and follow adult male orangutans. I trained them to collect data on male movements using the data sheet and daily range maps. Inter-observer reliability was not tested formally. However, I trained all of the male project assistants and monitored their data collection. Furthermore, the data collection was done on simple behavioural categories that did not require a high degree of interpretation. Two observers were always required to follow adult male orangutans, for both safety concerns and to get the most accurate view of focal animal activities. So, with these three assistants, I actually had two full teams of observers.

Food samples from focal animals were collected and identified. All orangutan food trees were tagged with an aluminum tag and a reference number. Tree height and diameter at breast height information were recorded as well. This information is part of the long-term data collection from the Cabang Panti research station.

The impact of the observer on the behaviours of male orangutans was variable. Roman was least affected by the presence of observers. He spent the least amount of time looking at or displaying to the observers below. He regularly foraged less than 15m from observers on the ground and was never aggressive to them. Jari Manis frequently displayed at observers through vocalizations and occasional branch throwing. However, these reactions were short-lived and only occurred at the beginning of observations. They typically lasted less than an hour, mostly on the first day of contact in a series of consecutive days of follow.

Sometimes, he would descend to the ground and charge the observers. For this reason, it was not always possible to follow him. Bones was most affected by the presence of observers. He vocalized regularly when observers were present. To lower the impact of the observer on the behaviour of focal male orangutans and to minimize the threat that the observers represented, a general rule of staying visible, but not being obtrusive was used. It was a way to let the focal male know where the observers were (i.e. the observers were never hiding) to avoid surprising the focal male, and to prevent him from concentrating on looking for the observers.

Data Analysis

Comparing Male Ranging Behaviours

My aim is to establish if the three males range in a similar fashion and to understand the variables that seem to influence their ranging behaviours. To accomplish this, the ranging data for the three males must be compared and the ecological factors (the amount of fruit in the diet and the presence of bark in a male's diet), climatic factors (rainfall patterns), and social factors (the presence of other orangutans) that might affect the ranging behaviours of the three subjects need to be identified. I compared the ranging behaviour of the males on days where a given variable is present to days when the variable is absent, to determine if the variable in question had a correlation with ranging behaviour.

Six measures of ranging behaviours were compared between the three male orangutans: daily range, the distance between nests, the speed of travel, the

pattern of travel, the directness of travel, and the day length. Then these measures of ranging behaviour were compared in relation to the four variables: fruit availability, amount of bark in their diet, rainfall patterns, and the presence of other orangutans.

Days of observation were considered independent for the analyses. It must be recognized, however, that some activities of the focal males on a given day could potentially have been influenced by activities on previous days. For example, if a day had heavy rainfall and the male did not spend much time eating, he may have dedicated more time to feeding on the following day than he would have otherwise. This potential effect of previous days on the behaviour of males on subsequent days was not tested. However, given a larger sample of days, it would be necessary to do so to maintain the assumption of independence of the unit of analysis.

Measures of Ranging Behaviours

Daily range was the total distance traveled by a focal animal in one day. This was calculated by plotting movements of the focal animal on the study site map throughout the day. That line was measured and calculated against the map scale to derive the distance traveled by the focal animal. Day range was only calculated for full-day follows.

Distance between nests was calculated by tracing a straight line between consecutive night nests of the focal animal. Full and partial day follows were used in this calculation when the location of the previous night's nest was known.

Speed of travel was the rate at which the focal animal traveled during the day in relation to the total distance covered. This resulted in a mean number of meters traveled per minute. Full and partial day follows were used in this calculation.

Pattern of travel was expressed as travel bout length, or the distance accumulated with each bout of movement. This was the mean travel bout distance traveled by a male orangutan per day. This was calculated by dividing the total day range length by the number of travel bouts recorded. A small value for bout length indicated that the male tended to move for short distances between stopping to rest or eat. A large value for bout length indicated that the male was moving long distances before stopping. These patterns of bout length are represented in Figure 2. Only full day follows were used for this calculation.

Directness of travel was the ratio of the distance between nests compared to the male's daily range. The directness of travel was not an independent measure, as it was a combination of two other measurements. A ratio of 1 would indicate that the male was traveling in a direct or linear way between nests. If a male's daily range was much longer than the distance between nests, the ratio would be closer to 0, indicating that the male was traveling in an indirect, or meandering fashion. These two styles of travel are represented in Figure 3. This measure could potentially discriminate between resident and transient ranging behaviours if transients keep moving through the forest in search of food and females. Resident males would be expected to travel in a less direct way over time, as they probably have a greater amount of range re-use. Transient males would be expected to have a more direct style of travel because they are more likely to move through an area to avoid competing with resident males.

Figure 2: Patterns of Travel

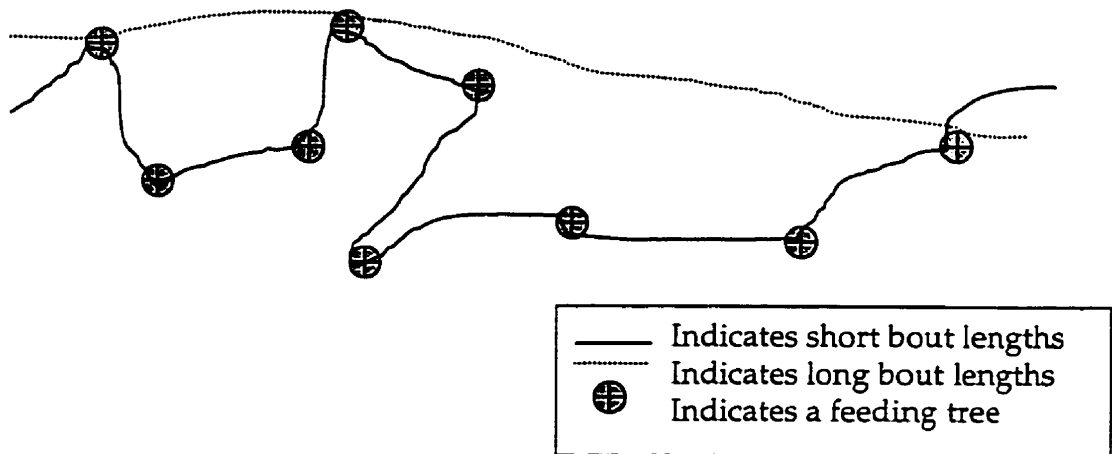
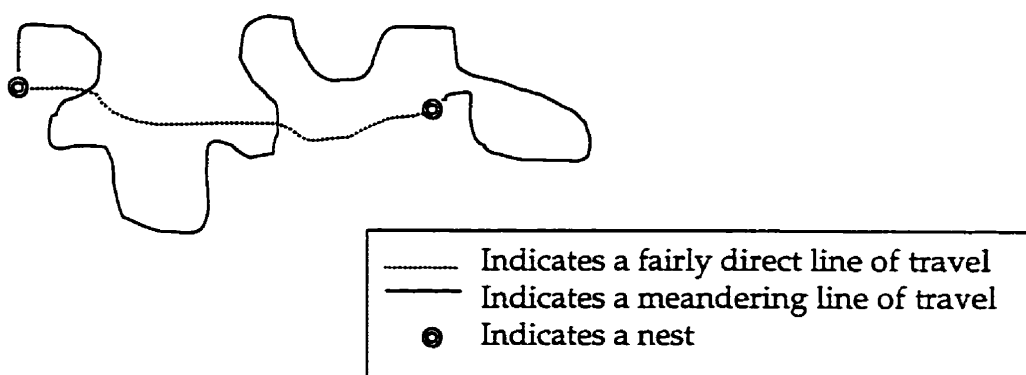


Figure 3: Directness of Travel

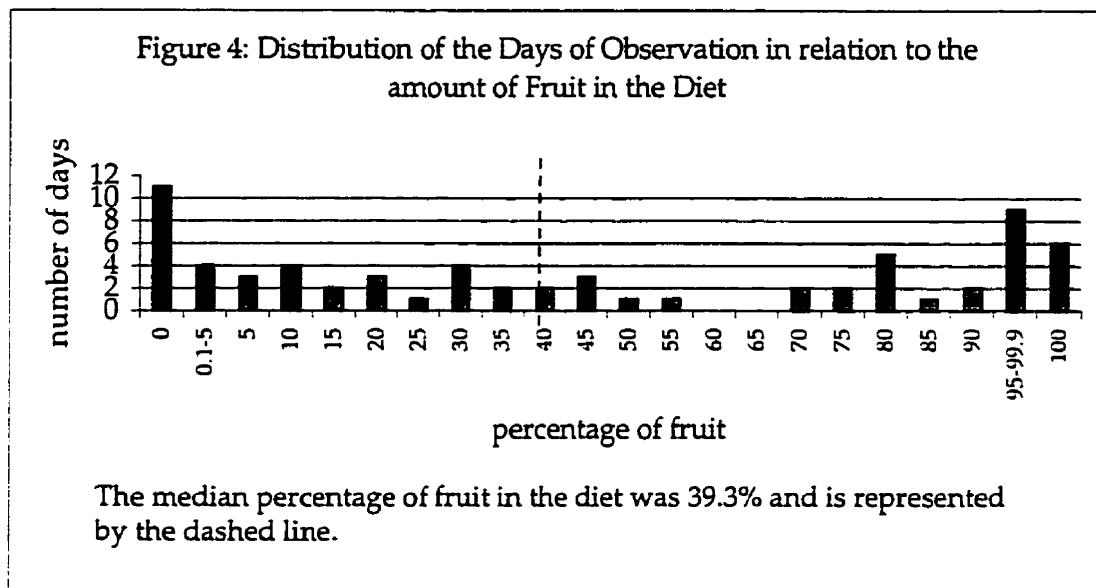


Day length is the amount of time a male orangutan is active during the day and could be potentially moving. It was expressed in minutes and calculated from the time that the male orangutan gets out of his previous night nest to the time he enters his next night nest. Only full day follows were used in these calculations.

Variables Potentially Influencing Male Ranging Behaviours

Fruit in the Diet

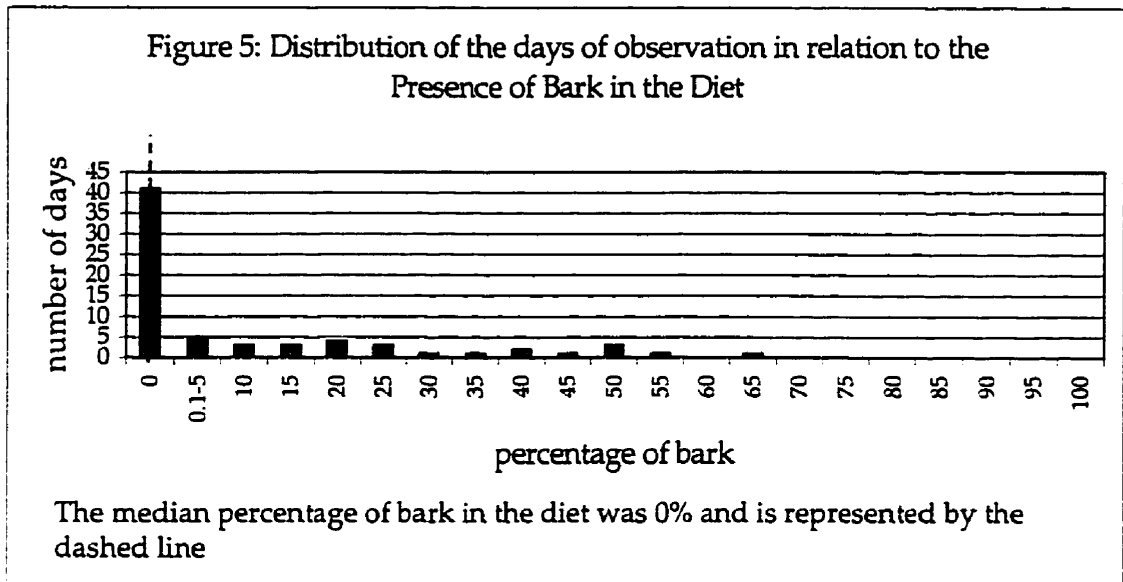
A “high fruit day” was a day during which the subject was feeding on fruit for at least 39.3% of the total foraging time. This threshold of 39.3% was used because it is the median percentage of time that male orangutans spent feeding on fruit in the data collected. The median was used as the measure of central tendency because the distribution of fruit in the diet of the focal males was skewed (Figure 4). Time spent feeding on fruit consisted of the time orangutans spent picking fruits and bringing them to their mouth, or pulling branches towards themselves and eating the fruit off the branch. It also included the processing time required to eat the fruit. This time did not include time apparently searching for fruit and moving between food sources. The term “fruit” applied to all parts of a fruit and ripeness stages of a fruit because orangutans feed on unripe fruits (Galdikas, 1988). Figure 4 shows the distribution of the days of observation, in relation to the percentage of fruit in the diet.



Bark in the Diet

Bark is time consuming for orangutans to harvest and is eaten in two ways.

Orangutans may selectively eat the inner cambium of the bark or eat the bark as a whole (Rodman, 1988). In this study, no bark was eaten on many days, resulting in a median percentage of bark in the diet of 0. Therefore, measures of ranging behaviours were compared between days when bark was present or absent on the diet. Figure 5 shows the distribution of days of observation in relation to the percentage of bark in the diet of adult male orangutans followed during this study.



Rainfall Patterns

Rainfall data were collected with a standard rain gauge in a forest clearing near the center of the field site. They were collected daily at 0600hours, therefore accounting for a 24-hour period of rainfall. A "high rainfall" day was a day that had 20mm of rainfall or more. Above this threshold was considered heavy rainfall because in the forest it indicated a short duration of intense rain or a longer duration of light rain.

The Presence of Other Orangutans

Another orangutan was considered to be present if he or she was visible and/or audible to the observer. I assumed that focal males would be able to detect any other orangutans that were noticeable to the observer. The maximum distance an observer could be expected to see or hear another orangutan was 50m unless

other observers were following the other orangutan. Another orangutan could be an adult female, another adult male, or a subadult male.

Home Range Estimate

A home range was calculated for Roman and Jari Manis for the time they were observed within the study site. In prior orangutan research where home range values were provided, the methods used by the authors were not given (MacKinnon, 1971; Rodman, 1973; Galdikas, 1978; Rijksen, 1978). In this study, the grid method was used, which has been used by many other primate studies (Vedder, 1984; Newton, 1992; Chapman and Wrangham, 1993). The grid of 3x3mm (equivalent to 50 x 50m in the forest) was superimposed over the daily range maps. The total number of grid squares entered over the total period of observation was calculated. This measure used full and partial days of follow. The sample size for days of observation on Bones was too small to produce a comparable home range estimate.

Long Call Comparisons

The intensity, duration, and frequency of long calls were compared between Roman and Jari Manis. Most of the long call data were obtained from Jari Manis, who long called more consistently than Roman. Long calls that occur more than thirty minutes apart were considered influenced by independent stimuli. This thirty-minute threshold was taken from research done by Mitani (1985b) where

he considers activities up to thirty minutes after a long call to be potentially influenced by the long call. Only independent long calls are included in this analysis.

The *intensity* was defined as the amount of “roars” in a long call (Mitani, 1985b). A long call begins and ends with vocals likened to gurgling sounds. In-between these gurgling sounds is a series of pulsing roars that can be heard through the forest for up to a kilometer away (Galdikas, 1983; Mitani, 1985b). The more intense a long call, the more likely it is to be heard, as modulating vocals travel best in the tropical rainforests (Mitani and Stuht, 1998).

The *duration* of a long call was estimated to the closest minute. I assume that the longer the duration of a long call, the higher the potential for it being heard by a larger audience.

The *frequency* of long calls was estimated as the number of long calls heard by the observer on days of observation for a given male.

Jari Manis’s ranging behaviour was analysed using the six measures of ranging behaviour to determine if long calling affected his movement decisions. The six measures of ranging behaviours were compared between days when he did call versus days when he did not. I also analyse long calls in terms of their frequency, intensity and duration. Roman and Bones had insufficient sample sizes of days with long calls to make any comparisons with their ranging behaviour.

Statistical Tests

All statistical comparisons were done using the Statview II program for MacIntosh computers; all tests are two-tailed unless otherwise stated. One-tailed tests were only performed when adequate background information was present to predict the direction of a comparison (see below). The level of significance used was $p < 0.05$. In all cases where I compare ranging behaviour between males and the influence of one of the four variables on ranging, the unit of analysis is the day of travel.

First, I tested if the three males had different ranging behaviours. I compared the six measures of ranging behaviour for the three males using a Kruskal-Wallis one-way analysis of variance (Siegel and Castellan, 1988). When there was a significant result, a multiple comparison test was done to determine the location of the significant differences. Then I compared the four potential influences on male ranging behaviors (fruit, bark, other orangutans, rainfall patterns) on days when they were present to days when they were absent using a Wilcoxon-Mann-Whitney test (Siegel and Castellan, 1988). This test determined if the variable had a significant association with ranging behaviour. As the same data set was used for four comparisons, I increased the probability of making a type I error. To circumvent this problem, I applied an "experimentwise error rate correction", which adjusted the alpha level in relation to the number of tests I had and maintained a confidence level of 0.95 overall. For these analyses, I thus had an alpha level of significance of $p < 0.0127$.

Formula: $\alpha' = 1 - (1 - \alpha)^{1/k}$ (Sokal and Rohlf, 1981).
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For the analyses of the long calls, I first compare long calls between the two males, Jari Manis and Roman. The long call frequency, intensity, and duration between the Jari Manis and Roman are compared using a Wilcoxon-Mann-Whitney test. Then, Jari Manis's measures of ranging behaviours are compared between days when he did long call versus days when he did not, also using a Wilcoxon-Mann-Whitney test. As the data used for this analysis is a small subset of the data analysed above, I applied a level of significance of $p < 0.05$.

Non-parametric statistics were used for this study due to the small sample size of three male orangutans and the fact that data were not normally distributed. Due to the use of non-parametric statistics, the median value will be presented in the results.

One-Tailed Tests

When considering fruit as an influence on daily range length, a one-tailed test was used. Previous research on female orangutans in this habitat had indeed found that daily range is shorter when fruit is more available (Knott, 1998).

The speed of travel in primates has been reported to increase with an increase in daily range (Strier, 1987). Therefore, if orangutans are seen to decrease their daily range on high fruit days, this decrease in ranging may also decrease their speed of travel. Thus, it was assumed that speed of travel would decrease on high fruit days.

On the basis of prior research and field observations, I predicted that day length for Roman would be shorter on days with high rainfall. This was based on observations that orangutans left their nests later in the morning and made new night nests earlier in the evening on days with high rainfall (MacKinnon, 1971).

Chapter Four: Results

This chapter presents the results of analyses to determine if the three males range in a similar way, and if the measures of male ranging behaviour were influenced by ecological, social or climatic factors. This chapter also presents the comparison of long calls between Roman and Jari Manis. Jari Manis's long call data were also analysed to determine their association with his ranging behaviour. Sample size may not equal 69 for all analyses due to occasional missing data in some categories.

A Comparison of the Ranging Behaviours of the Three Focal Males

The three focal animals were compared to determine if they had similar ranging behaviours. If analyses did not show significant differences in the measures of ranging behaviours of the three males, their data were combined for further analysis.

Day length was the only measure of ranging behaviours that was significantly different for the three adult male orangutans (Kruskall-Wallis one-way analysis of variance: $H=7.47$, $N=69$, $df=2$, $p=0.03$). The median day length is 566.50 minutes (range 340-760 minutes) for Roman, 545.50 minutes (range 342-703 minutes) for Jari Manis, and 707 minutes (range 702-716 minutes) for Bones. A multiple comparison test showed the ranging differences to be between Roman

and Jari Manis and between Jari Manis and Bones. Because the day length was significantly different for the three males, each male was analysed separately to determine the factors that were influencing their ranging behaviours.

The three focal males did not differ in the length of their daily range ($H=3.73$, $N=69$, $df=2$, $p=0.15$), their directness of travel ($H=4.98$, $N=66$, $df=2$, $p=0.08$), or in their distance between nests ($H=0.36$, $N=68$, $df=2$, $p=0.84$). The median daily range traveled by Roman was 583.34m (range 100-1750m), compared to 432.14m (range 107.14-1057.14m) for Jari Manis, and 857.14m (range 300-1171.43m) for Bones. The median directness of travel was 0.54 (range 0.05-0.94) for Roman, 0.68 (range 0.53-0.93) for Jari Manis, and 0.52 (range 0.26-0.55) for Bones. The median distance between nests was 338.69m (range 28.57-1508.33m) for Roman, 257.14m (range 85.71-735.71m) for Jari Manis, and 471.43m (range 78.57-607.14) for Bones.

The three males also did not differ in their speed of travel ($H=2.03$, $N=68$, $df=2$, $p=0.36$), or in their travel bout length ($H=1.43$, $N=67$, $df=2$, $p=0.49$). The median speed of travel was 1.05m/minute (range 0.18-2.80 m/minute) for Roman, 0.87m/minute (range 0.22-2.07m/minute) for Jari Manis, and 1.21m/minute (range 0.42-1.67m/minute) for Bones. The median travel bout length was 101.19m (range 16.67-875m) for Roman, 80.95m (range 50.45-164.29m) for Jari Manis, and 60m (range 53.25-122.45m) for Bones.

Ecological Factors that Potentially Influence
Male Orangutan Ranging Behaviours

This section presents how ecological, social, and climatic factors influenced male orangutan ranging behaviours. Table 2 provides an overview of the significant results of this section.

Table 2: Summary of Significant Results

	Fruit in the Diet	Bark in the Diet	Other Orangutans	Rainfall Patterns
Daily Range			A > P	
Distance between Nests				L > H
Speed of Travel				
Pattern of Travel	LF > HF		A > P	
Directness of Travel				
Day Length				

LF = Low fruit
HF = High fruit

A = Other orangutans absent
P = Other orangutans present

L = Low rainfall
H = High rainfall

Amount of Fruit in the Diet

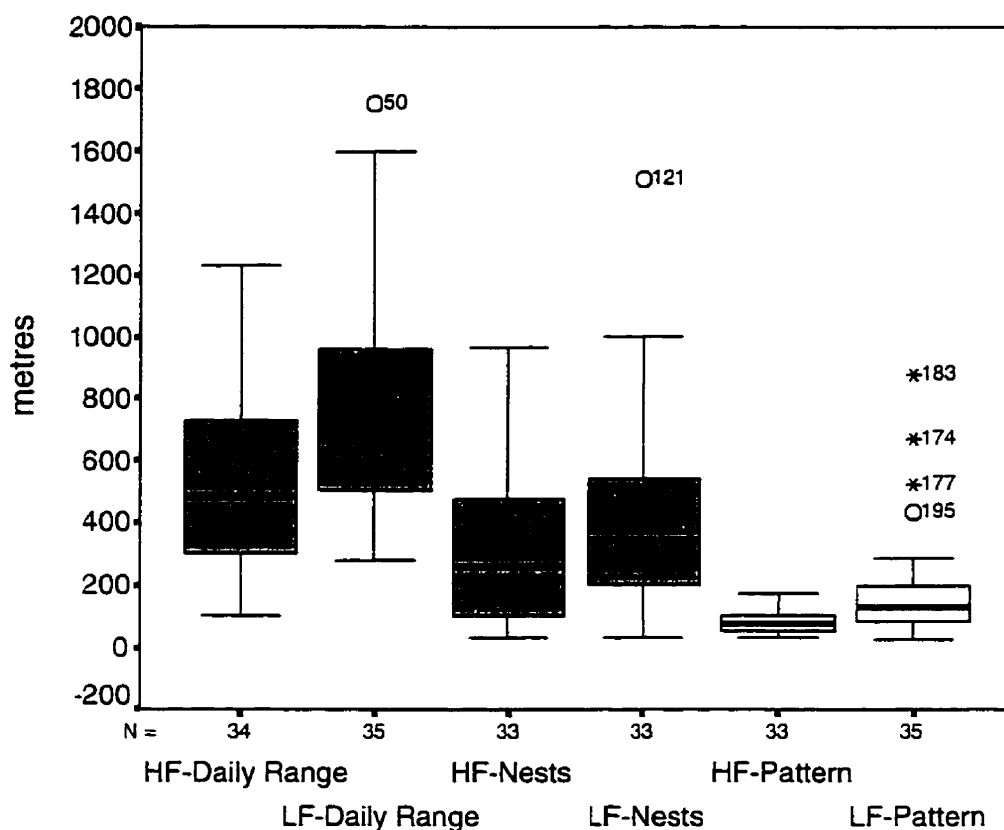
The pattern of travel, expressed as travel bout length, was significantly different on high fruit days versus low fruit days, with high fruit days showing shorter bout length (Wilcoxon-Mann-Whitney: $z=-3.16$, $n_1=35$, $n_2=33$, $p=0.002$, Figure 6). The median travel bout on high fruit days was 75m (range 30.61-183.33m), compared to 126.53m (range 22.22-875m) on low fruit days.

There was a tendency for male orangutans to shorten their daily range on high fruit days compared to low fruit days ($z=-2.22$, $n_1=34$, $n_2=35$, $p=0.03$ one-tailed test, Figure 6). The median daily range on high fruit days was 485.71m (range 100-1233.33m), as opposed to 628.57m (range 278.57-1471.43m) on low fruit days.

There was also a tendency for speed of travel to be slower on high fruit days compared to low fruit days ($z=-2.45$, $n_1=33$, $n_2=35$, $p=0.014$ one-tailed test, Figure 7), but this tendency was not significant. The median speed of travel on high fruit days was 0.85m/minute (range 0.18-2.07m/minute), compared to 1.16m/minute (range 0.23-2.80m/minute) on low fruit days.

The distance between consecutive nests ($z=-1.68$, $n_1=33$, $n_2=35$, $p=0.09$ Figure 6), and the directness of travel ($z=-0.39$, $n_1=32$, $n_2=34$, $p=0.69$, Figure 7) did not significantly differ between high and low fruit days. The median distance between nests on high fruit days was 257.14m (range 28.57-966.67m), compared to 357.14m (range 83.33-1508.33m) on low fruit days. The median value for directness of travel on high fruit days was 0.56 (range 0.16-0.94), compared to 0.55 (range 0.05-0.94) on low fruit days.

Figure 6: Variation in the daily ranges, distance between consecutive nests and pattern of travel between high fruit and low fruit days for the focal males.



This boxplot illustrates the variation (median, range, and quartiles) in the daily range, the distance between consecutive nests, and the pattern of travel for high fruit days (HF) and low fruit days (LF). It does not present a comparison between the six elements represented. The white boxes represent significant differences for the measure of ranging behaviour on high versus low fruit days. "N" is equal to the number of days of observation. Values outside of the whiskers between 1.5-3 times the box length are "O" outliers. The outlying values greater than 3 box lengths are "*" extreme values.

Guide to reading a boxplot:

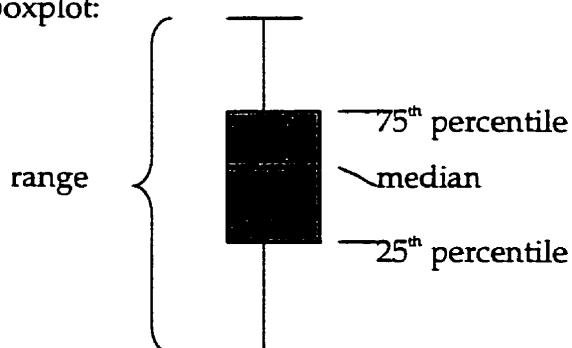


Figure 7: Variation in the directness of travel and the speed of travel on high fruit days (HF) versus low fruit days (LF) for the focal males.

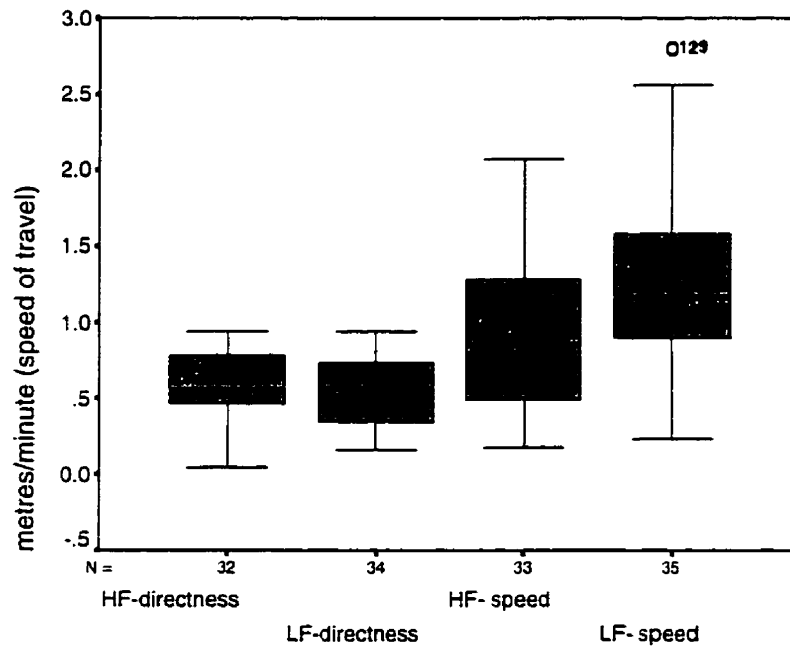
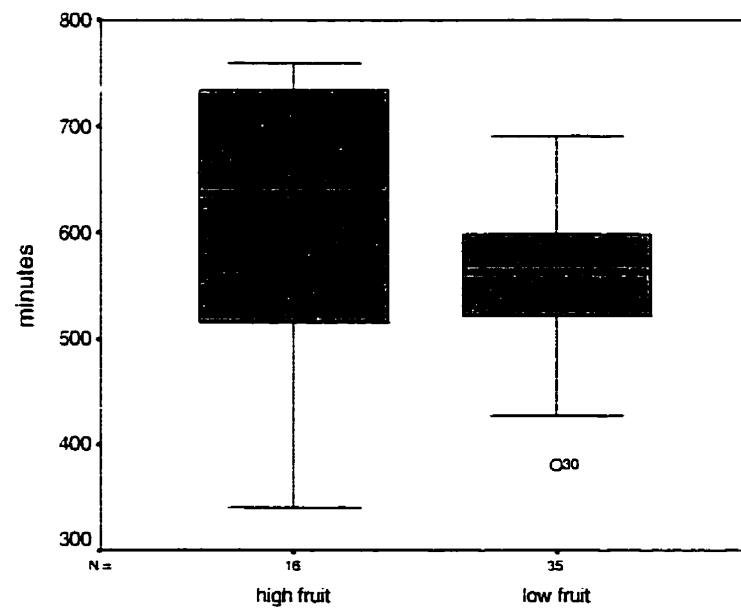


Figure 8: Variation in Roman's day length on high fruit versus low fruit days.



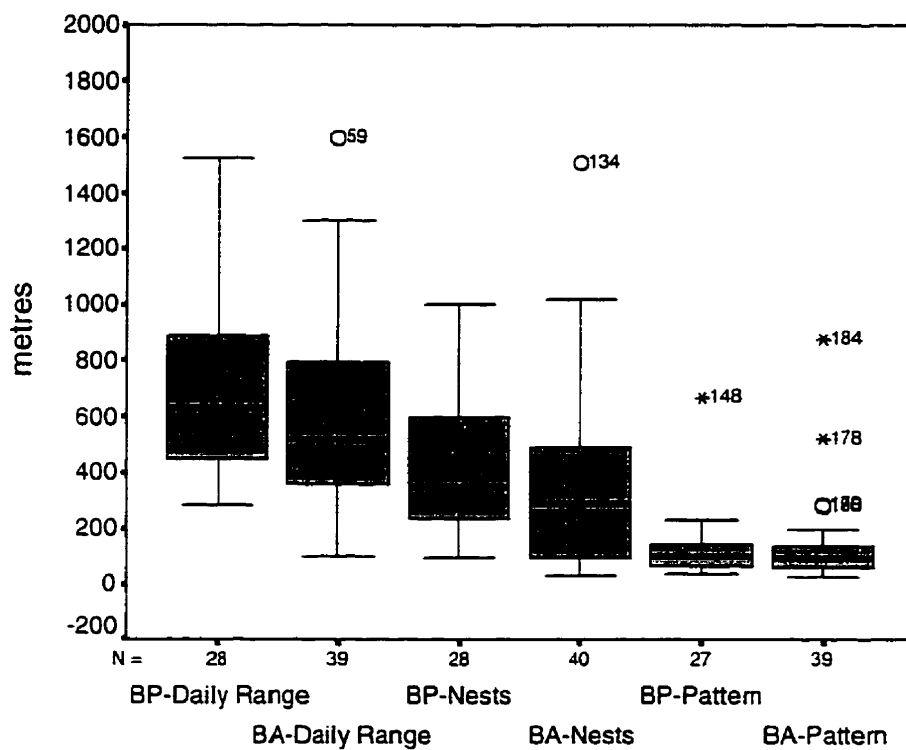
Roman's day length did not significantly differ between high and low fruit days ($z=-1.67$, $n_1=16$, $n_2=36$, $p=0.09$, Figure 8). Roman's median day length on high fruit days was 637 minutes (range 340-760 minutes), compared to 561 minutes (range 380-691 minutes) on low fruit days. All of the full follows for Jari Manis and Bones were high fruit days, and therefore a comparison could not be made between their day length on high fruit versus low fruit days.

Presence of Bark in the Diet

The presence of bark in the diet did not significantly influence any of the ranging behaviours of adult male orangutans in this study. The daily range ($z=-1.27$, $n_1=29$, $n_2=39$, $p=0.20$, Figure 9), the distance between their nests ($z=-1.59$, $n_1=28$, $n_2=40$, $p=0.11$, Figure 9), the speed of travel ($z=-1.69$, $n_1=27$, $n_2=41$, $p=0.09$, Figure 10), the directness of travel ($z=-0.79$, $n_1=26$, $n_2=40$, $p=0.94$, Figure 10), the pattern of travel ($z=-0.45$, $n_1=27$, $n_2=39$, $p=0.65$, Figure 9) and the day length (Roman: $z=-0.33$, $n_1=22$, $n_2=29$, $p=0.74$, Figure 11) (Jari Manis: $z=-0.87$, $n_1=5$, $n_2=9$, $p=0.39$, Figure 11) did not significantly differ between days when bark was present in the diet and days when bark was absent from the diet.

The median daily range length on days when bark was present in the diet was 628.57m (range 285.71-1528.57m), as opposed to 525m (range 100-1600m) on days when bark was absent from the diet. On days when bark was present in the diet, the median distance between consecutive nests was 338.69m (range 92.86-1000m), compared to 285.72m (range 28.57-1508.33m) on days when bark was absent. The median speed of travel was 1.17m/minute (range 0.52-2.56m/minute) on days with bark present in the diet, and 0.95m/minute (range

Figure 9: Variation in the daily range, the distance between consecutive nests and the pattern of travel between days when bark was present and absent in the diet of the focal males.



BP: Bark present in the diet on a given day.

BA: Bark absent in the diet on a given day.

Figure 10: Variation in directness of travel and speed of travel when bark was present and absent in the diet of focal males.

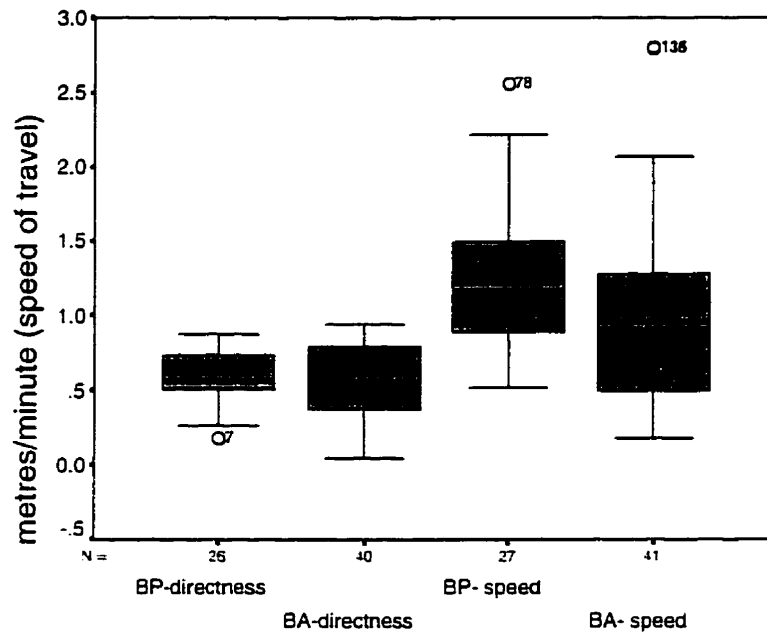
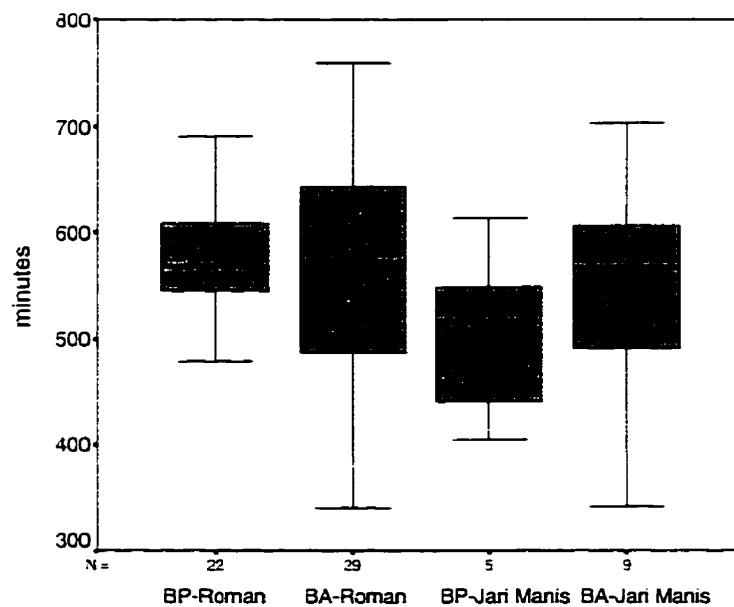


Figure 11: Variation in day length for Roman and Jari Manis on days when bark was present and absent in their diets.



0.18-2.80m/minute) on days with bark absent from the diet. The median directness of travel on days with bark present in the diet was 0.56 (range 0.18-0.87), as opposed to 0.55 (range 0.05-0.94) on days with bark absent from the diet. Travel bout length had a median of 100m (range 35-666.71m) on days with bark present in the diet, compared to 91.07m (range 22.22-875m) on days when bark was absent from the diet. The median day length when bark was present in their diet was 516 minutes (range 404-613minutes) for Jari Manis and 545 minutes (range 479-691minutes) for Roman. On days when bark was absent from their diet, median day length was 485.75 minutes (range 342-703 minutes) for Jari Manis, and 571 minutes (range 340-760 minutes) for Roman.

A Social Factor that Potentially Influence Male Orangutan Ranging Behaviours

Presence of Other Orangutans

The daily range of the three males differed significantly was significantly shorter on days when other orangutans were present compared to days when they were absent ($z=-2.69$, $n_1=27$, $n_2=42$, $p=0.007$, Figure 12). The median daily range when other orangutans were present was shorter, with a value of 457.14m (range 100-1378.57m), compared to 647.64m (range 278.57-1750m) when other orangutans were absent.

Travel bout lengths also showed a significant difference between days when other orangutans were present versus when others were absent ($z=-2.75$, $n_1=26$, $n_2=41$, $p=0.006$, Figure 12). The median travel bout length on days when other

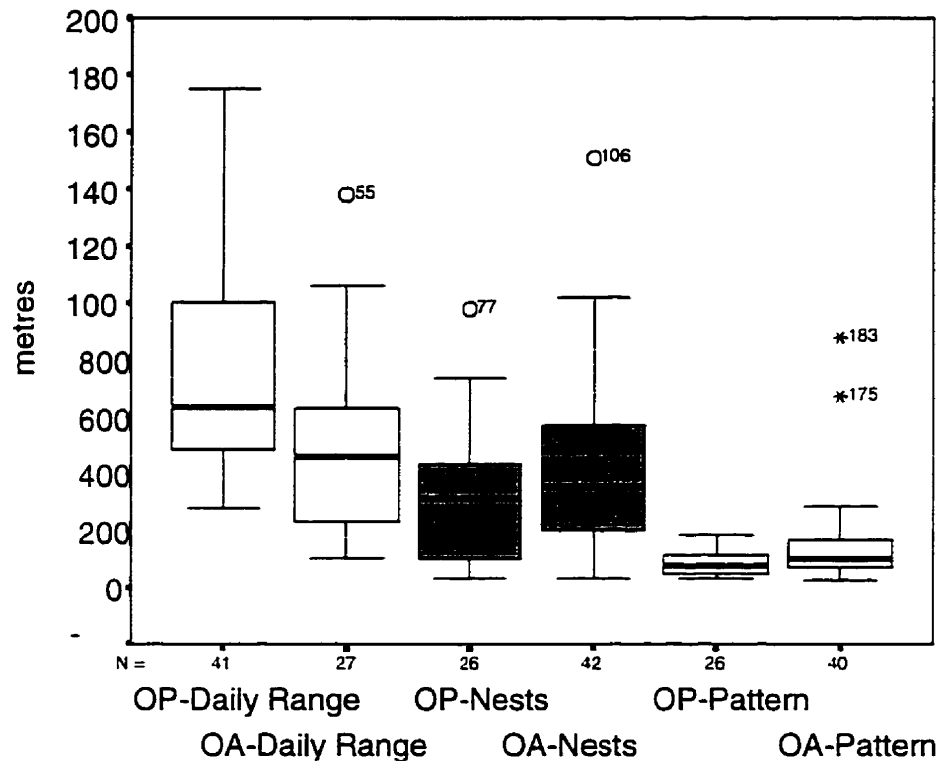
orangutans were present was shorter, at 72.52m (range 30.61-183.33m), compared to 102.04m (range 22.22-875m) on days when they were absent.

The speed of travel tended to differ on days when other orangutans were present, but this tendency was not significant ($z=-2.46$, $n_1=26$, $n_2=42$, $p=0.014$, Figure 13). The median speed of travel on days when other orangutans were present was 0.84 m/minute (range 0.18-2.22 m/minute), compared to 1.16 m/minute (range 0.23-2.80 m/minute) on days when they were absent.

The distance between nests ($z=-1.16$, $n_1=26$, $n_2=42$, $p=0.25$, Figure 12), and the directness of travel ($z=-1.79$, $n_1=23$, $n_2=43$, $p=0.07$, Figure 13) did not differ significantly between days with other orangutans present and days when they were absent. The median distance between nests on days when other orangutans were present was 312.50m (range 28.57-978.57m), compared to 350.84m (range 28.57-1508.33m) on days when they are absent. The median value for directness of travel on days when other orangutans were present was 0.68 (range 0.05-0.93), compared to 0.53 (range 0.06-0.94) on days when they were absent.

Both Roman's ($z=-0.07$, $n_1=14$, $n_2=38$, $p=0.94$, Figure 14), and Jari Manis's ($z=-0.91$, $n_1=12$, $n_2=2$, $p=0.36$, Figure 14) day length did not differ significantly when other orangutans were present compared to when they were absent. Roman's median day length was 554.50 minutes (range 363-756 minutes) on days when other orangutans were present, compared to 572 minutes (range 340-760 minutes) on days when others were absent. Jari Manis's median day length on days when other orangutans were present was 529.50 minutes (range 342-703), compared to 580.50 minutes (range 548-613 minutes) on days when others were absent.

Figure 12: Variation in daily range, distance between consecutive nests, and pattern of travel between days when other orangutans were present and when other orangutans were absent for the focal males.



OP: days during which other orangutans were present
 OA: days during which other orangutans were absent

Figure 13: Variation in the directness of travel and the speed of travel on days when other orangutans were present versus absent for the focal males.

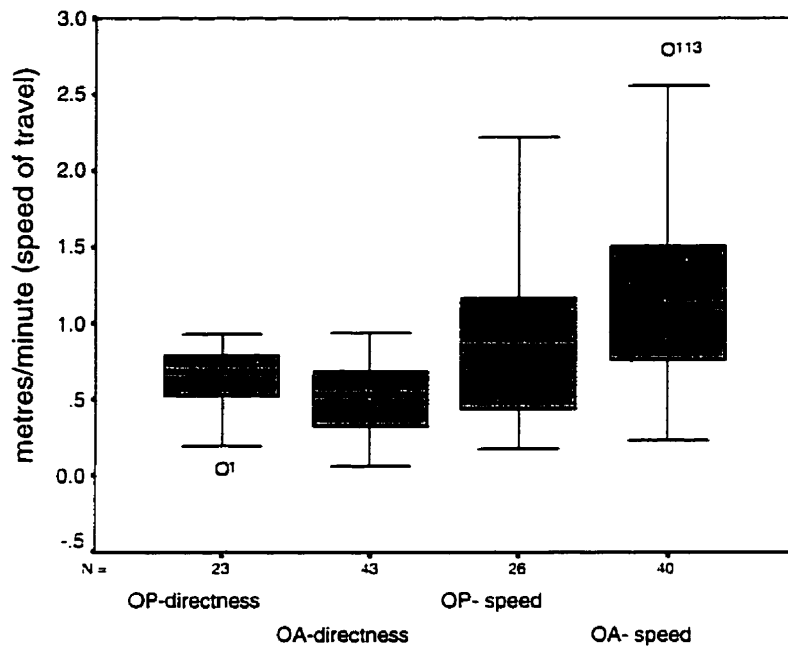
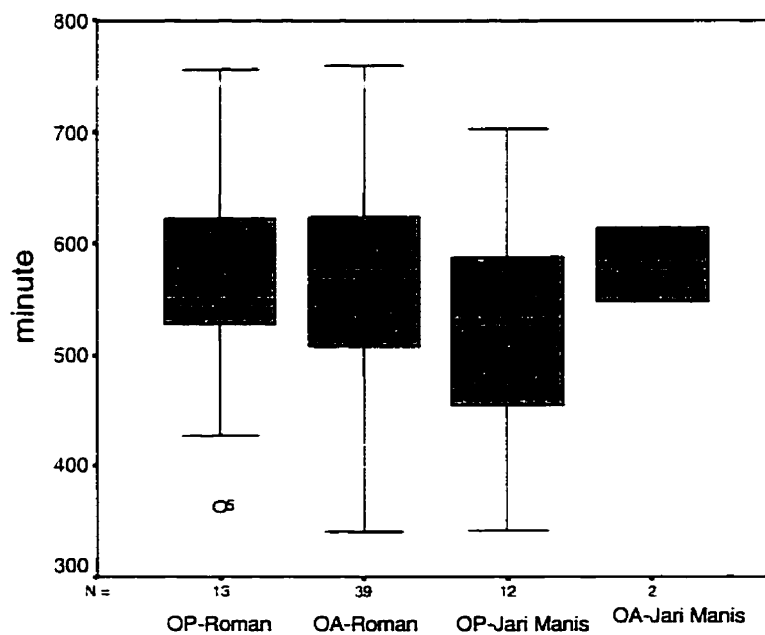


Figure 14: Variation in day length for Roman and Jari Manis on days when other orangutans were present versus days when other orangutans were absent.



A Climatic Factor Potentially Influencing
Male Orangutan Ranging Behaviours

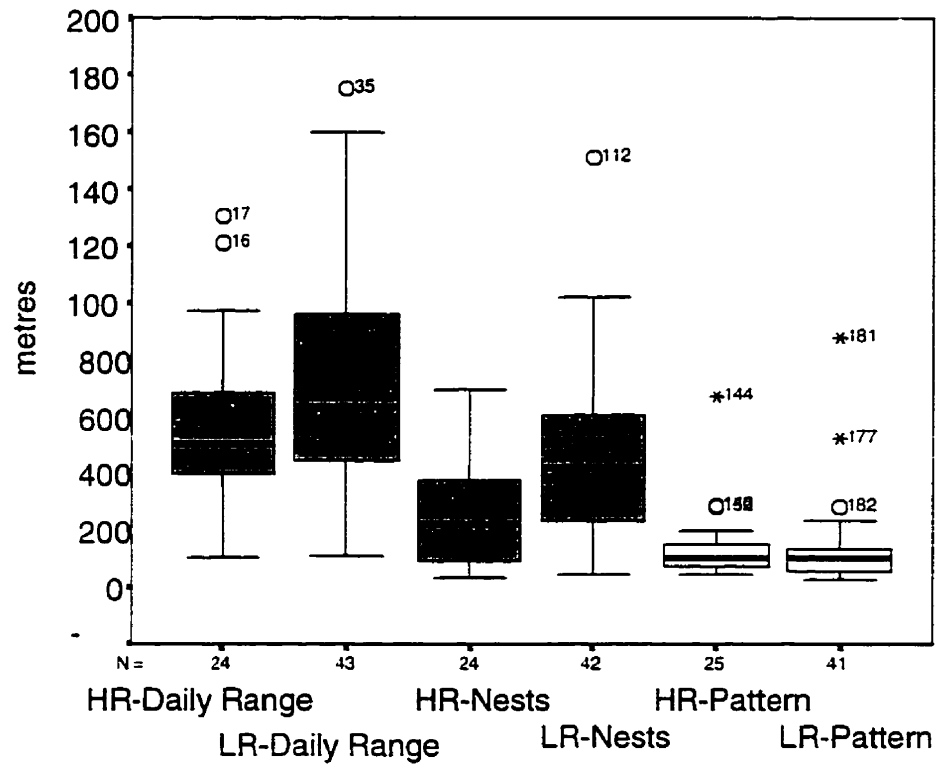
Rainfall

The distance between nests differed significantly between high rainfall days and low rainfall days ($z=-2.53$, $n_1=42$, $n_2=24$, $p=0.01$, Figure 15). The median distance between nests on high rainfall days was shorter, with a value of 217.86m (range 28.57-691.67m), compared to 420.83m (range 42.86-1508.33m) on low rainfall days.

Roman had a tendency to shorten his day lengths on high rainfall days ($z=-1.85$, $n_1=18$, $n_2=33$, $p=0.03$ one-tailed test, Figure 17). Jari Manis's day length was not shorter on high rainfall days versus low rainfall days ($z=-1.58$, $n_1=8$, $n_2=8$, $p=0.12$ one-tailed test, Figure 17). Roman's median day length on high rainfall days was 534 minutes (range 340-760 minutes), compared to 583 minutes (range 427-760 minutes) on low rainfall days. Jari Manis's median day length on high rainfall days was 554.50 minutes (range 404-703 minutes), compared to 455.50 minutes (range 136-606 minutes) on low rainfall days.

Speed of travel ($z=-1.82$, $n_1=25$, $n_2=41$, $p=0.07$, Figure 16), and daily range ($z=-1.66$, $n_1=24$, $n_2=43$, $p=0.10$, Figure 15) did not differ significantly between high rainfall days and low rainfall days. The median speed of travel on high rainfall days was 0.89 m/minute (range 0.18-2.07 m/minute), compared to 1.17 m/minute (range 0.22-2.80 m/minute) on low rainfall days. The median daily range on high rainfall days was 500m (range 100-1300m), as opposed to 628.57m (range 107.14-1750m) on low rainfall days.

Figure 15: Variation in daily range, distance between consecutive nests, and pattern of travel between days with high rainfall and low rainfall for the focal males.



HF: days with a high amount of rainfall

LF: days with a low amount of rainfall

Figure 16: Variation in the directness of travel and the speed of travel on high rainfall versus low rainfall days for the focal males.

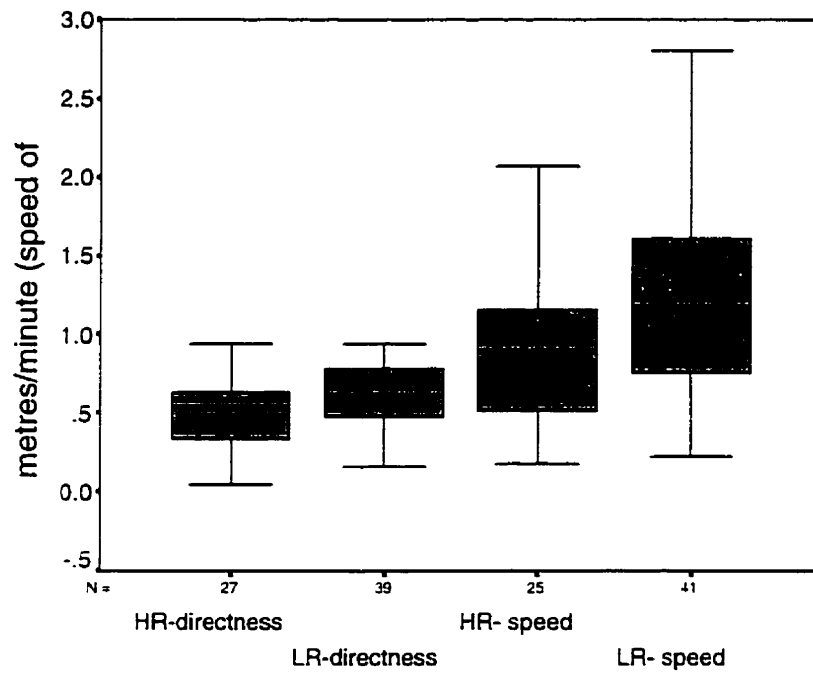
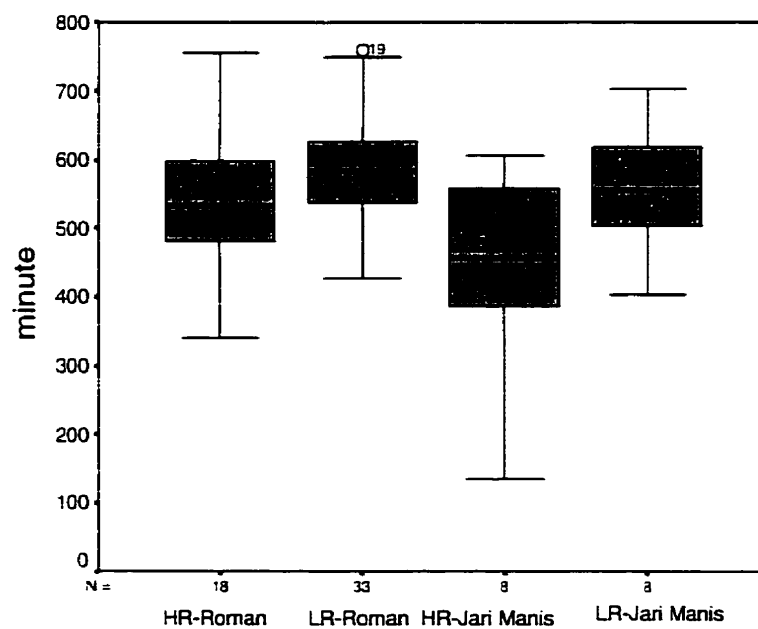


Figure 17: Variation in the day length for Roman and Jari Manis on high rainfall versus low rainfall days for the focal males.



The pattern of travel ($z=-0.84$, $n_1=25$, $n_2=42$, $p=0.40$ Figure 15), and the directness of travel ($z=-1.63$, $n_1=27$, $n_2=39$, $p=0.10$ Figure 16) did not differ significantly between high rainfall days and low rainfall days. The median travel bout length on high rainfall days was 100 m (range 45-666.71m), compared to 95.11 m (range 22.22-875m) on low rainfall days. The median value of directness of travel on high rainfall days was 0.53 (range 0.05-0.94) as opposed to 0.61 (range 0.16-0.94) on low rainfall days.

Comparison of Long calls

The frequency, intensity, and duration of long calls were compared between Roman and Jari Manis. The associations between Jari Manis's long calling and his ranging behaviours were also presented. Jari Manis long called 31 independent times during seven of his fourteen days of observation, while Roman long called twice during two of his 52 days of observation.

Jari Manis's long calls frequency and intensity varied significantly from Roman's (frequency: $z=-5.89$, $n_1=58$, $n_2=21$, $p=0.0001$, intensity: $z=-2.13$, $n_1=2$, $n_2=33$, $p=0.03$). The median frequency of long calls per day for Jari Manis was higher, with a value of 1 (range 0-9), compared to 0 (range 0-1) for Roman. The median intensity for Jari Manis was higher, with a value of 34 roars (range 3-67 roars), as opposed to Roman's long calls at 8.5 roars (range 5-12 roars).

Jari Manis's long calls had a tendency to differ from Roman in terms of duration ($z=-1.86$, $n_1=35$, $n_2=2$, $p=0.06$), although this was not significant. The median

duration for Jari Manis's long calls tended to be longer, with a value of 3 minutes (range 1-5 minutes), compared to one minute (no range) for Roman.

Two main factors were observed to stimulate the focal males to long call: loud crashes from tree falls and the presence of other orangutans or observers. Table 3 summarizes the presumed stimuli for Roman and Jari Manis's long calls. Jari Manis long called 5 times after a tree fall compared to Roman who long called once after a tree fell. Jari Manis long called 13 times while another orangutan was present, while Roman again long called once.

Table 3: Long Call Stimuli for Jari Manis and Roman

Stimulus	Jari Manis	Roman
Female Orangutan	6	0
Male Orangutan	7	0
Both Male and Female	0	1
Tree Fall	5	1
Observer	3	0
Unknown	10	0
Total	31	2

Long Calling and Jari Manis's Ranging Behaviour

This section presents the analyses comparing Jari Manis's ranging behaviours on days when he long called, to days when he did not.

Jari Manis's day length was significantly different on days when he long called compared to days when he did not long call ($z=-1.98$, $n_1=7$, $n_2=7$, $p=0.05$). The median day length on days when he did long call was longer, with a value of 606 minutes (range 404-703 minutes), compared to 491 minutes (range 342-566 minutes) on days when he did not long call.

Jari Manis's travel bout lengths were also significantly different on days when he long called compared to days when he did not long call ($z=-2.11$, $n_1=7$, $n_2=7$, $p=0.04$). The median travel bout length on days when Jari Manis did long call was shorter, with a value of 75m (range 50.45-96.11m), compared to 128.57m (range 53.57-971.43m) on days when he did not long call.

Jari Manis's daily range tended to differ on days when he did and did not long call ($z=-1.86$, $n_1=7$, $n_2=6$, $p=0.06$), but this tendency was not significant. The median daily range for days when he did long call tended to be longer, with a value 600 m (range 228.57-1057.14m), compared to 228.57 m (range 107.14-971.43m) on days when he did not long call.

The distance between Jari Manis's consecutive nests ($z=-1.35$, $n_1=7$, $n_2=7$, $p=0.18$), his directness of travel ($z=-0.32$, $n_1=6$, $n_2=6$, $p=0.75$), and his speed of travel ($z=-1.34$, $n_1=7$, $n_2=7$, $p=0.18$) did not significantly differ between days when he did and did not long call. The median distance between nests on days when he did long call was 335.71m (range 207.14-735.71m), compared to 214.29m (range 85.71-

657.14m) on days when he did not long call. The median directness of travel on days when he did long call was 0.68 (range 0.53-0.94), compared to 0.73 (range 0.53-0.93) on days when he did not long call. The median speed of travel on days when he did long call was 1.13 m/minute (range 0.38-1.69 m/minute), compared to 0.61 m/minute (range 0.22-2.07 m/minute) when he did not long call.

Home Range Estimate

During the 58 days that Roman was observed, he used a home range area of approximately 2.49km². Jari Manis used an area of approximately 0.92km² during the 21 days he was followed. This estimate of adult male orangutan home range size is limited to a small sample of observation days. The actual size of their home range could be much larger and would take much longer to estimate the full size accurately. Appendix 3 illustrates the home range area used by the three males during this study.

Chapter Five: Discussion and Conclusions

The main objective of this study was to analyse the ranging behaviours of adult male orangutans over a period of six months. Five measurements of ranging behaviours (the daily range, the distance between consecutive nests, the speed of travel, the pattern of travel, the directness of travel, and the day length) were compared in relation to ecological, social and climatic variables that may influence ranging decisions.

Summary of Results

Travel bout lengths were shorter on high fruit days. There was also a tendency for daily range to be shorter and speed on travel to be slower on high fruit days. The presence of other orangutans was associated with a tendency to show shorter daily ranges and travel bout lengths. There was also a tendency to show a slower speed of travel when other orangutans were present. High amounts of rainfall were associated with shorter distances between consecutive nests. One male in particular, Roman, had a tendency to shorten his day length on high rainfall days.

Jari Manis's long calls were significantly more frequent and more intense than Roman's. They also had a tendency to be longer. Days when Jari Manis long called, were associated with longer day lengths and shorter travel bout lengths. Jari Manis was more frequently stimulated to long call spontaneously, when other orangutans were present, or at the sound of trees falling than Roman.

Ecological Influences on Adult Male Orangutan Ranging Behaviour

The Amount of Fruit in the Male's Diet as an Influence on their Ranging Behaviours

Fruit is a resource that is spatially and temporally dispersed. Therefore, preferential frugivores must adapt their ranging decisions in relation to the distribution of fruits (Yamagiwa and Mwanza, 1994). Fruit availability does indeed influence orangutan movement decisions (Sugardjito *et al.*, 1987; van Schaik and van Hooff, 1996; Knott, 1988). Orangutans move to different areas of their home ranges depending on seasonal fluxes of fruit availability and choose trees with large fruit crop sizes (Leighton, 1993).

In this study, male orangutans had shorter travel bout lengths on days when fruit was prevalent in their diet; they also had a tendency to travel at a slower speed and to have shorter daily ranges. These results may be interpreted in two ways; male orangutans might decrease their movements when fruit was prevalent in their diet because fruit was readily available and they did not have to move far between sources, or alternatively, they increase their movements when fruit was low in their diet in order to search for fruit sources. All days of observation on Jari Manis and Bones were on the high fruit side of the median used to determine high versus low fruit days. This complicated the interpretation of the results because Roman was then responsible for all of the low fruit days and therefore it must be considered that shorter ranging behaviours on high fruit days were a characteristic of Roman's ranging behaviour.

Galdikas (1988) reported that when fruit was available in Tanjung Puting, the number of foraging bouts decrease significantly from 20.3 bouts to 8.5 bouts per

day. She attributed this to a need to visit fewer locations to obtain enough fruit per day. Galdikas's observations on foraging bouts can be considered equivalent with this study's measure of traveling bouts, as traveling primarily occurs in connection with seeking out and collecting food resources (Galdikas, 1981). It seems reasonable for males to have shorter travel bouts when they have a high amount of fruit in their diet, as they have probably been able to obtain adequate fruit resources from fewer locations.

It was not surprising that the amount of fruit in the male's diet did not influence the directness of their travel, or the distance between their consecutive nests. When fruit is dispersed in such an unpredictable way, it can be assumed that an orangutan does not increase its chances of finding a fruit source by traveling in a more direct line. With a more direct a line of travel, one would expect a larger distance between consecutive nests. Therefore, because it was not expected that directness of travel would be greater on high fruit days, it follows that distance between consecutive nests would not be significantly longer.

The effect of the amount of fruit in a male's diet on orangutan daily range is variable between sites. In this study, male orangutans tended to have shorter daily ranges on high fruit days, which has also been shown for females at the same site (Knott, 1998) and males at other sites (Rodman, 1979; MacKinnon, 1996). However, at one site, orangutans have longer daily ranges when they include a large daily intake of fruit in their diet (Galdikas, 1979; 1988). While these results may seem contradictory, they may simply reflect variation in habitats. Table 4 provides a comparison of adult male daily range at different sites. Galdikas (1988) reported that orangutans moved greater distances on days when fruit was available in Tanjung Puting National Park. Tanjung Puting is the only area of orangutan habitat without large strangler fig trees. In other

orangutan study areas, such as Cabang Panti, strangler figs are present and when in fruit, provide a large part of the fruit in the orangutan's diet. This "fig-effect" on ranging behaviour results in shorter daily movement because figs offer the largest crop size of any fruiting trees in the Southeast Asian rainforest. When a strangler fig, which is the largest fig tree, is in fruit, it can take multiple days for the fruit to be depleted by many fruit-eaters including numerous birds, primates and rodents all feeding together (MacKinnon, 1974; personal observation).

Therefore, when figs are available, daily ranges can be shorter because the orangutan essentially stays in the same place for several days to exploit the large resource. This fig-effect on male ranging behaviour was evident for one study subject, Jari Manis. He ate exclusively in a fig tree for four days straight, only leaving to nest within 200m. On these days figs made up close to 100% of the time he spent feeding. MacKinnon (1974) also observed similar behaviour in adult male orangutans. Jari Manis was even seen to re-use one of his night nests on this occasion, a behaviour I never saw others do. The fig tree was visited also by hornbills (*Buceros rhinoceros*), red leaf-eating monkeys (*Presbytis rubicunda*), gibbons (*Hylobates agilis*), crab-eating macaques (*Macaca fascicularis*) and on two days, a female orangutan, Marissa and her juvenile daughter, Misha. It has been suggested that orangutans may in fact locate fruiting figs trees from the sound of hornbills feeding (MacKinnon, 1971).

Thus, when fruit is available, I suggest that the crop size of the trees is a key element that influences the ranging decisions of male orangutans. Whether the crop size of fruit is large or small, or whether it is a time of fruit scarcity (which is essentially no crop), is a gradient that will influence the daily movements of orangutans differently.

The Effect of Large Crop Size Availability on Ranging Behaviours

When crop sizes are large, such as when figs are in fruit, the daily range will be shorter. This is due to the fact that larger crop sizes will take longer for orangutans to deplete, and therefore will allow them to remain in the same area for longer. This hypothesis presumes that orangutans will stay to exploit a fruit resource until the fruits are depleted before searching for another. Living in such an unpredictable environment, orangutans probably make the most of a resource when it is available to them. It is interesting to note that of the four sites listed in Table 4, only Tanjung Puting does not have large fig trees. This seems to be reflected in the higher mean daily range at this site than at the three others.

Table 4: A Comparison of Ranging Behaviours of Adult Male Orangutans at Different Study Sites

Field Site	Mean Daily Range (metres)	Mean Day Length (minutes)	Sample Size	Reference
Tanjung Puting	850	586	100 days, 4 males	Galdikas, 1978
Ketambe	480	n/a	n/a	Rijksen, 1978
Mentoko	500 (includes females)	688	7 days, 1 male	Rodman, 1984
Cabang Panti	653	571	69 days, 3 males	This study

As with orangutans, daily range decreases in the Taï forest chimpanzees when large crops of figs are available. Their percent of traveling time is lowest when their prime food source is figs, and they show a decrease in their travel bout length and overall daily range (Doran, 1997). These chimpanzees spend several consecutive days feeding and resting near the same fig tree (Doran, 1997).

Other solitary animals such as jaguars, mountain lions and black bears also alter their daily range to access clumped food resources. Mountain lions (*Puma concolor*) will decrease their daily range when they are exploiting clumped food resources, such as carrion (Beier *et al.*, 1995). Likewise, when prey is abundant, and they are not required to search far, jaguars (*Panthera onca*) decrease their daily range (Rabinowitz *et al.*, 1986). After the mating season is over, black bear males concentrate on eating to increase their fat storage before the winter and they hibernate again. During this transition period, black bears (*Ursus americanus*) decrease their daily range when large clumps of resources, such as juniper berries, are available (Rogers, 1987).

The Effect of Small Crop Size Availability on Ranging Behaviours

When fruit is difficult to find, or when crop sizes of available fruit are small, orangutans may have longer daily ranges to search for fruit. When large figs were not fruiting, and when as a result, the proportion of fruit in the diet was low, male orangutans in this study had longer daily ranges, possibly to search further for fruit sources. Small fruit crop sizes require males to have longer daily ranges because they can deplete the fruit, requiring them to keep moving to find more fruit sources. Orangutans in Tanjung Puting have longer daily ranges when they have a large proportion of fruit in the diet, but this is most probably

because trees in their habitat produce smaller crop sizes of fruit due to the lack of large fig trees.

In lowland gorillas (*Gorilla g. gorilla*), Tutin (1996) also observed that daily range was longer when fruit was abundant in the diet of the animals. Lowland gorillas are large group-living animals, which require a large amount of fruit to meet the nutritional requirement of each individual in the group. However, fruit patches are generally small in their lowland forest environment, which induces the members of the group to compete for access to the fruit and to have large group dispersion (Doran and McNeilage, 1998). The rapid depletion of small fruit patches also probably requires the group to increase their daily range to include more fruit in their daily diet. This increased competition for fruit resources is also reflected in a faster speed of travel on days when fruit is available. The gorillas literally race each other to the fruit sources, presumably knowing that not everyone will be able to feed (Tutin, 1996).

Similar to orangutans, black bears have a solitary, dispersed polygynous social structure. However, bears follow a strict cycle of seasons during which their ranging behaviours change. During post-hibernation, which corresponds to the mating season, males compete for access to females. During this time, male bears decrease their use of clumped resources, such as garbage dumps, which reduces aggressive conflict between adult males over access to females and leads to an increase in daily range (Roger, 1987). When fruit availability decreases, these bears increase their daily ranging behaviours and extend the peripheral edges of their home ranges in search of food (Rogers, 1987).

The Effect of Resource Scarcity on Ranging Behaviours

During times of marked fruit scarcity, frugivores generally decrease their daily range and rely on a diet of low quality, highly abundant foods, such as leaves and bark. These foods have been referred to as "fallback foods" (Wrangham, 1980; Tutin, 1996; Wrangham *et al.*, 1996).

When fruit is decidedly scarce, orangutans conserve their energy by decreasing their daily range, and broaden their diet to incorporate more readily available foods such as leaves and bark (MacKinnon, 1996; Knott, 1998). This strategy was not seen in this study, possibly because data was not collected during a time of marked fruit scarcity. Indeed, fruit was never totally unavailable and high fruit days were interspersed with low fruit days. Therefore, this study was not able to observe orangutans decreasing their range and broadening their diet.

While consumption of bark did not seem to influence the ranging behaviours of male orangutans in this study, it is still an interesting element of a male's diet to try to understand. Orangutans may use bark as a fallback food in a similar way that lowland gorillas, chimpanzees and bonobos use terrestrial herbaceous vegetation in times when fruit availability is low. In fact, when fruit availability was low, lowland gorillas have also been observed to increase their consumption of bark (Tutin, 1996; Doran and McNeilage, 1998).

Galdikas (1979) observed that when orangutans were exploiting permanent resources (leaves and bark), they usually traveled shorter distances per day. This paralleled her finding that when fruit was abundant in the diet, daily range was increased at that site. However, in Gunung Palung, when fruit was high in the diet, daily range was shorter, therefore it was difficult for me to expect a further

shortening to be visible when the orangutans were eating high levels of bark. Essentially, eating high levels of bark may have been mimicking the effect of a high fruit diet on daily range because they were both foods are time consuming to exploit. When orangutans eat bark they usually dedicate long periods of time to its extraction and processing. It was this dedication of time to one resource that promoted the consideration of bark as an influence on male orangutan ranging.

While the amount of bark consumed by a frugivore is not generally tested as a potential influence on ranging behaviour, bark is considered to be an important food source, to which Rodman (1988) believes orangutans have an intriguing dependence. During his observations at Mentoko, Rodman (1988) estimated that bark constituted 37.5% of the orangutans diet, whereas it was only 24.5% of the diet for orangutans in Tanjung Puting (Galdikas, 1988). In this study, bark is represented a weighted mean of 19.8% of the male orangutan's diet. Despite this variation between sites, bark remains an important part of the diet of orangutans and its effect on ranging ought to be investigated more closely.

Chimpanzees in the Taï Forest (Doran, 1997) and gorillas in the Lopé Reserve (Tutin, 1996) have developed social and dietary adjustments for times of fruit scarcity. Travel time is decreased and their diet is broadened to include higher amounts of lower quality, more fibrous foods such as leaves and nuts (Doran, 1997). These apes also decrease the size of their feeding party and become much more solitary, presumably to decrease intra-group competition (Tutin, 1996; Doran, 1997). In the Taï Forest, the chimpanzees decrease their party size from a mean of 3.45 individuals to 1.80 individuals when fruit is scarce (Boesch, 1991; Doran, 1997). This decrease in party size is only seen when there are no estrus

females available in the community, as the presence of estrus females significantly increases party size (Doran, 1997).

Fruit is the most important dietary component for bonobos, and when it is scarce, they resort to terrestrial herbaceous vegetation as an alternative resource (Malenky and Stiles, 1991). Bonobos have comparatively low intra-group competition for prime food resources, because they have abundant terrestrial herbaceous vegetation resources to use as fallback food (Wrangham, 1986; White, 1989; Malenky and Stiles, 1991; Doran, 1997), and presumably because food availability is not influenced by sympatry with another ape (Wrangham, 1986). This allows bonobos to have larger, more stable party size compared to chimpanzees. An increase in prime food (THV or fruit) patch size correlates with an increase in party size in both bonobos and chimpanzees (Wrangham, 1986; White, 1989).

Climatic Factors as Influences on Male Orangutan Ranging Behaviours

Rainfall Patterns

Despite the fact they live in wet habitats where rain occurs frequently, heavy rainfall may still influence the movements of rainforest animals in general. Rainfall patterns could affect ranging behaviours in direct or indirect ways. Directly, high rainfall would probably make movements more precarious on slippery branches and lead to a decrease in forest temperature and visibility.

Indirectly, rainfall patterns will influence vegetation growth, which may influence the ranging behaviours of rainforest animals.

In this study, high rainfall days were associated with a shorter distance between night nests. There was also a tendency for Roman's day length to be shorter on high rainfall days. Other studies have stated that heavy rain makes orangutans stay in their nest longer in the morning, and that they make their night nests earlier in the afternoon (MacKinnon, 1971; 1974). In this study, Roman would regularly stay in his nest until after 9am when it was raining, and on one day of heavy rain he made his night nest at noon.

If heavy rainfall was directly influencing males to decrease their activity time, it could also be expected that their daily range and the distance between their nests would decrease as they travel less and rest more during periods of heavy rain (MacKinnon, 1971). However, the daily range of the males in this study was not influenced by rainfall patterns. They did significantly shorten the distances between their night nests on high rainfall days, possibly indicating they were using an area in a concentrated fashion on rainy days even though they still traveled as far. To support this argument, I would have expected the directness of travel to be lower on days of high rainfall, demonstrating a more meandering style of movement. However, the data did not show a difference in directness of travel between high and low rainfall days.

The absence of significant differences in ranging behaviours on high versus low rainfall days may be explained by the method of collecting rainfall data. Rainfall data was not specifically collected while observing the male orangutans. Instead, rainfall data was collected for the study site in general, resulting in an amount of rainfall for a 24-hour period. This led to two problems with the rainfall data.

First, the rainfall data did not indicate if the rain fell in a heavy downpour over a short period of time, or if it fell lightly throughout the 24-hour period. Second, the rainfall data did not discriminate between times when the orangutans were out of their nests and potentially moving, from times when they were asleep. Isbell (1983) also collected pooled rainfall data and found no significant correlation between rainfall patterns and ranging behaviour of red colobus in the Kibale Forest.

This study did not test the indirect influence of rainfall patterns, however. The amount of rainfall could be influencing the abundance of food resources available to orangutans, which was seen to influence their ranging behaviours (Rodman, 1973, this study).

Vedder (1984) analysed the influence of rainfall patterns (as an indication of food availability) on the ranging behaviours of mountain gorillas. She determined the abundance of terrestrial herbaceous vegetation available for the gorillas to eat depending on the mean monthly rainfall. In months with high rainfall, she found that the gorillas decreased their range size and their travel rate. She attributes this to an increase in terrestrial herbaceous vegetation. Despite the fact that heavy rainfall has been seen to halt movements in mountain gorillas (Goodall, 1977), Vedder does not agree that it could be the rainfall itself that slowed their movement, as she found no correlation between daily rainfall patterns and changes in movements. Rainfall patterns may be useful to determine the availability of terrestrial herbaceous vegetation, however, fruit generation is more time consuming than for foliage and therefore, its availability may be difficult to determine using rainfall patterns alone.

Social Factors Influencing Ranging Behaviours

The Presence of Other Orangutans

Adult male orangutans are considered highly solitary. In fact, they are alone from 62% (Rijksen, 1975) to 91% (Galdikas 1985a) of the time. This range may be explained as variation between sites in food distribution and population density and by the fig-effect on ranging behaviours. Rijksen's observations on orangutans in Northern Sumatra were done at a site where large fig trees are present. Galdikas's observations were done in Tanjung Puting where fig trees are comparatively absent. With large accumulations of fruit available, orangutans are able to feed together without increasing feeding competition (van Schaik, 1996).

Wrangham *et al.* (1993) define a "constraint-free day-range" as the day range of a solitary individual without the influence of competition from conspecifics. Essentially, the addition of another orangutan in the vicinity of the focal male constitutes an increase in group size and therefore an increase in daily range would be expected. Two animals competing for similar resources would have to move farther to obtain adequate food than if they ranged alone. However, the results of this study suggest that male orangutans had shorter daily ranges and travel bout lengths when other orangutans were present. In Tanjung Puting, Galdikas (1988) also observed that daily range decreased when orangutans contacted, even briefly, other orangutans. Mean daily range for adult males in Tanjung Puting was 852m when they were alone, compared to 838m when in contact with other orangutans (Galdikas, 1988), although it is not known if this difference is statistically significant.

Male orangutans would be expected to react in different ways depending on the sex of the other orangutan present. Adult males are intolerant of each other so the presence of another adult male would probably elicit one of two responses depending on the dominance rank of the males involved; males should either avoid each other or attack each other (Rijksen, 1975; Galdikas, 1985b; Mitani, 1985a). A subordinate male may choose to flee (MacKinnon, 1971). A dominant male might stand his ground, or possibly chase the approaching male (MacKinnon, 1973). When the male is in association with an adult female, he would probably be more aggressive towards intruding males, as the receptivity of the adult female has been associated with increased levels of male-male association (Rijksen, 1975; Mitani, 1985a).

Galdikas (1988) observed that adult male orangutans had their shortest daily ranges when they were maintaining proximity with adult female orangutans. The males that were interested in mating with females would probably try to maintain exclusive access by following them. Females forage at more food sites and for less time at each site than males. Therefore, a male following a female would have to decrease his foraging bout length and increase his travel bout length which would result in him expending more energy, and replenishing less energy, than usual (van Schaik and van Hooff, 1996). However, the extent of these constraints on males would depend on the spatial distribution of females. If females lived in relatively small home ranges they would probably have access to fairly reliable food resources. If these food resources also had large crop sizes, the male would not have to compromise his energy expenditure as much as he would if females had large home ranges resulting from highly dispersed and small food sources. In Tanjung Puting, male orangutans in association with females also tended to increase their day lengths (Galdikas, 1978; 1988). Adult

females have a longer day length than males which may account for this increase (Horr, 1977).

During this study, a focal male was not observed with another male orangutan or in consortship with an adult female. Sometimes the focal male was seen feeding in the same tree as a female orangutan, but that never constituted a consortship, because there was no copulation, and no proceptive behaviour from the female. They simply happened to feed together in the same tree. The orangutans in proximity were Marissa, an adult female, and Misha, her juvenile offspring. Marissa was in proximity with Jari Manis frequently over the past few years and mated with him five times in January 1998 (Knott, pers. comm.). When Marissa and Misha entered the fig tree, Jari Manis showed no obvious response. It was a very large tree and Marissa maintained a distance of approximately 20 meters from Jari Manis. After approximately 15 minutes of Marissa and Misha being in the fig tree with him, Jari Manis charged Misha and she fled from the tree. Marissa continued to eat the figs. Marissa and Misha ate for periods of time less than one hour for 2 alternate days while in the same tree as Jari Manis. When they left the area to continue traveling, Jari Manis remained in the area of the fig tree for another day. Male orangutans may have some understanding of the receptivity of an adult female based on the size of their offspring. At this time, Misha was not yet fully-grown, at about 75% the size of her mother. It is difficult to know if Jari Manis did not inspect Marissa physically because he somehow knew she was pregnant (she gave birth 3 months later on October 30, 1998 (Knott, pers. comm.)), or because he knew he had mated with her recently. This does not mean that the presence of females could not have affected male ranging behaviours. Males may still need to monitor the reproductive status of females and try to exclude other males from monitoring these females.

I also need to specify that the presence of another orangutan did not necessarily mean that they were together for a long time. It simply means that at some point in the day, the focal male was within visual or audible contact of another orangutan. In further work, a more precise measure could be used that could distinguish between time spent with another orangutan, from the presence within visual or audible contact of another orangutan at some point during the day, as an influence on ranging behaviour.

The Presence of Other Orangutans on High Fruit Days

It was interesting that the results showed the similarities of ranging behaviours when other orangutans were present and when fruit was abundant. This may be because on 25 of the 43 (58%) days when fruit was considered high, there were also other orangutans present. This may explain the fact that no conflicts were seen between Roman and Jari Manis, even though they were ranging in the same area for 10 days. The presence of a high amount of fruit may have decreased the competition for fruit, allowing males to range more closely than usual (van Schaik, 1996). The presence of an estrus female would have probably increased the tension between the males and they might not have been seen to range so closely.

Long Call Comparison between Roman and Jari Manis

Long calls are generally considered to be spacing mechanisms between adult male orangutans (Mitani, 1985a). Males vocally defend the area around them from rival males (MacKinnon, 1971), an area that presumably encompasses both food and mate resources. Long calls and ranging behaviours are associated to help a male defend a core (Galdikas, 1979). Long calls allow for “purposeful avoidance” by males, rather than leaving it to chance (Horr, 1975), which reduces the number of physical contacts between males.

In this study, long call behaviour varied greatly between Roman and Jari Manis. Based on the observations of previous researchers that long calls were most frequently given by the dominant male, Jari Manis was probably dominant over Roman. This was supported by the physical characteristics of Jari Manis, who was larger than Roman.

Males were consistently observed to long call after certain stimuli such as tree fall, branches breaking, other long calls, or presence of the observers. However, many long calls have been considered spontaneous, i.e. there was not obvious direct stimulus to the observer. It has been suggested that these spontaneous long calls are given by the dominant males and they use them to announce their location to other males in the forest and possibly to announce their arrival in an area (Mitani, 1985b; van't Land, 1990). Jari Manis more readily long called spontaneously, as if to announce his presence. This also supported the idea that he was dominant. Roman only long called rarely and briefly, as if to conceal his location, or at least not announce it.

Table 5 summarizes the frequencies of long calls by adult males heard at other sites. The differences in long call frequencies between sites may be due to sampling and/or regional differences, or to differences in male dominance. Differences in long call frequency may also be due to differences in population density, as higher densities increase the frequency of long calls (MacKinnon, 1971).

Table 5: Long Call Frequencies from Other Study Sites

Study Site	Mean Number of Long calls	Length of Study	Reference
Northern Borneo	1/day	26 months	Horr, 1975
Kutai	2/month	12 months	Rodman, 1973
Tanjung Puting	1.5/day 3.6*/day	48 months	Galdikas, 1981; 1983
Ulu Segama	0.2-0.7/day	17 months	MacKinnon, 1974
Cabang Panti	0.04-2.21*/day	89 days	This study

* Indicates the home range of a known resident male

The Association between Long Calling and the Ranging Behaviours of Jari Manis

In one of the few studies on long calling in male orangutans, males traveled in the direction in which they long called and moved in a more direct fashion on days when they long called frequently (van't Land, 1990). Unlike van't Land, in this study, the directness in which Jari Manis traveled on days when he long called was not significantly straighter than on days when he did not. He had significantly longer day lengths on days when he did long call and his travel bout length was significantly shorter. By moving short distances within an area, long calling frequently, and having an increased day length, Jari Manis may have been attempting to announce or reaffirm his presence in the area. Jari Manis did not long call while moving. When long calling spontaneously, he sat on a high, open branch and long called above the forest canopy.

Home Range Size

Based on the limited time of data collection, it must be reiterated that these estimates only represent a limited home range size. Focal males used these areas for approximately two months and are known to leave this area every year for long periods. Most estimates of adult male orangutan home range size (Table 6) should also be considered limited due to the small study sites, and relatively short study lengths. Roman's home range estimate of 2.49km^2 was similar to early estimates done at Kutai and Ketambe where the length of the study was longer, but the size of the study area was smaller.

Table 6: Home Range Estimates for Adult Male Orangutans

Study Site	Size of Study Site	Home Range Estimate	Length of Study	Reference
Ulu Segama	varied	>5km ²	17 months	MacKinnon, 1971
Sabah		*5.1km ²	2 years	Horr,1975
Kutai	3km ²	*1.2km ²	15 months	Rodman, 1973
Tanjung Puting	35km ²	*5-6km ² >35km ²	4 years	Galdikas, 1978
Ketambe		*2km ²		Rijksen, 1978
Cabang Panti	15km ²	*0.92km ² (JM) *2.49 km ² (RM)	21 days 58 days	This study

Limitations of This Study

One of the most crucial elements missing from this research was information on actual fruit availability. As it is now, fruit availability is inferred from the amount of fruit orangutans accessed. If fruit availability data had been collected, this study would have been able to determined if in fact orangutans were exploiting fruit as their prime resource when it was available, and if they move to areas of higher fruit availability. Other studies have collected food availability

information and were able to determine the distribution, abundance and seasonality of fruit in relation to ranging behaviours (*Presbytis melalophos*: Bennett, 1986; *Gorilla gorilla berengei*: Watts, 1991; *Presbytis entellus*: Newton, 1992; *Presbytis entellus*: Koenig *et al.*, 1998). Also, Isbell (1998) proposed a new technique for measuring habitat quality by looking at species-specific preference. She looked at the distance between feeding bouts, and the length of feeding bouts to estimate the quality of food in the habitat. This new technique presents an interesting way to collect ranging data and food availability data at the same time.

There were other information about adult male orangutan ranging behaviours that would have been interesting to investigate more fully. Satellite camps at the edges of the study site would have potentially allowed transient males to be followed. More accurate rainfall data would have been more useful in analysing male ranging behaviours, i.e. data collected per hour, or per bout of rain as opposed to lumping 24 hours of rain collection.

It is difficult to make comparisons between orangutan ranging behaviours and those of other solitary mammals. This is mainly due to different data collection techniques. Many large mammals are tracked using radio collars. This technique provides home range size data and sometimes day range data, but there is still little known about what factors influence the animal's ranging decisions. Radio collars are not used to track movements of orangutans due to the difficulty of sedating such a large, arboreal ape and the large throat pouches on male orangutans would make it difficult to fit a collar on without possible injury to the animal. Traditional methods for following orangutan movements are time and energy consuming but they provide a higher level of understanding of orangutan ranging behaviour.

This study showed some interesting trends in adult male orangutan ranging behaviours under different influences, but it represents a “snapshot” of male orangutan ranging behaviour. The tropical rainforest is a complex environment with many fluctuating variables. The results of this study must be taken within the context they were extracted from. Caution must be used when comparing them to orangutans in different areas and at different times of the year. Now that orangutans really only exist in National Parks, each pocket of habitat has different elements and pressures imposed on it. The absence or presence of large fig trees seemed to be an obvious difference between Tanjung Puting and other orangutan study sites that may be influencing the ranging behaviour of adult male orangutans.

Conclusions

1. In this study, the amount of fruit in the diet of male orangutans may influence their ranging behaviours. A high level of fruit in the diet was associated with a shorter daily range, and travel bout lengths as well as slower speed of travel for male orangutans in this study.
2. The influence of high amounts of fruit in the diet on ranging behaviours may be a result of the fig-effect on ranging. Large crop sizes on fig trees may hold a male in an area, even for multiple days, before he has depleted the fruit.

3. The amount of bark in the diet of male orangutans did not influence their ranging behaviours. This is probably due to the reliability of bark resources acting as a fallback food in a similar way THV resources act for gorillas, chimpanzees and bonobos.
4. The presence of other orangutans was associated with a shorter daily range and travel bout length. However, many days when other orangutans were present were also high fruit days. Therefore, it is difficult to determine which factor influenced males to decrease their ranging behaviours.
5. Rainfall patterns had little effect on male orangutan ranging behaviours. However, the distance between consecutive nests and Roman's day length were shorter on high rainfall days.
6. Jari Manis long called significantly more frequently and more intensely than Roman. He also showed a tendency to long call for a longer duration than Roman. Jari Manis also long called more spontaneously, than Roman, suggesting Jari Manis was the more dominant male in the area.
7. Jari Manis showed longer day lengths and shorter travel bout lengths on days when he long called which suggests an association between long calling and at least some measures of ranging behaviour.

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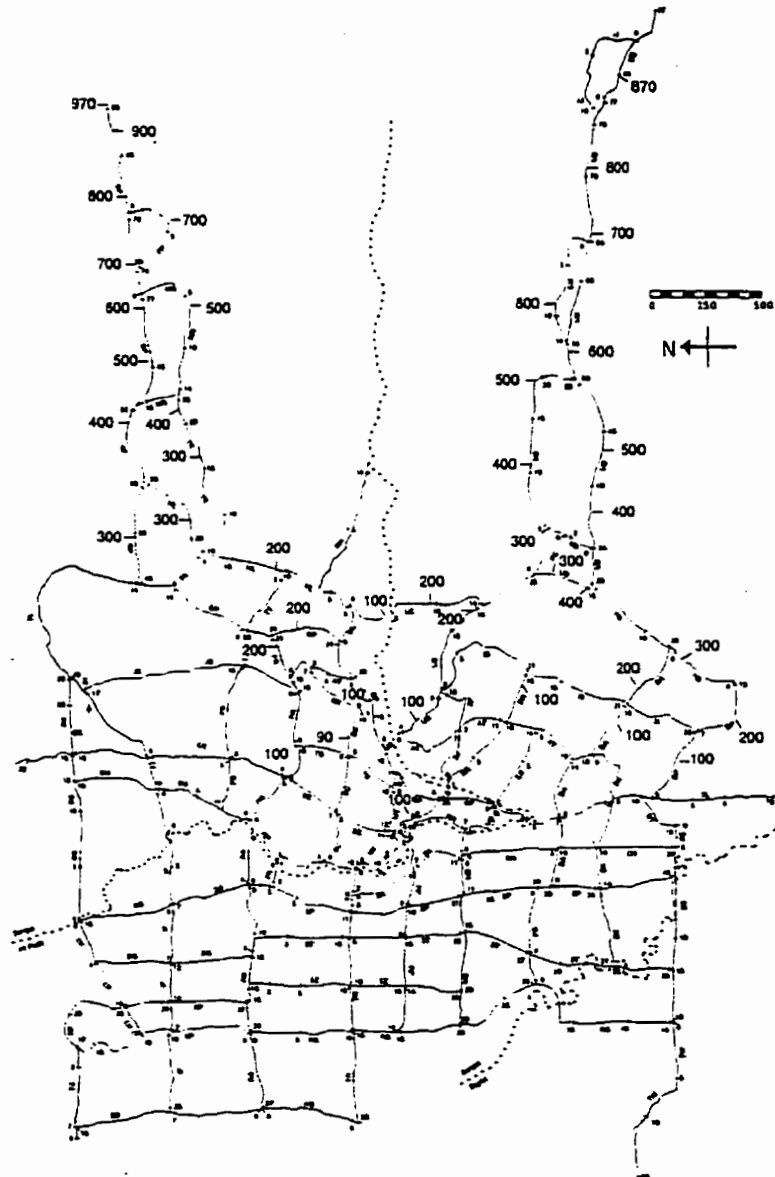
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Appendix 1: Data Collection Sheet

Categories	Description
Time	Scan samples, recorded every five minutes unless activity changed
Location	Of focal animal from nearest trail
Direction of travel	Of focal animal
Distance of travel	Each travel bout in metres
Activity 1	Travel, rest, eat, sleep
Activity 2	Long Call, watch observer, urinate, defecate
Body Position	Sitting, standing, hanging, lying
Position in Tree	Trunk, branch, crotch, ground
Height in Tree	Metres
Comments	Rainfall information, long calls from other orangutans...
Foraging	Fruit, bark, leaves...
Food Tree	Height, Diameter at Breast Height
Fruit Crop Size	<50, 50-250, 250-500, 500-1000, >1000

Appendix 2: The Cabang Panti Study Site Trail System



- Solid lines Represent trails.
- 40 Small numbers represent each 20m along the trail (numbers starting from the beginning of the trail).
- Dotted lines represent rivers.
- 300 Large numbers represent elevation.

