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# RANGING BEHAVIOUR AND SEASONAL MOVEMENTS OF SUMATRAN ORANGUTANS (*Pongo pygmaeus abelii*) IN SWAMP FORESTS

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Submitted for the degree of
DOCTOR OF PHILOSOPHY

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Dedicated to
MAM and DAD

# ABSTRACT

The ranging behaviour of Sumatran orangutans was studied in a swamp forest within the Leuser Ecosystem, Sumatra, Indonesia. The use of line transect techniques for estimating orangutan densities from nests was also examined. The densities obtained, in conjunction with raw numbers of new nests along transects were then compared with estimates of forest productivity in an attempt to identify how orangutan movements are influenced by resource availability.

Using nests as an indicator of orangutan numbers produced serious underestimates of absolute densities for a variety of reasons. These were considered to stem mostly from the use of decay rates estimated from total time to nest disappearance, whilst under-detecting older nests in censuses, and from the difficulties of detecting nests on or above transects and accurately estimating distances. The number of new nests along a transect was still considered a reliable indicator of fluctuations in absolute densities.

Orangutan home ranges at Suaq Balimbing were found to be distinctly larger than previously reported elsewhere. Females appear to utilise core areas of at least 500 ha, whilst also using a peripheral excursion zone so that total home ranges probably lie between 900 ha and 1500 ha. Adult male and subadult male ranges were considered to be in excess of 3000 ha and perhaps as much as 10000 ha. There was no evidence that adult females or adult males need necessarily be transient or nomadic as previously proposed. Subadult males, however, may constitute a dispersal phase.

Orangutan movements were related to fruit availability, in that they will move to areas where fruit is abundant, but also into other areas when fruit is generally scarce. Thus there was evidence that orangutans shift diets during lean periods rather than travelling large distances. There was no evidence to support the occurrence of large-scale seasonal movements of orangutans.

There was evidence to suggest that dominant adult males behave differently to other, non-dominant males, in that they occupy smaller ranges, probably as a result of being able to restrict access by other males to receptive females. Non-dominant adult males tended to avoid the dominant male, whereas subadult males did not.

Evidence was also found to support the existence of clusters of females with similar ranges, who may be related, preferentially associate with each other, and are to some degree synchronised reproductively.

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# TABLE OF CONTENTS

# LIST OF TABLES

**Table** **Page**

# LIST OF FIGURES

# CHAPTER 1

# INTRODUCTION

## 1.1. TAXONOMY

Orangutans (*Pongo pygmaeus*) are members of the great apes (Family Pongidae) which includes the gorilla (*Gorilla gorilla*), chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*). All great apes have larger bodies and larger brains than other primates, and are to some extent sexually dimorphic (Rowe 1996). The last common ancestor of all living Pongidae and Hominidae was probably the genus *Kenyapithecus*, which lived around 15 million years ago in the middle of the Miocene of eastern Africa (Nowak 1999).

Traditionally, two subspecies have been recognised; namely *Pongo pygmaeus pygmaeus* (Linnaeus 1760) in Borneo, and *Pongo pygmaeus abelii* (Lesson 1827) in Sumatra, which has been geographically isolated for at least 10,000 years, and possibly much longer (Rijksen and Meijaard 1999). However, there is currently considerable support for reclassifying the two subspecies as distinct species, with three additional subspecies within the Bornean population (e.g. Courtenay *et al.* 1988; Groves et al. 1992; Ryder and Chemnick 1993; Nowak 1999; Rijksen and Meijaard 1999; but see Muir *et al.* 1995, for an opposing view).

In appearance, no single clearcut physical characteristic distinguishes the two subspecies and they readily hybridise in captivity, producing fertile offspring (Mallinson 1978; Muir *et al.* 1995). Some subtle differences do exist, however, with respect to body and facial hair (i.e. colour, length and morphology), and facial shape, including the shape of the adult male's cheek flanges (MacKinnon 1975; Courtenay *et al.* 1988). Sumatran orangutans tend to have longer, more oval faces, with males possessing more 'diamond-shaped' flanges, and paler, more pointed beards. Bornean orangutans tend to have less facial hair, and body hair tends to be darker in colour. Viewed under a microscope Bornean hairs are flattish with a thick column of black pigment down the centre, whereas Sumatran hair is thinner and rounder, and has a finer, often broken column of black pigment down the centre (MacKinnon 1975).

## 1.2. DISTRIBUTION

During the Pleistocene, the orangutan occurred throughout Southeast Asia, from Java in the south, to the Tropic of Cancer in southern China (von Koenigswald 1982; Rijksen and Meijaard 1999). It currently survives only in dwindling areas on the islands of Borneo and Sumatra, and hence primarily within Indonesia, but also in the Malaysian states of Sabah and Sarawak. No reliable records exist for orangutans in Brunei Darussalam (Rijksen and Meijaard 1999).

Throughout their present distribution orangutans occur in rainforest habitats ranging from sea level swamp forests to mountain slopes (Rodman and Mitani 1987; Knott 1999). Few orangutans are found at high altitude. In Sumatra orangutan densities above 1200 m tend to be less than 10% of those in the lowlands (Djojosudharmo and van Schaik 1992), whilst in Borneo sightings are rare above 500 m (Rijksen and Meijaard 1999).

The dramatic historical decline in the orangutan's distribution can realistically only be ascribed to two causes: climate change and hunting by humans, of which the latter is probably the major factor (van Schaik *et al.* in review). Even their present distribution on the two islands tends to coincide with areas in which the indigenous people do not hunt orangutans for religious reasons (MacKinnon 1992).

## 1.3. CONSERVATION AND RESEARCH

### 1.3.1. CONSERVATION STATUS

On paper the orangutan has been the most strictly protected species in Indonesia since 1924 (with a brief reduction in protected status in 1996/1997), and has been protected in Sarawak and Sabah since 1957 and 1965 respectively (Rijksen and Meijaard 1999). Their protected status resulted in some decades of only steady decline in orangutan populations on both islands, which led to their current classification as vulnerable (rather than endangered) in the IUCN/SSC Red Data List (Baillie and Groombridge 1996). To prevent any international commercial trade in orangutans they have also been listed on Appendix 1 of the Convention on International Trade in Endangered Species (CITES) for many years. Despite these listings, however, they are again coming under increasing threat from habitat destruction, through both legal and illegal logging and fires, and illegal hunting (more for the commercial pet trade than as a food resource; Rijksen and Meijaard 1999; van Schaik *et al.* in review; EIA/Telepak 1999). A Population and Habitat Viability Analysis (PHVA) in Medan, Sumatra, in 1993 concluded that there were between 10,282 and 15,546 orangutans in Borneo at that time (Rijksen *et al.* 1995) and around 9,200 in Sumatra (van Schaik *et al.* 1995a). More recent estimates, however, suggest that the populations of both islands are currently each declining at a rate in excess of 1000 individuals per year and that as much as 46% of the Sumatran population has probably been lost since 1993 (van Schaik *et al.* in review; J. R. MacKinnon pers. comm.). As a consequence their long-term survival in the wild is in immediate jeopardy.

### 1.3.2. REHABILITATION PROJECTS

An indirect result of the loss of suitable habitat is the capture of infants, which are then either kept locally as pets or enter international trade. In an attempt to combat this problem a number of rehabilitation projects have been established over the years to provide havens to which confiscated orangutans could be taken.

The first was established in 1961 in Sarawak's Bako National Park, Malaysia, by Barabara Harrison and the Sarawak Museum (Lardeux-Gilloux 1995), but was terminated in 1964, and the animals transferred to a newly established station at the 43 km$^2$ Sepilok Forest Reserve in Sabah, Malaysia (Rijksen 1978; Rijksen and Meijaard 1999). In 1971 the first Indonesian rehabilitation station was established by the Indonesian Nature Conservation Service (then known as PPA) at Ketambe in Aceh, Sumatra, which also eventually ceased operations, in 1979 (Lardeux-Gilloux 1995). It was soon followed by a second Indonesian centre in the then Tanjung Puting wildlife reserve in Borneo (Galdikas-Brindamour 1975; Rijksen 1978) and in 1973 by a second Sumatran project, at Bohorok, on the eastern side of the Gunung Leuser National Park (Aveling and Mitchell 1982). In 1977 another small Malaysian station was founded in a 6.4 km$^2$ forest plot at Semengok in Sarawak (Lardeux-Gilloux 1995; Rijksen and Meijaard 1999) and finally, in 1992 the most recent project was established at Wanariset Samboja in East Kalimantan (Rijksen and Meijaard 1999; Smits *et al.* 1995; Yeager 1997).

During the late 1960's and early 1970's it was believed that whenever possible all confiscated apes should be used to replenish a steadily declining meta-population in the wild (Rijksen and Meijaard 1999). And indeed to date, only the Semengok and the now defunct Bako National Park projects in Sarawak, and the most recently established Wanariset Samboja project in East Kalimantan are, or were, in forest areas with no existing wild population (Rijksen 1978; Smits *et al.* 1995). All others do (or did) release ex-captive orangutans into existing wild populations (Galdikas-Brindamour 1975; Aveling and Mitchell 1982; Lardeux-Gilloux 1995; Smits *et al.* 1995; Rijksen and Meijaard 1999).

### 1.3.3. PREVIOUS STUDIES

Incidental observations of wild orangutans were made by a number of early travellers and naturalists (see Röhrer-Ertl 1988 for review), but the first real attempts at fieldwork were by Schaller, who spent two months in Sarawak in 1961, and Davenport, who spent six months in Sabah prior to 1967 (Rijksen 1978). In 1967 Horr began a three year study in the Lokan area of Sabah (Horr 1975), and in 1968 MacKinnon began a 16 month study in the Ulu Segama area, also in Sabah (MacKinnon 1974). Between 1969 and 1971 Rodman observed orangutans for approximately 14 months, dividing his time between Horr's Lokan site, and the Mentoko (Kutai) area of East Kalimantan (Rodman 1973a). The Mentoko site has since been used occasionally by other researchers despite being severely burnt in 1982, e.g. Mitani between 1981 and 1983, and Suzuki, for several periods between 1982 and 1989 (MacKinnon 1989; Mitani 1989; Suzuki 1990). In 1971 Galdikas commenced her work at Tanjung Puting in Central Kalimantan, which still continues today (Galdikas 1979; Galdikas-Brindamour 1975). At present, at least three additional major orangutan research sites exist in Borneo. One is the Cabang Panti Research Site in the Gunung Palung National Park, West Kalimantan (Knott 1998), another lies in the Sebangau catchment area in Central Kalimantan (Husson *et al.* 1999, unpubl.), and a third in the Kinabatangan catchment area in Sabah (Lackman-Acrenaz and Acrenaz 2000, unpubl.). A further location, at Danum Valley in Sabah, has also been used for orangutan research in recent years (Ghaffar unpubl.). All except the Kinabatangan and Danum Valley sites in Sabah lie within Indonesia.

Research on Sumatran orangutans began when MacKinnon undertook a 7 month study in the Ranun area of the then Gunung Leuser reserve in 1971, and later the same year Rijksen established the Ketambe station, also in the Gunung Leuser reserve, and began a field study lasting 3 years (MacKinnon 1974; Rijksen 1978). The study area at Ketambe has been used intermittently by several researchers studying orangutans, most notably Schurman (1975-1979), Sugardjito (1979-1983) and Utami (1993-1996; Rijksen and

Meijaard 1999). The only additional site for research on Sumatran orangutans is at Suaq Balimbing Research Station in Aceh, Sumatra, where the present study was conducted (see Chapter 2).

## 1.4. BASIC NATURAL HISTORY

### 1.4.1. PHYSICAL CHARACTERISTICS AND LIFE HISTORY VARIABLES

Adult head and body length tends to range from around 1.25 to 1.50 metres (Nowak 1999) and wild adult body weights have been estimated at 30-50 kg for females, and 50-90 kg for adult males (Markham and Groves 1990). Considerably heavier individuals have been recorded in captivity (MacKinnon 1989). The maximum ages of males and females known from captivity were 58 and 57 years, respectively (Perkins 1999), but a more conservative estimate of maximum longevity for both sexes in the wild of *circa* 45 years is generally accepted (Leighton *et al.* 1995). Orangutans possess the longest inter-birth interval of any land-based mammal at around 8 years (Leighton *et al.* 1995), and mature male orangutans exhibit pronounced bimaturism that divides them into fully adult males and subadult males (Kingsley 1982; Maggioncalda *et al.* 1999; Utami 2000a). Fully adult males possess striking secondary sexual characteristics (SSCs) such as large size, fatty cheek flanges and a muscular throat pouch, whilst subadult males lack all of these characters (Horr 1975; Mitani 1985a; Rodman and Mitani 1987; Winkler 1989; van Hooff 1995). Subadult males are sexually mature, however, and can sire offspring (van Hooff 1995, Maggioncalda *et al.* 1999; Utami 2000a). Furthermore, males may retain the subadult form for many years (te Boekhorst *et al.* 1990; van Hooff 1995), and there is long-standing speculation that the presence of fully adult males in the same area is responsible for this through some form of suppression (Kingsley 1982; van Schaik and van Hooff 1996).

Fully adult males also emit loud vocalisations known as long calls that can carry for some distance (Mitani 1985a). The long call has a ‘bubbly’ introduction which builds up slowly into a climax of full roars, then tails off gradually into a series of sighs (MacKinnon 1974). Some differences have been noted between the long calls of Bornean males and Sumatran males, Bornean calls tending to be longer and with more ‘call units’ and longer intervals between ‘units’ than Sumatran calls (MacKinnon 1974). The purpose of the long call remains uncertain but it has been speculated that it serves as a spacing mechanism for adult males (MacKinnon 1974; Mitani 1985a), and possibly also as a means for females to locate potential mates (Rodman 1973a; Rijksen 1978; Galdikas 1983).

### 1.4.2. LOCOMOTION

Orangutans are primarily arboreal and diurnal (Rowe 1996; Nowak 1999), and are thus the largest extant arboreal animal (Cant 1987; Knott 1999). Locomotion through the canopy is usually by quadrumanous clambering (using all four hands and feet to grasp and pull themselves along), often also using their momentum to bridge gaps by swaying small trees, and occasional brachiation (Sugardjito 1982; Knott 1999). Wild orangutans rarely descend to the ground, although adult males do so more often than females (MacKinnon 1974; Galdikas 1978; Rodman and Mitani 1987), and Bornean orangutans appear to more frequently than Sumatran. For example, Galdikas (1978) found that adult males at Tanjung Puting spent a daily mean of 66 mins travelling on the ground, with a range from 19 mins to 2 hours, whilst Sugardjito (1982) observed ground walking only once in 136 hours of observing wild Sumatran adult males.

### 1.4.3. DIET

Orangutans are predominantly frugivorous with the proportion of the diet comprising fruit fluctuating around 60% for most studies (e.g. MacKinnon 1974: 62%; Rijksen 1978: 58%; Rodman 1973: 61%; Galdikas 1978: 62%), though this proportion can vary considerably on a daily basis, up to 100% (Knott 1999). A wide variety of fruit species is eaten, e.g. around 200 at Ketambe (Rijksen and Meijaard 1999), though orangutans have a clear preference for fruits with soft pulp, arils or seed-walls around the seed, including drupes and berries (Djojosudharmo and van Schaik 1992; Leighton 1993). When and where available the fruit of large fig trees appears to comprise the staple food of orangutans (Rijksen and Meijaard 1993), although Leighton (1993), demonstrated a relatively low preference for figs by establishing that they were eaten only when fruit pulp and seeds were rare. In addition, the large strangling figs often utilised by orangutans in much of their range tend to be scarce in lowland swamp forests (pers. obs.; Galdikas 1988) and are consequently replaced by other fruit species as staple food resources in such habitats.

Other major food sources include leaves, plant and liana stems, the inner cambium layer of bark, roots and insects (Knott 1999), though it appears that at Ketambe and Suaq

Balimbing Sumatran orangutans feed considerably more on insects, and at Ketambe, Suaq Balimbing and Ranun, distinctly less on cambium, than Bornean orangutans (van Schaik *et al.* 1999). Occasionally wild orangutans have been seen to catch and eat slow lorises, *Nycticebus coucang* (Utami 1997; van Schaik unpubl.), a gibbon, *Hylobates lar* (Sugardjito and Nurhada 1981), a squirrel (B.M.F. Galdikas pers. comm.) and a rat (Knott 1998a), yet unlike the chimpanzee there are so far no indications that the orangutan is an active hunter (Rijksen and Meijaard 1999).

### 1.4.4. PREDATION

Due to their large size and arboreal nature orangutans have few natural predators. Only clouded leopards (*Neofelis nebulosa*), reticulated pythons (*Python reticulatus*) and estuarine crocodiles (*Crocodylus porosus*) on both islands, and Sumatran tigers (*Panthera tigris sumatrae*) and possibly dholes (*Cuon alpinus*) in Sumatra, are likely to be capable of preying upon them. It can be said, however, that despite occasional casualties these predators almost certainly exert little influence on the population density of orangutans (Rijksen 1978).

### 1.4.5. COGNITION

The cognitive abilities of orangutans are well known. Psychological research has demonstrated that the orangutan, like the other great apes, has a distinct consciousness regarding the 'self', and possesses an extraordinary ability for learning, deduction and invention (Rijksen and Meijaard 1999). Orangutans are also capable of learning sign language (Shapiro 1995; Byrne 1995; Miles *et al.* 1996). Tool use by captive and ex-captive individuals has been well documented (Rijksen 1978; Maple 1980; McGrew 1989; Bard 1993; Byrne 1995; Russon and Galdikas 1995; Russon 1996; Miles *et al.* 1996) and is at least as complex as that of chimpanzees (van Schaik *et al.* 1996). However, not until van Schaik established a field station in the swamp forests of northern Sumatra were truly wild orangutans discovered to regularly manufacture and use tools (van Schaik *et al.* 1996, 1999; Fox *et al.* 1999).

## 1.5. SOCIO-ECOLOGY

### 1.5.1. RANGING BEHAVIOUR AND DISPERSAL

Previous studies have estimated range sizes for orangutans that vary from 40 ha (Rodman 1988) to 600 ha (Galdikas 1988) for adult females, and from 60 ha (Rodman 1988) to 700 ha (Suzuki 1992) for males, though some authors simply stated that male ranges are larger than those of females (e.g. Mitani 1989; Rijksen 1978; Galdikas 1988). All seem to agree that the home ranges of individuals of both sexes overlap with those of others of the same sex. All ranging data to date have been obtained by following individual orangutans through the forest and mapping their movements. No attempts have yet been made to radio collar orangutans due to the difficulties of affixing or implanting a device with adequate range and battery life, that will withstand the attentions of the individual concerned and not result in injury. Furthermore, there would also be problems in attempting to anaesthetise such a large animal without risk of injury from falls. There has been some progress in the chemical immobilisation of wild orangutans, however, and darting has been successfully employed for some translocations (see Hiong *et al.* 1995).

Rijksen and Meijaard (1999) suggest that orangutans can be divided into three classes based on dispersal activity:

1) Residents, who are found for many years to be present for most of each year in one particular area.
2) Commuters, who are seen regularly for several weeks or months each year for many years and appear to live a 'nomadic' existence.
3) Wanderers, who are seen very infrequently (or once) in a period of at least three years and may never return to the area.

Rijksen and Meijaard (1999) also state that at Ketambe, the relative proportions of residents, commuters and wanderers are, respectively, approximately 30%, 60% and 10%. Furthermore, they state that it is considered that the development of many young orangutans follows the sequence from dependent resident (during infancy and juvenile stage) to (social) commuter (during adolescence and sub-adulthood) to (quasi-solitary) resident (as adult), if and where the habitat and an individual's pattern of social relationships permits. An individual may be obliged to remain a commuter during adulthood, or to become a wanderer, if its relative social status remains low (Rijksen and Meijaard 1999). However, to distinguish between transience or simply very large home ranges requires knowledge of the size of home ranges, and yet to date, the true extent of home ranges has only been inferred using relative presence and absence of individuals within study areas of limited size. In fact the Ketambe study area is even today only 450 ha (Utami 2000b) and during Rijksen's study was only around 150 ha (Rijksen 1978) whilst estimates of home range sizes for adult females (which possess the smallest home ranges), appear to reach 600 ha and even higher (see Chapter 4; Galdikas 1988; Singleton and van Schaik in press). Furthermore, it is likely that many of the previous estimates of home ranges are in fact serious underestimates. Thus the distinction between resident and transient individuals may be highly speculative.

MacKinnon (1989) noted that many frugivorous mammals in the Segama area of Sabah exhibited large scale seasonal movements (e.g. pigs, fruit bats, and elephants), and that these movements are possible because although most forest areas have good and poor fruit seasons, these are not in synchrony. He also reported that 'influxes' into his study area corresponded to periods of high local fruit abundance, and that males tended to be more dispersive than females. In addition, Rodman (1973b) predicted a highly dispersive sub-adult phase based on the observation that small, but sexually mature males appeared transient.

### 1.5.2. SOCIAL ORGANISATION

Orangutans are unusual, at least among diurnal primates, for several reasons. They are largely solitary, have low interaction and association rates, show extreme sexual dimorphism in body size and appearance, engage in forced copulations (so called 'rape'), display female mating preferences in favour of some males and in strong opposition to others (rapes), and range in irregular movements (van Schaik and van Hooff 1996). These facts make it difficult to distinguish any spatially discrete communities or social units (van Schaik and van Hooff 1996). Indeed, despite more than 30 years of field research the orangutan's social organisation remains enigmatic. The basic units of orangutan populations are considered to be solitary individuals and mother-offspring dyads (Rodman 1973a; MacKinnon 1974; Horr 1977; Rijksen 1978; Galdikas 1979; Suzuki 1992; Schürmman and van Hooff 1986). Galdikas (1978) suggested that multi-unit groupings are relatively infrequent and seldom lasted more than one day, although she acknowledged that groupings of two females and offspring were sometimes more stable. MacKinnon (1989) also stated that encounters between different independent members or primary units (mother-infant dyads) of the population were only occasional and associations where more than one primary unit may temporarily travel together were generally short lived. Sumatran orangutans, however, are believed to be more gregarious than their Bornean counterparts, probably as a result of higher densities on the former island (Rijksen and Meijaard 1999). At Ketambe it has been shown that orangutans may congregate in large fruit trees, and may even form travel bands that can stay together for several days (Sugardjito *et al.* 1987; van Schaik 1999). Furthermore, there is evidence that mean party sizes for adult females in the swamps of Suaq Balimbing are higher than the drier hill and alluvial forests elsewhere in the region, e.g. Ketambe (van Schaik 1999). Therefore, despite some association between individuals, and unlike the other great apes, that either maintain permanent social groups, or more frequently congregate in social aggregations, orangutans appear to form no readily identifiable social units other than the basic units, and hence possess no group or community structure (Singleton and van Schaik in press.).

Current theory on mammalian social systems considers that "variation in male mating behaviour is related to the effect of male assistance in rearing young and to the defensibility of females by males. The latter is, in turn, related to female ranging behaviour and to the size and stability of female groups. Much of the variation in mammalian mating bonds and systems of mate guarding can be attributed to differences in these three variables" (Clutton-Brock 1989: p. 339). Thus mammalian mating systems are widely thought to reflect the female's response to environmental factors, unless the need for male parental care is unusually great. This is the now classic approach which postulates that female distribution and relationships are above all a response to the distribution of risks and resources in the environment, whereas male distribution and relationships reflect above all the spatiotemporal distribution of mating opportunities (Ims 1988; Davies 1992). However, rarely considered by students of non-human primates is the influence male behaviour can exert on female behaviour (van Schaik and van Hooff 1996).

According to MacKinnon (1989), all authors have agreed that the spatial distribution of orangutan males is to a large extent determined by opportunities for access to oestrus females, and strong competition between males for such access. MacKinnon (1989) also suggests that different females in local populations are somehow in phase in their breeding so that in one locality there are years when several females give birth, interspersed by several years when very few females give birth. Such groupings or clusters of reproductively synchronised females were also observed within relatively localised areas at Suaq Balimbing (see Chapter 6; Singleton and van Schaik in press). This led MacKinnon (1989) to deduce that much of the male orangutan population is highly mobile and ranges rather widely in search of areas where the female population is most likely to provide reproductive opportunities. He adds, however, that we still do not know what the wider social units of orangutans are. The orangutan social system has been regarded as a roving male strategy (Clutton-Brock 1989), and even a 'lek'-type system (Rijksen and Meijaard 1999). Van Schaik and van Hooff (1996) suggest that there are two plausible models, both partly consistent with existing evidence. These are a roving male promiscuity system, in which there is no higher level social unit, or a spatially dispersed but socially distinct community organised around one or more large adult males.

Thus despite a number of field projects, some long-term, there remains much conflicting information as to the size of orangutan ranges, what the main determinants of ranging patterns are, if seasonal movements occur, whether or not some individuals are transient (and if so which age or sex groups they are), and above all, if any social organisation exists other than the basic units of solitary individuals and mother-offspring dyads. However, since individual home ranges are normally larger than the study areas of previous researchers, and orangutan movements also therefore, on a larger scale, it is reasonable to assume that any social organisation that exists, may also function on a larger scale. For this reason a detailed study of orangutan ranging behaviour may serve as the best practical means of elucidating the still enigmatic orangutan social system.

There can also be little doubt that attempting to delineate forest areas for the conservation of a species whose social organisation and even home range sizes are unknown, could result in unwitting, but nonetheless catastrophic underestimation of their requirements. This is of particular concern in light not only of the current rapid pace of forest destruction within the orangutan's distribution, but also in view of their extremely slow reproductive rate. For these reasons alone it is imperative that attempts are made to determine range sizes and movement patterns within orangutan populations as rapidly as possible.

## 1.6. AIMS AND OBJECTIVES

As outlined above, many aspects of orangutan socio-ecology are still relatively poorly understood and are the result of speculation and inferences made from relatively scant, but gradually accumulating data. The primary aim of this study is therefore to add to the information currently available, by examining various aspects of orangutan socio-ecology, but in particular ranging behaviour, in the swamp forests of northern Sumatra, and to compare and contrast the findings with observations from elsewhere.

To achieve this four main areas are explored. In Chapter 3 an attempt is made to estimate absolute densities, and to determine the degree to which densities fluctuate over large and small areas. The accuracy of such estimates is then discussed, along with some possible explanations for spatial and temporal variation in densities. Home range sizes and relative presence of individuals of the various age and sex classes are estimated in Chapter 4, along with the degree of stability and overlap of ranges. Some inferences are then drawn regarding the age and sex composition of the population, the degree to which transience exists, and which age/sex class is the most likely dispersal phase. In Chapter 5 the relationship between fluctuating densities and various aspects of forest productivity and orangutan diets is explored to determine if seasonal movements do indeed occur, and what their most likely causes might be. Chapter 6 examines association rates between individuals and subsets of the population and discusses possible interpretations of these data, particularly with regard to observations made concerning ranging behaviour. An attempt is then made in Chapter 7 to provide a synthesis, and discuss the results within the context of what has been deduced from other field studies, and the implications for orangutan social organisation and conservation. The specific aims are therefore as follows:

1. To determine absolute densities of orangutans in Sumatran swamp forests.
2. To determine if seasonal movements occur and why.
3. To determine which age and sex classes are transient (migratory) if any.
4. To determine home range sizes of the various age and sex classes.

# CHAPTER 2

# STUDY AREA, CLIMATE AND GENERAL METHODS

## 2.1. STUDY AREA

### 2.1.1. LOCATION

This study was conducted at the Suaq Balimbing Research Station (03°04'N, 97°26'E), in the Kluet region of what is now the Leuser Ecosystem (formerly Gunung Leuser National Park). The Leuser Ecosystem lies predominantly within the province of Aceh, Sumatra, Indonesia, but also straddles the border to the south, into the province of North Sumatra. The Kluet region lies within the Kabupaten of Aceh Selatan, on the coastal plain between the Barisan mountains and the coast. The research station was established in 1994 by van Schaik of Duke University, USA, under the auspices of the Wildlife Conservation Society (WCS), but in 1997 came under the control of the Leuser Management Unit (LMU). Only one other major orangutan study, by Fox (1994-1996), also of Duke University, has been undertaken at the site other than the present study and the on-going work by van Schaik.

### 2.1.2. VEGETATION AND FOREST TYPES

Along the coast in both directions, the original forest cover has been replaced by agriculture. The only remaining forested connection to the rest of the Leuser Ecosystem, and therefore to other orangutan populations, is now via a narrow expanse of contiguous forest to the north-east that grades into the Barisan mountain range.

The study area is bordered to the west by the Krueng Lembang river, and to the east by low hills, reaching 500 m (Figure 2.1). Southwards the swamp extends to the main coast road, approximately 11 km away from the station at its nearest point. To the north, the forest grades into swampy, near impenetrable rotan (*Calamus* spp.) scrub, and after 700 m or so probably harbours few orangutans except for occasional visitors. The degraded nature of this area may in some part be a result of illegal logging in the past, but could also be a natural consequence of frequent and deep flooding.

Within the area as a whole, van Schaik (1999) distinguishes four main habitat types:

1. Tall riverine forest along the Krueng Lembang river (floodwater pH 6-7).
2. Regularly flooded 'backswamps' near the river and foothills, on muddy soils with a very irregular and open forest (floodwater pH 5-6.5).
3. Structurally simple, but generally closed canopy peat swamp forest whose peat layer becomes deeper away from the backswamps (floodwater pH 3.5-5.5). Also termed 'transitional swamp'. Further south, in the area of the southernmost trails added by this study, the floodwater pH of the peat swamp forest can reach as low as 2.5.
4. Mixed dipterocarp hill forest.

Examples of common tree species in the most extensive habitat, the peat swamp forests, were mempelam (*Gluta cf malayana* (Corner) Ding Hou), puwin (*Sandoricum beccarianum* Baillon), meranti (*Shorea* sp.), and malaka (*Tetramerista glabra* Miq.). Of these *S. beccarianum and T. glabra* constituted major food species for orangutans. In the backswamps, cemengang (*Neesia* sp.), and in the hills, durian hutan (*Durio* sp), were significant food species. Notably, large strangling figs (*Ficus* spp.) that are typically the staple diet species for orangutans at most other research sites (Rijksen 1978; Leighton 1993; Rijksen and Meijaard 1999), were virtually absent except for a very few, widely scattered trees, even in the hills.

### 2.1.3. FAUNA

The area harbours much of the fauna typical of the rest of the Leuser Ecosystem (see Rijksen 1978; van Schaik and Supriatna 1996), although the Sumatran elephant (*Elephas maximus sumatranus*) and Sumatran rhinoceros (*Dicerorhinus sumatraensis*) have not been recorded in the immediate vicinity for many years (M. Griffiths pers. comm.). Other primates regularly encountered in the study area were siamang (*Hylobates syndactylus*), white-handed gibbon (*Hylobates lar*), Thomas' langur (*Presbytis thomasi*), silvery langur *(Trachypithecus cristata*), long-tailed macaque (*Macaca fascicularis*), pig-tailed macaque

(*Macaca nemestrina*) and slow loris (*Nycticebus coucang*), all of which will compete for food with orangutans to some degree. Other significant competitors include Malayan sun bear (*Helarctos malayanus*), binturong *(Arctis binturong*), fruit bats (Chiroptera) and several species of hornbill (Bucerotidae).

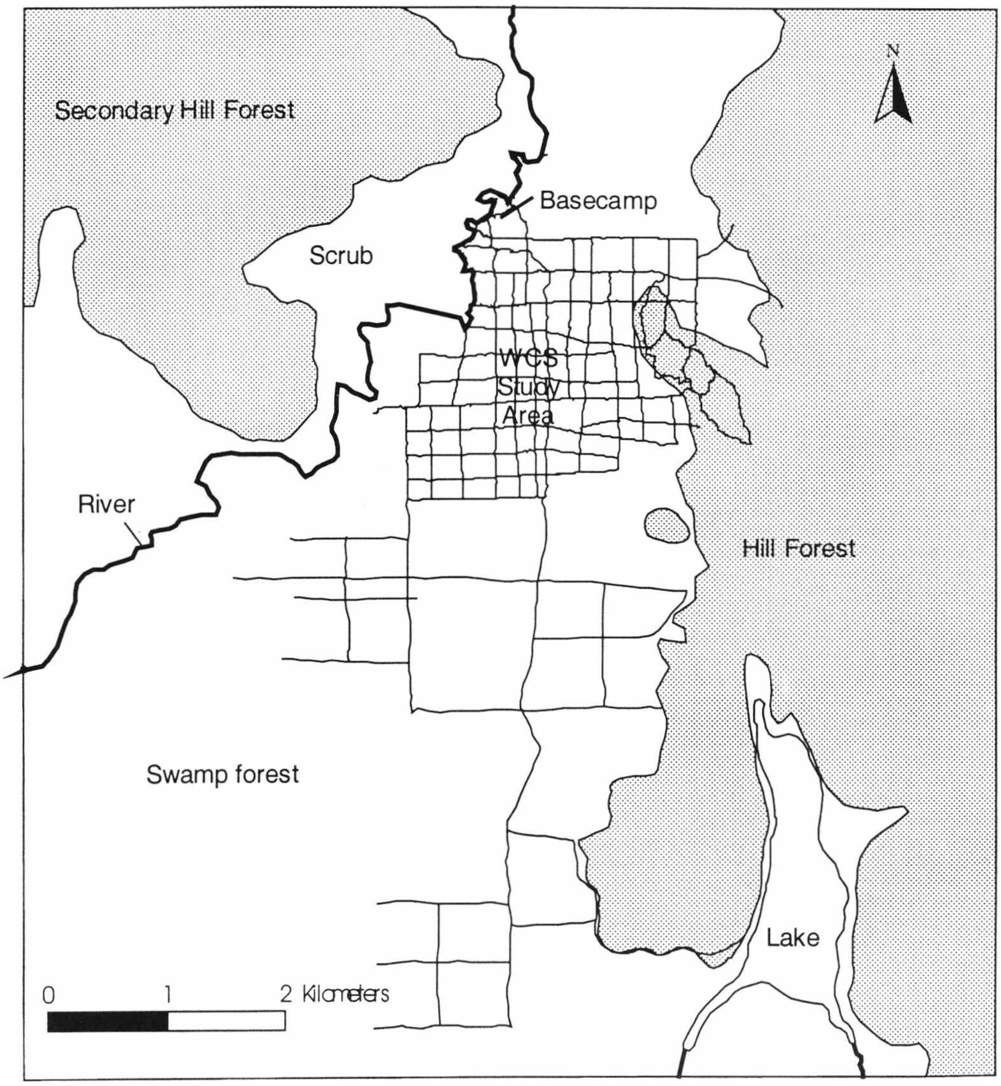
### 2.1.4. TRAIL SYSTEM

The original WCS study area comprises a comprehensive trail system within an area of approximately 460 ha of predominantly swamp forest, at less than 5 m above sea level. For clarity, this 460 ha area shall be consistently referred to as the WCS study area. The station itself is located at the north-western tip of this area, on a small hill by the river. At the onset of the present study, additional trails were cut extending the existing trail system approximately 5 km to the south and south-west, and 1.5 km to the east (see Figure 2.1). This larger area shall be referred to simply as the study area, or the whole area, to distinguish it from the WCS study area. All trails were tagged and marked at 50 m intervals. Three trails had been improved with the construction of a rudimentary boardwalk (HJPLX, X and W), to enable quicker access through the swamps to the hills in the east, and to the central and southern parts of the WCS study area, from the base camp.

### 2.1.5. DISTURBANCE

Logging, both legal and illegal, has impacted the area across the river to the extent that orangutans are likely to be largely absent, or surviving at much reduced densities there. At the time of the study, logging had also been carried out at some points along the river banks, mostly south-west of the WCS study area, but had not yet extended further inland than 100 m to 200 m at most. Hence the orangutan population (excepting individuals that may have routinely crossed the river), had been relatively undisturbed other than by occasional fishermen working in the swamps.

**Figure 2.1**: Locality of study area. Grey area denotes drier hill areas. Narrow lines represent forest trails. The dense trail system to the North is the original WCS study area.



## 2.2. CLIMATE

### 2.2.1. METHODS

Maximum and minimum temperatures were measured at chest height in the shade of the forest, at 1800 each day. Rainfall was measured twice daily at 0600 and 1800 using a standard rain gauge (precipitation tube) located in a clearing beside the station. Daily rainfall totals therefore represent the sum of these two measures. River levels were also measured twice daily at the same times as rainfall, with the aid of a wooden ruler fixed vertically on the river bank and marked at 10 cm intervals (zero being arbitrary). Mean daily values were calculated as the mean of both levels, and used to calculate the mean monthly values which do not therefore represent the absolute maxima and minima observed. Table 2.1 gives a summary of climate data for the period October 1996 to September 1998 inclusive.

### 2.2.2. RAINFALL

Total annual rainfall between October 1996 and September 1997 (inclusive) was 2703 mm, and 146 days experienced more than 1 mm of rain. Between October 1997 and September 1998 this rose to 3648 mm in 185 days of greater than 1 mm of rain. The average of the two periods was thus 3176 mm per year. Most rain fell during the night with only 32.4% falling during daylight hours. All months experienced at least 8 days of greater than 1 mm of rainfall whilst the most days with greater than 1mm of rain in a single month was 25 in August 1998. Total monthly rainfall is plotted in Figure 2.2, which shows a distinct wet season beginning around August, rising to a peak around September to November and declining again by February or March. Consequently, the driest part of the year would seem to be around April to June.

Rijksen (1978) noted two relatively dry seasons per year during his three year study in lowland hill forest area at Ketambe, namely January to February and July to August, and these did appear to be present in the first year of this study, (though slightly earlier in December 1996 and June 1997), but were less clearly defined in 1998 when March, April and June were the driest months.

### 2.2.3. TEMPERATURE

Mean annual forest temperature was 26.2 °C between October 1996 and September 1997 and 26.7 °C between October 1997 and September 1998. The highest mean monthly maximum temperatures occurred at the beginning of the drier spells in both years, i.e. over 31 °C in January 97 and in February and March 98. Of particular note is that mean monthly

**Table 2.1**: Climate data; October 1996 to September 1998 inclusive.

|  | Rainfall (mm) |  |  |  |  | Mimimum temp |  | Maximum temp |  | River levels (monthly) |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | Total (mm) | Mean/day | SD | No. days >1mm | % of days >1mm | Mean | SD | Mean | SD | Max | Min | Mean | SD |
| Oct-96 | 387 | 12.484 | 17.964 | 23 | 74.194 | 22.597 | 0.554 | 28.403 | 1.513 | 14.00 | -3.75 | 5.774 | 5.130 |
| Nov-96 | 406 | 13.520 | 23.613 | 17 | 56.667 | 22.317 | 1.046 | 29.233 | 1.897 | 11.75 | -1.50 | 4.608 | 5.144 |
| Dec-96 | 106 | 3.423 | 8.737 | 11 | 35.484 | 22.097 | 0.768 | 29.839 | 1.350 | 9.00 | -2.25 | 2.129 | 3.429 |
| Jan-97 | 257 | 8.303 | 27.680 | 9 | 29.032 | 22.274 | 0.740 | 31.452 | 1.207 | 10.75 | -4.00 | 0.944 | 4.305 |
| Feb-97 | 228 | 8.139 | 17.765 | 7 | 25.000 | 22.161 | 1.028 | 30.607 | 1.235 | 12.50 | -2.00 | 2.370 | 4.032 |
| Mar-97 | 168 | 5.413 | 11.694 | 13 | 41.935 | 22.903 | 0.790 | 30.452 | 1.135 | 10.50 | -2.00 | 4.782 | 3.391 |
| Apr-97 | 195 | 6.503 | 14.749 | 9 | 30.000 | 22.933 | 0.807 | 29.933 | 1.278 | 11.50 | -1.00 | 2.933 | 3.686 |
| May-97 | 241 | 7.781 | 19.559 | 13 | 41.935 | 22.339 | 1.036 | 30.065 | 1.476 | 11.75 | -2.00 | 2.427 | 3.701 |
| Jun-97 | 74 | 2.457 | 5.668 | 8 | 26.667 | 22.533 | 0.681 | 30.317 | 0.886 | 1.75 | -4.00 | -2.475 | 1.218 |
| Jul-97 | 157 | 5.071 | 12.529 | 10 | 32.258 | 22.435 | 0.761 | 29.919 | 1.050 | 2.00 | -6.00 | -4.419 | 1.592 |
| Aug-97 | 291 | 9.394 | 30.735 | 13 | 41.935 | 22.145 | 0.594 | 29.984 | 1.084 | 10.25 | -6.50 | -2.016 | 5.157 |
| Sep-97 | 193 | 6.437 | 12.146 | 13 | 43.333 | 22.767 | 0.838 | 29.067 | 0.954 | 10.25 | -3.75 | 1.633 | 4.803 |
| Oct-97 | 409 | 13.184 | 23.017 | 18 | 58.065 | 23.016 | 0.769 | 28.016 | 0.979 | 11.50 | 1.50 | 7.137 | 2.604 |
| Nov-97 | 514 | 17.130 | 25.390 | 23 | 76.667 | 23.033 | 0.656 | 28.683 | 1.030 | 13.25 | 6.50 | 9.908 | 1.715 |
| Dec-97 | 341 | 11.000 | 20.294 | 17 | 54.839 | 23.145 | 0.685 | 29.258 | 1.132 | 13.50 | 0.50 | 7.282 | 3.341 |
| Jan-98 | 242 | 7.797 | 24.214 | 12 | 38.710 | 23.435 | 0.929 | 30.661 | 1.583 | 13.50 | 2.00 | 6.718 | 3.086 |
| Feb-98 | 303 | 10.829 | 29.949 | 8 | 28.571 | 23.857 | 0.756 | 31.036 | 1.247 | 12.00 | -1.25 | 2.473 | 3.564 |
| Mar-98 | 124 | 4.000 | 8.044 | 13 | 41.935 | 23.871 | 0.785 | 31.258 | 0.835 | 0.50 | -4.00 | -2.331 | 1.003 |
| Apr-98 | 119 | 3.963 | 8.349 | 12 | 40.000 | 24.133 | 0.955 | 30.933 | 0.935 | 2.50 | -4.63 | -3.092 | 1.595 |
| May-98 | 232 | 7.468 | 18.721 | 11 | 35.484 | 23.790 | 0.938 | 30.774 | 1.182 | 10.25 | -3.50 | 1.633 | 3.983 |
| Jun-98 | 128 | 4.250 | 8.095 | 14 | 46.667 | 23.433 | 1.425 | 30.150 | 1.543 | 3.25 | -3.75 | -2.404 | 1.300 |
| Jul-98 | 291 | 9.387 | 16.297 | 14 | 45.161 | 22.968 | 1.176 | 30.274 | 1.966 | 11.13 | -5.50 | -0.770 | 5.341 |
| Aug-98 | 481 | 15.516 | 23.147 | 25 | 80.645 | 22.871 | 1.511 | 29.210 | 1.778 | 14.75 | -1.63 | 7.081 | 5.234 |
| Sep-98 | 466 | 15.527 | 25.199 | 18 | 60.000 | 23.050 | 1.778 | 30.267 | 2.192 | 13.75 | 7.50 | 9.921 | 1.496 |
| Total | 6352 |  |  |  |  |  |  |  |  |  |  |  |  |

**Figure 2.2**: Total monthly rainfall with mean monthly maximum (○) and minimum (●) temperatures; October 1996 to September 1998.

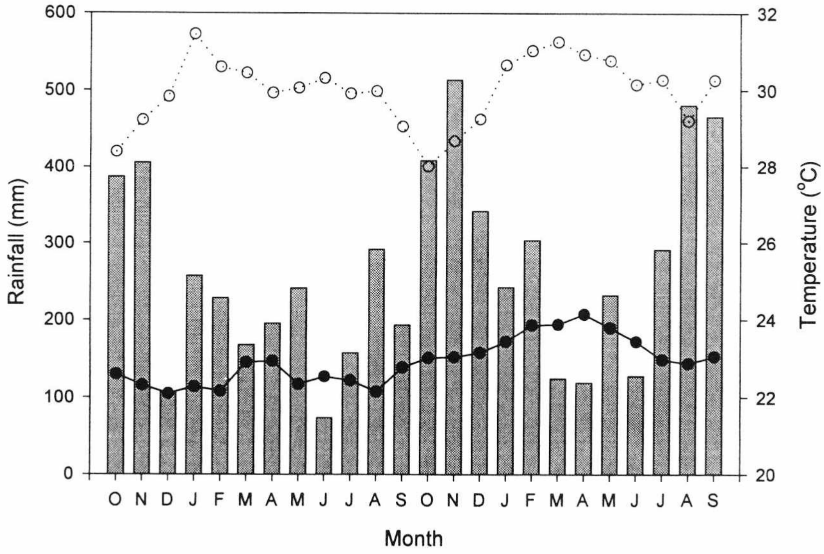
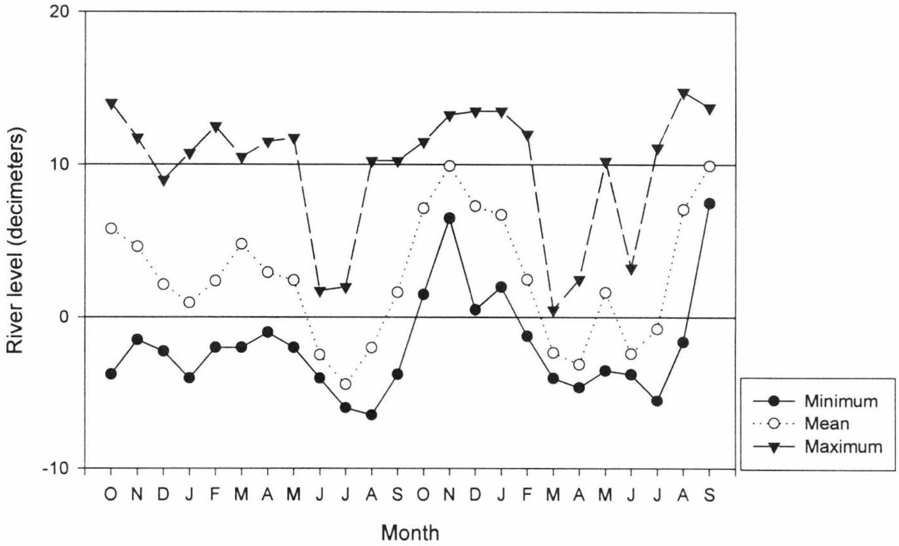


**Figure 2.3**: Mean monthly maximum, minimum and daily river levels (in decimeters +/- an arbitrary zero; daily level = mean of am and pm levels); October 1996 to September 1998.



minimum temperatures did not reach 23 °C for the whole period until October 1997, after which only two months (July and August 1998), were below 23 °C. Figure 2.2 shows this slight rise in minimum temperatures during the second period and also three distinct troughs in the plot of mean monthly maximum temperatures around September in both 1996 and 1997, and August in 1998, though as with minimum temperatures the latter trough does not reach as low as the previous two. These troughs also occur immediately before the months with greatest rainfall.

### 2.2.4. RIVER LEVELS

River levels are an indicator of flood levels in the swamp and examination of Figure 2.3 shows that river levels tend to peak around the same time that precipitation peaks, as might be expected. However, the river can also rise or remain high during periods of low or no rainfall in the study area, presumably as a result either of floodwater slowly feeding back into the river channel, or of rainfall further upstream. On a day-to-day basis, strong and sudden increases in river level were not always accompanied by heavy rainfall in the study area, whereas heavy rains in the study area were always accompanied by high water. The swamps often retained high water levels long after river levels dropped, but that river levels often rose sharply for no obvious reason suggests a strong rainfall gradient from the coast inland. This is supported by old records from Kandang, at the river mouth, which show a lower mean annual total of around 2880 mm (C. P. van Schaik pers. comm.).

### 2.2.5. DISTURBANCE

It should be noted that the latter half of 1997 was the period during which much of Indonesia was ablaze and a considerable amount of smoke was drifting around in the atmosphere. The degree to which this may have affected the climate in the region during the study period is not known. Furthermore, minimum river levels appeared to peak much higher during late 1997 and mid 1998, than in 1996. Again it is not known to what extent this is a natural phenomenon or not since there was known to be a considerable amount of logging in progress upstream from the study site.

## 2.3. GENERAL METHODS

Data for this study were primarily collected by myself and local field assistants, between October 1996 and September 1998 inclusive. Three basic methods were employed:-

1) Focal individual follows;
2) Phenological observations in vegetation plots; and,
3) Nest censuses along transects.

An overview of each of these is given below, but each is described in more detail in the relevant chapters. Data on the movements of individual orangutans within the WCS study area, since early 1994, were made available from the WCS database for inclusion in this study. Nest census and phenological data pertaining to WCS transects and plots, that overlapped the period of the present study were also made available so that the WCS transect sites could be incorporated, thus increasing the size of the area being monitored. All data collected by myself and assistants have also been made available to the WCS project.

### 2.3.1. FOCAL INDIVIDUAL FOLLOWS

Individual orangutans were normally located by searching the WCS study area. For the present study (i.e. from late 1996) search effort was concentrated on the periphery of the WCS trail system, whilst the WCS study followed animals only when they were within it. Individuals were then followed for as long as was found to be practical. A large number of the orangutans regularly found within the WCS study area had been previously habituated by the WCS project prior to this study. Some, however, either encountered outside the WCS study area, or which were previously unknown but found within it, were not previously habituated. Individual orangutans can normally be easily recognised by their distinguishing features and records describing all those that were known and named at Suaq Balimbing have been kept since the onset of the WCS study. These records contain information pertaining to the general appearance of the animal, often with drawings, and details of any unique features they may possess (e.g. warts, scars, damaged fingers etc.). In the case of adult females, the sex and approximate age of their infants was also noted. The majority of recognisable individuals were assigned names, though a small number of relatively new animals were still being known by numbers at the end of the present study.

Whenever possible follows lasted from nest to nest i.e. from when an orangutan left its night nest in the morning, to when it completed and relaxed in its subsequent night nest. Orangutans were rarely 'lost' but on occasions follows were abandoned due to weather, or the individual leaving the area (particularly by the WCS project), or to switch to another individual, which for various reasons, might yield more data. Examples of why an individual may have been considered likely to yield more data could be if it was one that had not previously have been followed very much, if it was outside of its known range or if it looked like it might leave the study area.

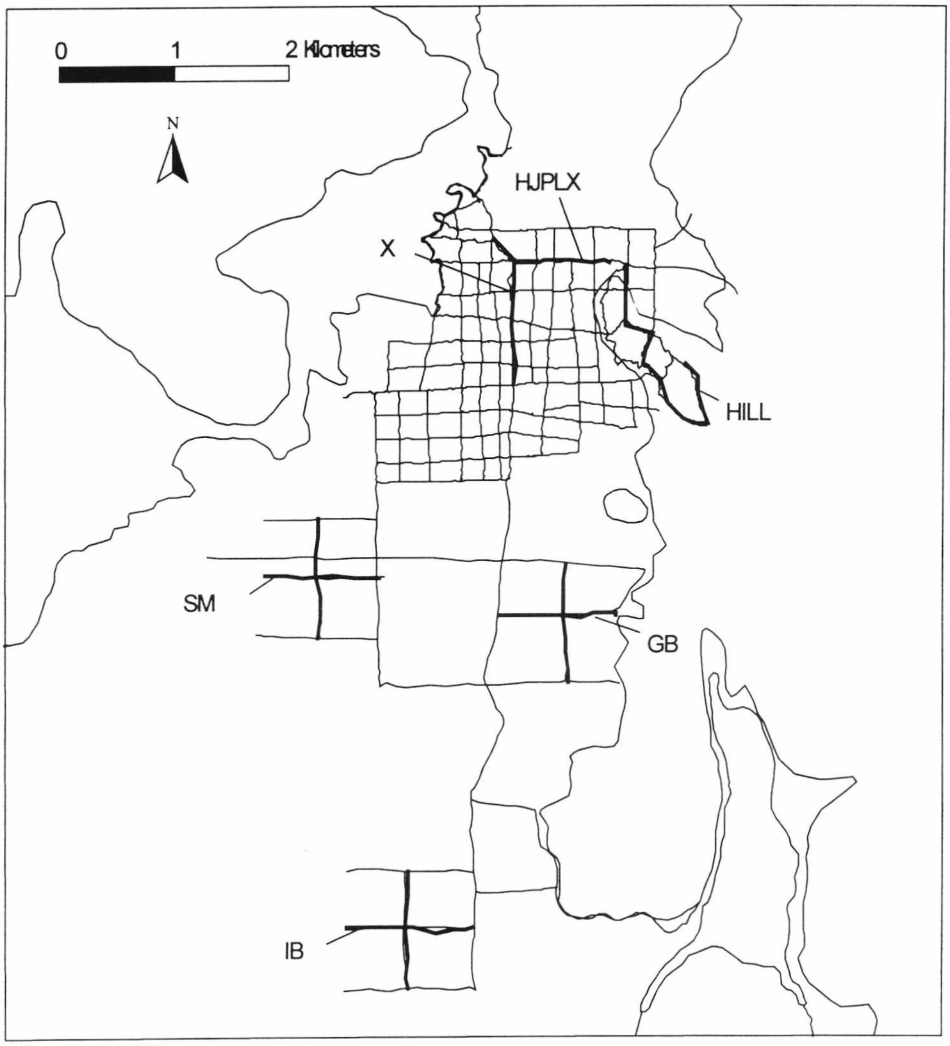
Behavioural data were collected on all individual orangutans followed using focal animal sampling and point sampling at an interval of two minutes (see Martin and Bateson 1986). Some behaviours, such as interactions between individuals (e.g. copulations, play, social behaviours etc.) were recorded by taking notes on an all-occurence basis.

In addition to behavioural data, the movements of focal individuals were recorded during all follows by estimating the distance travelled each time the individual moved from one tree to another, noting the direction with a compass, and plotting these on a map of the trail system. Outside the WCS study area the distance and direction travelled were plotted in similar fashion on a grid of 100 m x 100 m, and positions recorded at sporadic intervals, when forest conditions or time permitted, using a hand-held Global Positioning System (GPS).

### 2.3.2. NEST TRANSECTS

Several sites for the monitoring of nest densities and phenology were established throughout the area, in locations considered likely to encompass slightly different habitat types, or to give reasonable distances between sites (see Figure 2.4). Three of these sites (HJPLX, HILL and X) have been monitored for several years by the WCS project and tend to run along existing trails, whereas those to the south (GB, IB and SM) were set up as new in early 1997 and extend overall coverage to a much greater area. At each site nest transects were established to monitor monthly fluctuations in nest densities over a wide area, and to estimate absolute densities of orangutans in the area as a whole. Transects were monitored monthly, and the location, height, position in tree, tree species used (where known) and the estimated age of all nests seen were recorded. New nests (less than one month old) could be readily identified since they were not recorded during previous censuses.

**Figure 2.4**: Transect and phenology plot locations.



Transects in the south (SM, IB and GB) formed a cross, with two trails of approx. 1 km each bisecting each other perpendicularly at each location, giving a total transect length at each site of approximately 2 km. Actual transect lengths and the duration of montioring are given in Table 2.2. New nests could only be identified on the second visit to the nest transects and so the number of months in which new nests were recorded is one less than the number of months given in the table.

**Table 2.2**: Nest transect lengths and duration of monitoring.

| Plot name | Start month | End month | No. of months | Transect length (m) |
|---|---|---|---|---|
| HILL | Mar-97 | Sep-98 | 19 | 3085 |
| HJPLX | Mar-97 | Sep-98 | 19 | 1550 |
| X | Mar-97 | Sep-98 | 19 | 1865 |
| IB | Mar-97 | Sep-97 | 7 | 1972 |
| SM | Mar-97 | Sep-98 | 19 | 1955 |
| GB | Aug-97 | Sep-98 | 14 | 1865 |

### 2.3.3. PHENOLOGY PLOTS

At each plot, monthly observations were made pertaining to levels of fruit, flower and young leaf production. For each tree and each phenophase a score was assigned to represent the abundance, and for fruit and flowers, also the stage of development (e.g. ripe or unripe fruits, fully open flowers or buds).

At the same locations as nest transects, several phenology plots were established although shorter stretches of the same trails (approximately 1 km in most cases) were used. The locations of all phenology plots and nest transects are shown in Figure 2.4. The length of each phenology plot and the duration of monitoring are given in Table 2.3. In locations HJPLX, HILL and X, phenology plots simply ran along the nest transects for a section of their overall length whereas at GB, IB and SM, the phenology plots ran along only the East-West section of the nest transects.

Plot (and transect) locations were selected to provide coverage of what were initially perceived to be a variety of different forests types. Both X and SM lay in the slightly drier 'transitional swamp' locations with more of the main (staple) food species of orangutans (e.g. malaka and puwin). HJPLX and GB were in areas of deeper 'backswamp', closer to the foothills or the river. These areas tended to be deeper due to run off and floodwater, contained tree species associated with the deeper water, and also included some food species that are favoured by the orangutans and which they appeared to actively seek out when available. Most notable in these areas was the presence of cemengang (*Neesia* sp.). The HILL location comprised lowland mixed dipterocarp hill forest which appeared not to support large numbers of orangutans for much of the time, and contained tree species typical of the drier conditions (e.g. Dipterocarps). The most difficult site to classify was IB, because despite the fact that it was located at least a kilometre from the nearest hills it still tended to be slightly wetter than SM or X and hence would appear at first glance to be in a transition area between the very wet foothill 'backswamp' type habitat and the slightly drier 'transitional swamp' central zone.

**Table 2.3**: Phenology plot sizes and duration of monitoring.

| Plot name | Start month | End month | No. of months | Plot length (m) | Plot Area ($m^{-2}$) |
|---|---|---|---|---|---|
| HILL | Mar-97 | Sep-98 | 19 | 1800 | 15425 |
| HJPLX | Mar-97 | Sep-98 | 19 | 840 | 7750 |
| X | Mar-97 | Sep-98 | 19 | 850 | 4250 |
| IB | Mar-97 | Sep-97 | 7 | 1000 | 5000 |
| SM | Mar-97 | Sep-98 | 19 | 1050 | 5250 |
| GB | May-97 | Sep-98 | 17 | 980 | 4900 |

A summary of the tree and liana composition of each plot is given in Table 2.4. This shows that in terms of overall stem density, X and HJPLX were the highest whilst HILL and IB were the lowest. Species density suggests similarities between X and GB and between IB and SM whilst HILL and HJPLX came out highest.

What is not clear from these figures, however, is the degree of similarity between plots in terms of species composition. A more useful assessment of the degree of similarity between plots may therefore be provided by Soerenson's index, which is a measure of similarity of species composition, rather than overall abundance. Soerenson's index is calculated by the following formula (Kent and Coker 1994):

$$S_s = \frac{2a}{2a + b + c}$$

where a = no. of species common to both plots,

b = no. of species in plot 1,

c = no. of species in plot 2.

Multiplying 'a' by 2 gives weight to the species common to both plots rather than to those that only occur in one of the two samples (Kent and Coker 1994). Results are given in Table 2.5 along with the distances between plots, the index being expressed as a percentage of similarity with a higher percentage thus reflecting greater similarity. Distances were calculated between the mid-points of transects. The table shows more clearly the degree of dissimilarity between the HILL plot and all others since all values for this plot are less than 11%. It also illustrates some difference between HJPLX and both SM and IB (Soerenson's index less than 30).

These results show firstly that the HILL plot is quite distinct from all other plots in both species composition and species abundance, combining a high species density with a low stem density. Van Schaik (1999) also found that in general, fruiting levels are at least five times higher in the swamp habitats than in the hills at Suaq Balimbing. Secondly, whilst there were subtle differences between all the other plots, there was considerable overlap between them. There is also the suggestion that a difference did exist to some degree between the most distant plots (i.e. between HJPLX and both SM and IB) as similarity values were less than 30%. However, between X (which lay between HJPLX and the southern plots) and HJPLX, Soerenson's index was 36.76%, and X also had values greater than 30% with both SM and IB. This therefore suggests that dissimilarity increases as distance between plots increases, but that the transition between distant plots is gradual.

**Table 2.4**: Tree and liana stem and species density in phenology plots ($ha^{-1}$). * includes unknown liana species as one species and unknown tree species as one species.

| Veg. type | Category | GB | HJPLX | HILL | IB | SM | X |
|---|---|---|---|---|---|---|---|
| Trees | Stem density | 708.16 | 833.33 | 555.56 | 598.00 | 758.10 | 821.18 |
| | Species density* | 73.47 | 123.81 | 111.11 | 60.00 | 57.14 | 77.65 |
| Lianas | Stem density | 55.10 | 0.00 | 0.00 | 42.00 | 19.05 | 2.35 |
| | Species density* | 14.29 | 0.00 | 0.00 | 6.00 | 7.62 | 2.35 |
| All stems | Stem density | 763.27 | 833.33 | 555.56 | 640.00 | 777.14 | 823.53 |
| | Species density* | 87.76 | 123.81 | 111.11 | 66.00 | 64.76 | 80.00 |

**Table 2.5**: Soerenson's index of similarity between plots (expressed as a percentage), and distance between plots (metres).

| | HILL | | HJPLX | | IB | | SM | | X | |
|---|---|---|---|---|---|---|---|---|---|---|
| Plot | $S_s$ | Distance | $S_s$ | Distance | $S_s$ | Distance | $S_s$ | Distance | $S_s$ | Distance |
| GB | 9.03 | 2079 | 36.49 | 3192 | 39.67 | 3035 | 42.42 | 2188 | 40.63 | 2675 |
| HILL | | | 10.65 | 1613 | 4.41 | 5109 | 5.67 | 3398 | 8.28 | 1495 |
| HJPLX | | | | | 27.83 | 5976 | 29.51 | 3493 | 36.76 | 758 |
| IB | | | | | | | 41.44 | 3111 | 38.10 | 5409 |
| SM | | | | | | | | | 31.94 | 2874 |

# CHAPTER 3

# ORANGUTAN DENSITIES

## 3.1. INTRODUCTION

Density estimates constitute a fundamental prerequisite for effective conservation strategies for any species. By extrapolating estimated densities for different habitat types estimates of total populations over wide areas can be obtained, and by monitoring temporal fluctuations in densities, movements of individuals and declining populations can be detected. Until relatively recently, however, reliable estimates of orangutan densities were available for only a handful of sites where long term studies had been conducted. Furthermore, these sites may have been selected due to their unusually high densities, as fieldworkers may actually select areas most likely to provide adequate data (Leighton *et al.* 1995; van Schaik *et al.* 1995a).

Various methods are available to estimate forest primate densities. Rodman (1973) in Borneo, and Rijksen (1978) and te Boekhorst *et al.* (1990) at Ketambe, utilised records on the presence or absence of individual orangutans within the study area to estimate densities. This involves estimating for each individual orangutan, the percentage of its time that it spent within the study area, then summing the percentages over all individuals known to use the area, and dividing by the size of the study area. Recording presence or absence, however, assumes that individuals are always seen when present, and absences can only be inferred from a lack of presence records. Presence and absence methods also require long periods for data acquisition. For some small study areas the practical difficulties of adequately searching for orangutans may to some extent be overcome, but in the majority of situations this is unlikely to be the case. Hence this method is likely to produce errors due to the orangutan's cryptic, semi-solitary nature and the inherent difficulty of adequately searching an area. If home range sizes were known, then knowledge of the total number of individuals using an area could be used to calculate densities, but as is shown in Chapter 4, estimating range sizes of orangutans also remains difficult.

Brockelman and Ali (1987), have illustrated the use of line transects, or distance sampling techniques, to estimate primate densities relatively quickly and easily, based on direct sightings of individuals or groups. The orangutan's cryptic nature and the low densities involved again, however, make these techniques based on direct sightings impractical for estimation of orangutan densities. Previous density estimates for this species range from <1 km$^{-2}$ to 7 km$^{-2}$ (see Rijksen and Meijaard 1999), over a variety of different habitats, with the majority of habitats at the lower end of this range. Therefore with an actual density of 1 km$^{-2}$, and an effective strip width of 20 m either side of the transect, only one sighting every 25 km of transect would be expected (van Schaik *et al.* 1995b). In a similar manner, Payne (1987) calculated that in Sabah, to obtain 15 sightings of individual orangutans from surveys on the ground, as much as 290 km would need to be surveyed.

All great apes use nests in which to sleep during the night and also frequently to rest in during the day (Sugardjito 1983). Nests are much more commonly encountered than the animals themselves, and hence provide an indicator of actual animal densities. Therefore, efforts to estimate great ape densities have more recently focused on counting nests along line transects as opposed to individual animals (e.g. Ghiglieri 1984, Plumptre and Reynolds 1996, for chimpanzees *Pan troglodytes*; Tutin and Fernandez 1984, White 1994a, for chimpanzees and gorillas *Gorilla gorilla gorilla*; Djojosudharmo and van Schaik 1992, van Schaik *et al.* 1995b, Husson *et al.* unpubl., Lackman-Ancrenaz and Ancrenaz unpubl., for orangutans).

In principle, nest counts could be obtained by carefully searching an area of known size, but with this approach an unknown number of nests would inevitably still be missed. Also, spatial clumping of orangutan nests has been reported (MacKinnon 1974; Rijlksen 1978; Payne 1987), which would necessitate several smaller plots scattered over the area. For these reasons the line transect approach seems the most straightforward and easily repeatable method. It also allows nests to be labelled or identified as they can be located more accurately relative to a trail than within a large area, and hence new nests can be easily distinguished from those present during previous censuses (van Schaik *et al.* 1995b).

If nests are to be used to estimate absolute densities of orangutans, the density of nests themselves is first estimated, and must then be calibrated using estimates of the rate at which nests are produced $r$, and the proportion of the population that actually builds nests $p$. In addition, if nests of all ages, as opposed to only new nests are to be used, the duration of nest visibility $t$, must also be taken into account. Furthermore, these parameters should be estimated for each habitat type and each population, as variability is to be expected between local environmental conditions, and between different orangutan populations or 'cultures'.

The aim of this chapter is therefore to attempt to obtain accurate density estimates for the forests around Suaq Balimbing, and to assess the degree to which the various parameters differ from other locations. By estimating monthly densities at several locations as well as overall densities the results can then be used to evaluate seasonal movements, population structure, and range sizes. The accuracy of the estimates obtained and any problems with the methodology will also be explored and discussed.

## 3.2. METHODS

### 3.2.1. FIELD PROCEDURE

Six line transects were established for density estimation, as described in Chapter 2. The observer walked each transect once per month locating all nests recorded the previous month that were still visible, and any new nests not observed previously. For each nest, its location on the transect (each trail being marked at 50 m intervals by tree tags), and its perpendicular distance from the transect in metres, were recorded. To ensure that nests could be accurately located and identified in ensuing months, nest height (in 5m classes), and position in the tree (e.g. adjacent to trunk, at apex of trunk, on bough away from trunk, or using two or more trees combined), were noted. Each nest was also assigned an age (or stage of decay) class each month, according to the following criteria:

(1) Leaves still green/fresh in appearance,
(2) Leaves still attached and nest still firm and solid,
(3) Leaves falling, some small holes appearing in structure,
(4) Leaves are gone and holes visible in structure,
(5) Twigs and branches still present but no longer in original shape of nest.

The fundamental formula for estimating densities using line transects is given by Krebs (1999) as:

$$\hat{D} = \frac{n}{2La}$$

where;

$D$ = density of animals (or sign) per unit area,

$n$ = number of animals (or sign) seen along transect,

$L$ = total length of transect,

$a$ = half the effective strip width (a constant that must be estimated).

The constant 'a' is simply the total area under the detection function, and estimates how wide the strip would be if every organism (or sign) was seen and none were missed (Krebs 1999). The detection function itself is simply the rate at which detectability declines with increasing distance from the transect (Burnham *et al.* 1993).

The computer program DISTANCE (Thomas *et al.* 1998) was used to estimate densities. DISTANCE attempts to fit several possible models for calculating the detection function, based on the distribution of perpendicular distances from the transect, and evaluates the relative fit of each to the data. The model with the best fit according to Akaike's Information Criterion (AIC; see Buckland *et al.* 1993) is then selected.

Observations were truncated at 50 m perpendicular distance from the transect line during data collection, and DISTANCE was allowed to group the perpendicular distances itself whilst fitting the models. Buckland *et al.* (1993), suggest truncating at least 5% of the data to remove outliers, and it was considered that ignoring observations greater than 50 m from the trail in the field would achieve a similar result. After selecting the model DISTANCE then estimates the density of nests km$^{-2}$, and allows this result to be calibrated using additional parameters such that:

$$D = \frac{d_n}{r \times p \times t}$$

where;

$D$ = orangutan density,

$d_n$ = estimated nest density,

$r$ = the rate at which orangutans build nests,

$p$ = the proportion of the population that builds nests,

$t$ = the duration of nest visibility.

In order to monitor monthly variation, densities were first estimated using only nests that had been built since the previous month's census (the 'new nest' method). For this purpose only the parameters $r$ and $p$ were required. In order to assess the precision of the new nest method, densities were also estimated at each site using nests of all ages (the 'all nest' method), for which the additional parameter $t$ is required. Estimates using all nests were only possible during the first month of monitoring at each site since it was considered that previous knowledge of the location of some nests in subsequent months could bias the estimates produced. New nests on the other hand can only be identified after the first census. Therefore, since densities do fluctuate the usefulness of such comparisons between the two methods is limited but it was still considered that potential flaws in the methodology may be highlighted in this way.

In anticipation of a need to calibrate density estimates produced using nests as an indicator of animal densities with an estimate of absolute densities, a further method was also employed. For this purpose data were also collected on the location and distance from the trail of all orangutans encountered during searches outside and to the south of the WCS study area during 1998. This allowed density estimates to be made using direct sightings of orangutans rather than using nests as a 'sign'. The program DISTANCE was again used but without the need for the parameters $r$, $p$ and $t$.

## 3.3. RESULTS

### 3.3.1. JUSTIFICATION OF NEST METHOD

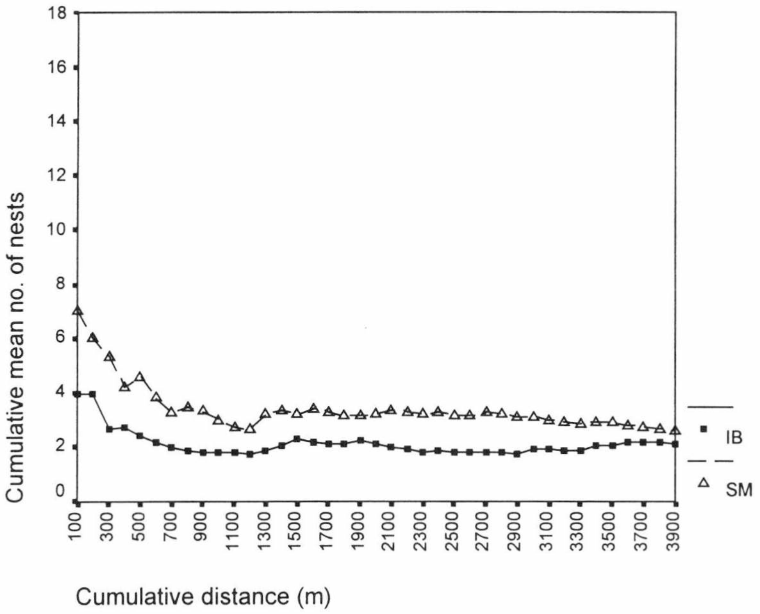
#### 3.3.1.1. *Minimum transect length required*

To determine the length of transect line required to ensure a realistic estimate of density approximately 4 km of transect, were surveyed at both the IB and SM sites in March and April 1997. Thus it was possible to calculate the cumulative mean number of new nests and of all nests, per 100 m of transect, with increasing cumulative length of transect surveyed. The results of this are shown in Figure 3.1. For clarity, 'new nests' refers to nests not identified in any previous censuses and therefore comprises only those built during the preceding month, whilst 'all nests' includes all nests that were present the previous month as well as new nests.

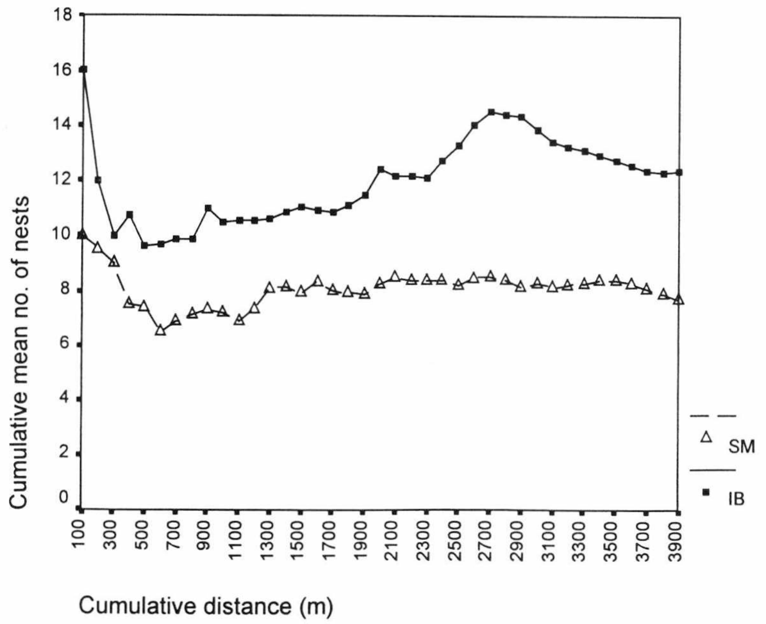
As can be seen, the rank order of the two sites remains constant throughout, both for new nests (Figure 3.1a) and for all nests (Figure 3.1b), but after an initial drop the cumulative mean number of new nests appears to level off, fluctuating around 3.0 at SM and 2.0 at IB after approximately 700 m. When all nests are considered, however, it can be seen that the IB area is unusual in that a distinct increase occurred between 2500 m and 3000 m along the trails. This was also apparent in the field as an exceptionally large number of nests were encountered along one stretch of trail there (trail SJ, approximately 1 km in length). This stretch of trail ran parallel to the IB trail, but 500 m to the south. The fourth trail at this site (trail NI, also 1 km in length and which is represented in the graph as the area from 2900 m to 3900 m), similarly ran parallel to, but 500 m to the north of IB. In contrast to trail SJ, however, trail NI had fewer nests per 100 m than both the IB and FR trails (trail FR running N-S, joining the three other trails at their midpoints). For these reasons the 1900 m combined length of IB and FR was used, since IB and FR were intermediate between the two extremes.

**Figure 3.1**: Cumulative mean number of (a) new nests, and (b) all nests, per 100 m along transects SM and IB in April 1997.

(a) New nests



(b) All nests



### 3.3.1.2. *Estimating nest-building rate 'r'*

To estimate densities of orangutans from nest densities, it is first necessary to estimate the rate at which orangutans build nests *r*. All orangutans, with the exception of infants and younger juveniles, construct new nests most nights (night nests) and frequently build one or more nests during the day for resting or play (day nests). Infants and younger juveniles invariably share nests with their mothers whilst older juveniles will sometimes construct their own, especially during the day. Occasionally orangutans will re-build or re-use already extant nests though this is generally considered a rare event (van Schaik *et al.* 1995b).

**Table 3.1**: Nest building rates (new nests/day/individual), based on nest to nest follows.

| Age/sex class | No. of individuals | No. of follows | No. of nests built | Mean no. of nests built/day | SD |
|---|---|---|---|---|---|
| Adult males | 12 | 126 | 208 | 1.651 | 0.752 |
| Subadult males | 11 | 73 | 180 | 2.466 | 1.248 |
| Adolescent males | 4 | 16 | 36 | 2.250 | 1.528 |
| Adult females | 18 | 410 | 757 | 1.846 | 0.981 |
| Immature females | 7 | 35 | 74 | 2.114 | 0.900 |
| All males | 27 | 215 | 424 | 1.970 | 1.080 |
| All females | 25 | 445 | 831 | 1.870 | 0.980 |
| All orangutans | 52 | 660 | 1255 | 1.902 | 1.012 |

Table 3.1 shows the rate (in nests/day/individual) at which orangutans belonging to each of the main age/sex categories construct new nests, with the exception of infants and juveniles. These data were collected over 660 full day focal individual follows (i.e. nest to nest), and show that the overall mean build rate for all orangutans was 1.902 nests/day/individual of nest building age. Some variation does appear to exist between age/sex classes but a one-way ANOVA failed to detect any significant differences between them ($F_{(5,47)} = 0.417$, $p = 0.834$). Therefore the value of 1.9 for $r$ represents the best available, and was adopted in conjunction with an estimate of the proportion of the population that builds nests $p$.

### 3.3.1.3. *Estimating proportion of population building nests 'p'*

MacKinnon (1974) found 49 of 346 individuals were young infants (i.e. 14%), in both Sumatran and Bornean forests. Van Schaik *et al.* (1995b) examined this for Suaq Balimbing and noted that 4 out of 40 individuals were small infants, and Mitrasetia (cited in van Schaik *et al.* 1995b) found 4 out of 39 at Ketambe. Consequently both of the latter authors estimated that around 10% of these populations were young infants. The figure obtained by this study, using all records of known and identified individuals within the WCS study area, supports these estimates as 9 out of 86 (excluding two that disappeared shortly after birth), were found to be young infants (below age 5) giving 10.47%. Thus approximately 90% of the population are nest builders and an estimate for $p$ of 0.9 therefore seems reasonable. It also allows for easier comparison of the results with van Schaik *et al.*'s (1995b) estimates.

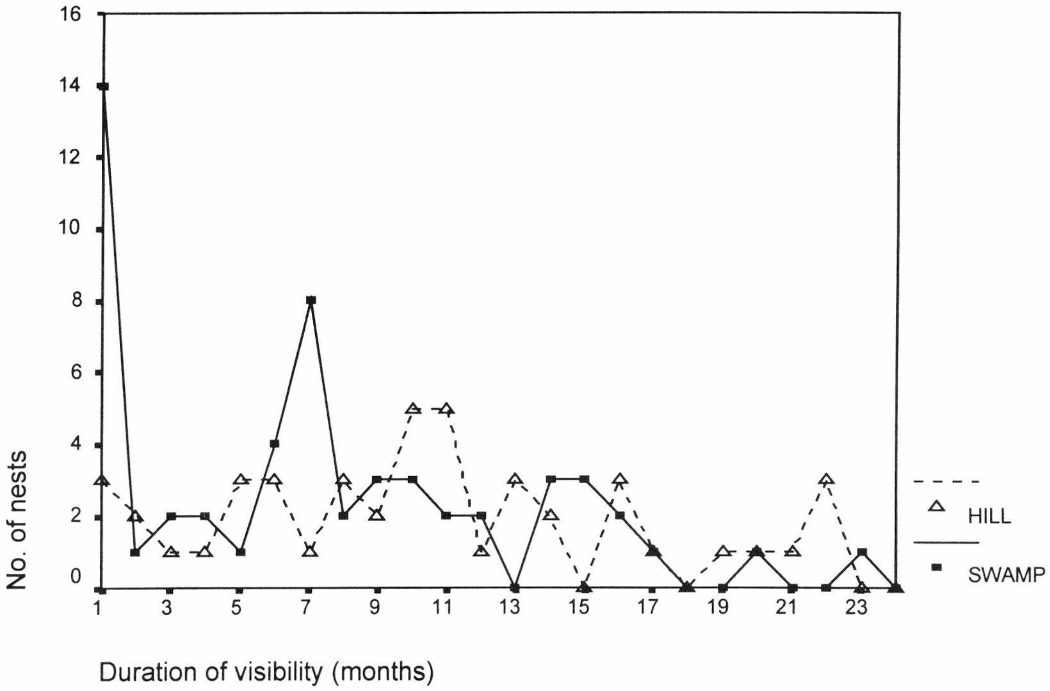
### 3.3.1.4. *Estimating duration of nest visibility 't'*

For the estimates using 'all nests' the same values of the parameters $r$ and $p$ could be used but with the addition of $t$, to account for the duration of visibility of nests, or nest decay rate. A total of 108 nests that were constructed in the WCS plots during April and May of 1997 were monitored until final disappearance, or in the case of four of these nests, to February 1999. Their location in terms of swamp or hill forest, and the mean and median duration of visibility (in months) are shown in Table 3.2, with a frequency graph in Figure 3.2. Nests that were known to have been re-built at some point during their lifespan, by a change of age class from an older to a newer nest, were excluded from the calculations (a total of 8 nests). Of the four nests still extant at the end of February 1999, one was assumed to disappear after one additional month as it had been class 4 for nine months. The others were assumed to disappear before the end of the next month (i.e. after 22 months) as each had already been class 5 for two or more months. These nests would appear to be exceptional and assigning these values was considered unlikely to significantly affect calculation of the mean duration of visibility *t*.

**Table 3.2**: Median and mean duration of visibility of nests in months, for nests recorded as new in April and May 1997, in two swamp plots combined, and the Hill plot.

| Location | No. of nests | Median | Mean | SD |
|---|---|---|---|---|
| Hill | 45 | 10 | 10.47 | 5.94 |
| Swamp (HJPLX and X) | 55 | 7 | 7.51 | 5.65 |

**Figure 3.2**: Duration of nest visibility (months) for both swamp and hill habitats.



An independent-samples t-test showed that mean nest decay rates in the two habitat types were significantly different (t = 2.546; df = 98; p = 0.012). In addition, Figure 3.2 shows that a large number of nests disappeared very quickly (within 1 month) in the swamp habitats. This almost certainly represents less durable day nests disappearing more rapidly than stronger night nests. After the disappearance of these nests, the frequency distribution of nest decay rates does appear to exhibit a moderate increase to a peak (or median) of around 7-8 months in the swamps. Thus the duration of nest visibility appears to be bimodal in the swamps, as flimsy nests (probably mostly day nests) disappear quickly and sturdy ones more slowly.

A potential error in estimating decay rates is the accidental inclusion of nests that are re-built, hence prolonging their observed duration, though as stated, those nests known to have been re-built were excluded. However, this may not have included all re-built nests, as some improvements made by orangutans, such as reinforcing the base of a nest from the inside, could easily have gone undetected in the monitoring process, whilst nonetheless prolonging nest life-span. To assess the likelihood of this, some comparisons were made between various estimates of the ratio between the rate of re-building to the rate of building nests from scratch.

**Table 3.3**: Rate of re-using/re-building already extant nests (nests/day/individual), based on nest to nest follows.

| Age/sex class | No. of individuals | No. of follows | No. of nests | Mean/day | SD |
|---|---|---|---|---|---|
| Adult males | 12 | 126 | 5 | 0.040 | 0.196 |
| Subadult males | 11 | 73 | 2 | 0.027 | 0.164 |
| Adolescent males | 4 | 16 | 4 | 0.250 | 0.577 |
| Adult females | 18 | 410 | 54 | 0.132 | 0.392 |
| Immature females | 7 | 35 | 3 | 0.086 | 0.373 |
| All orangutans | 52 | 660 | 68 | 0.103 | 0.351 |

Table 3.3 shows the rate at which orangutans were observed to re-build or re-use old nests during focal animal follows, a mean of 0.10 nests/individual/day for all age/sex classes. From this it follows that the ratio of nests re-built and re-used to nests built from scratch is 0.1:1.9. Thus for every 19 nests actually built from scratch, a further 1 nest would be expected to be re-built or re-used (or in other words that of a sample of nests built, roughly 5% would be expected to be re-used or re-built at some time during their lifespan). It should be noted that this figure refers to nests both re-used and re-built i.e. not physically re-built alone, and as such, should be higher than the proportion of nests observed to be re-built during nest censuses.

If the nests used in the estimation of $t$ are then considered, we find that of 108 nests, 8 (7.41%) were observed to be re-built during their life-span, when the expected number would be 108/19 or 5.68 nests. This suggests that re-building of nests should be adequately accounted for if these 8 nests are excluded from the estimation of $t$, particularly if it is remembered that the 5% figure also includes re-using of nests, which would go undetected during censuses. Similarly, an examination of all the nests monitored along transects between April 1997 and September 1998, shows that a total of 119 incidences of re-building were observed among 2196 nests when the expected number (2196/19) would be 115.58 nests. Also, among 726 nests recorded as new in the same period, 36 incidences of re-building were recorded, with an expected value of 38.21. Both the latter estimates are liable to be slightly biased as many nests will not have been monitored for their entire life-span, being already present at the onset of monitoring (in the case of the 2196 nests), or still extant at the end. Despite this problem, the large sample sizes involved, combined with the fact that nests already present at the onset should roughly cancel out those still present at the end, suggests that the methods employed do adequately identify cases of re-building, and that the estimate of around 5% as the rate of re-building is close to reality.

Hence, since the assessment of the number of re-built nests (which were excluded from the estimation of nest disappearance times) did not yield any obvious biases, the observed values being so similar to expected values, the $t$ estimates of Table 3.2 were used.

The parameters used for estimating densities are therefore: nest construction rate $r = 1.9$ nests/day/nest building individual, the proportion of the population that builds nests $p = 0.9$, and the duration of nest visibility $t = 7.5$ months for swamp habitats and 10.5 months in the hills (equating to approximately 228 days and 319 days respectively). To equate the measurement units of $r$ and $t$, $r$ was multiplied by 365/12 i.e. the mean number of days in a month, to give 57.79.

### 3.3.2. DENSITY ESTIMATES

#### 3.3.2.1. *Estimates using direct sightings*

During mid-1998, whilst searching outside and to the south of the WCS study area for individual orangutans, I walked some 73.157 km along the trails surrounding the SM and GB transects. In anticipation of a need to calibrate densities estimated using nests I also recorded the location of all orangutans encountered, and estimated their distance from the trail at the time they were first located. This resulted in encounters with 43 orangutans ranging from 0-70 m from the trail. Using DISTANCE and the uniform and cosine or Fourier series model (shown below to produce results highly comparable to other models), a density estimate for the area surrounding and including the GB and SM transect locations of 5.34 km$^{-2}$ was obtained (%CV = 21.20, df = 42, LCL = 3.500, UCL = 8.158), with an estimated strip width of 54.997 m (%CV = 14.72, df = 42, LCL = 0.952, UCL = 73.908). Lower and upper confidence limits (LCL and UCL) are 95% throughout.

### 3.3.2.2. *Estimates using nests*

#### 3.3.2.2.1. *New nests*

Using new nests, densities were estimated each month at each transect in order to explore possible relationships between orangutan movements and forest productivity (see Chapter 5). Using new nests alone, rather than 'all nests', is necessary if monthly fluctuations are to be identified, as the interval between censuses is far less than the mean duration of nest visibility.

When using DISTANCE in this manner, two options exist for attempting to fit the model. Buckland *et al.* (1993) suggest that where censuses are conducted in the same area by the same observer over regular time intervals it may be prudent to pool the data for each month over a longer time period and to fit the model to this larger sample. The alternative is to attempt to fit the model on a monthly basis (i.e. for each plot, each month), but the small number of new nests in some months, along some transects, precluded this, producing errors and on the whole greater coefficients of variation. Therefore, as the various habitats sampled contained few or no deciduous trees and hence that visibility was considered unlikely to vary noticeably between months, and as transects were monitored by the same observer each month, the first option was subsequently used.

An additional option that was investigated was to use the uniform and cosine model provided in DISTANCE. This is the same as the Fourier series model of Crain *et al.* (1979) and Burnham *et al.* (1980), which has often been adopted in previous primate studies (e.g. Brockelman and Ali 1987; van Schaik *et al.* 1995b; Blouch 1997). All estimates were therefore re-calculated using this model. The results were found to be highly comparable to those obtained using the model selected by DISTANCE using minimum AIC, though in most cases the Fourier series estimates were slightly lower (by around 0.1 of an individual), and with slightly higher coefficients of variation. For these reasons the results from the initial procedure were considered to be the most reliable and are shown in complete form in Table 3.4 and summarised to give density estimates and estimated strip widths at transect level in Tables 3.5 and 3.6.

Using the minimum AIC selection criteria, DENSITY selected the hazard rate and cosine model for all of the swamp-based transects, whilst choosing the uniform and simple polynomial model for the HILL transect (Table 3.6). The results shown give an overall area-wide density estimate of 2.87 $km^{-2}$ ± 0.869 (i.e. the mean of all transects from Table 3.5). Without the HILL transect the mean of the five swamp-based plots is higher, at 3.16 $km^{-2}$ ± 0.583. It should be noted here, however, that for some transects the first month's density estimates appear remarkably high (Table 3.4) and almost certainly reflect the observer noticing for the first time some nests that were in fact present, but not seen during the initial survey. As a result, area-wide estimates (from Table 3.5) will be slightly biased upwards, though the effect is likely to be negligible.

To verify the area-wide mean of 2. 87 $km^{-2}$, area-wide densities were estimated a second time by pooling the three swamp-based transects for which 17 months of data were available, thereby effectively using the combined data, and combined length of all three transects as a single long transect. The results are tabulated in Appendix 1 and the resultant area-wide temporal variation shown graphically in Figure 3.3. From this it appears that over the swamp area covered by these three plots, densities do vary over time whilst the mean overall density (across all months) was 3.027 $km^{-2}$ ± 0.923.

To assess the accuracy of these density estimates, the frequency distributions of the perpendicular distances of new nests were plotted (Figure 3.4). The number of new nests in a given distance class represents the number of all the nests recorded as new in any month, and along any transect, during the whole period. Thus all new nests are included, but each is included only once. The figure clearly indicates some heaping of perpendicular distances in the 20-24 m category. Despite this, however, DISTANCE should at least in part, reduce any errors resulting from spiked distributions by fitting appropriate models (Buckland *et al*. 1993).

**Table 3.4**: Monthly density estimates (km$^{-2}$) obtained by DISTANCE, using new nests for transects (a) GB, (b) HJPLX, (c) HILL, (d) IB, (e) SM and (f) X.

| | Month | No. of nests | Density | %CV | 95% LCL | 95% UCL |
|---|---|---|---|---|---|---|
| (a) GB | Sep-97 | 51 | 7.903 | 14.98 | 5.892 | 10.599 |
| | Oct-97 | 14 | 2.169 | 27.25 | 1.280 | 3.676 |
| | Nov-97 | 21 | 3.254 | 22.46 | 2.102 | 5.039 |
| | Dec-97 | 14 | 2.169 | 27.25 | 1.280 | 3.676 |
| | Jan-98 | 13 | 2.014 | 28.24 | 1.167 | 3.477 |
| | Feb-98 | 18 | 2.789 | 24.16 | 1.744 | 4.460 |
| | Mar-98 | 8 | 1.240 | 35.75 | 0.626 | 2.456 |
| | Apr-98 | 9 | 1.395 | 33.76 | 0.730 | 2.664 |
| | May-98 | 5 | 0.775 | 45.04 | 0.332 | 1.807 |
| | Jun-98 | 14 | 2.169 | 27.25 | 1.280 | 3.676 |
| | Jul-98 | 21 | 3.254 | 22.46 | 2.102 | 5.039 |
| | Aug-98 | 17 | 2.634 | 24.83 | 1.627 | 4.266 |
| | Sep-98 | 21 | 3.254 | 22.46 | 2.102 | 5.039 |
| (b) HJPLX | Apr-97 | 20 | 4.467 | 22.97 | 2.857 | 6.985 |
| | May-97 | 8 | 1.787 | 35.75 | 0.902 | 3.540 |
| | Jun-97 | 12 | 2.680 | 29.34 | 1.521 | 4.723 |
| | Jul-97 | 9 | 2.010 | 33.75 | 1.052 | 3.841 |
| | Aug-97 | 11 | 2.457 | 30.61 | 1.362 | 4.432 |
| | Sep-97 | 12 | 2.680 | 29.34 | 1.521 | 4.723 |
| | Oct-97 | 18 | 4.020 | 24.15 | 2.514 | 6.429 |
| | Nov-97 | 12 | 2.680 | 29.34 | 1.521 | 4.723 |
| | Dec-97 | 8 | 1.787 | 35.75 | 0.902 | 3.540 |
| | Jan-98 | 7 | 1.564 | 38.16 | 0.756 | 3.234 |
| | Feb-98 | 6 | 1.340 | 41.16 | 0.614 | 2.923 |
| | Mar-98 | 17 | 3.797 | 24.82 | 2.345 | 6.149 |
| | Apr-98 | 19 | 4.244 | 23.54 | 2.685 | 6.708 |
| | May-98 | 14 | 3.127 | 27.24 | 1.845 | 5.299 |
| | Jun-98 | 8 | 1.787 | 35.75 | 0.902 | 3.540 |
| | Jul-98 | 12 | 2.680 | 29.34 | 1.521 | 4.723 |
| | Aug-98 | 3 | 0.670 | 57.98 | 0.232 | 1.936 |
| | Sep-98 | 15 | 3.350 | 26.35 | 2.010 | 5.584 |
| (c) HILL | Apr-97 | 1 | 0.098 | 100.00 | 0.019 | 0.504 |
| | May-97 | 48 | 4.689 | 15.80 | 3.442 | 6.389 |
| | Jun-97 | 41 | 4.006 | 16.89 | 2.879 | 5.573 |
| | Jul-97 | 35 | 3.419 | 18.09 | 2.402 | 4.868 |
| | Aug-97 | 26 | 2.540 | 20.64 | 1.699 | 3.798 |
| | Sep-97 | 4 | 0.391 | 50.41 | 0.153 | 0.997 |
| | Oct-97 | 15 | 1.466 | 26.61 | 0.876 | 2.453 |
| | Nov-97 | 18 | 1.759 | 24.43 | 1.095 | 2.825 |
| | Dec-97 | 7 | 0.684 | 38.34 | 0.330 | 1.418 |
| | Jan-98 | 8 | 0.782 | 35.94 | 0.394 | 1.552 |
| | Feb-98 | 14 | 1.368 | 27.49 | 0.804 | 2.327 |
| | Mar-98 | 11 | 1.075 | 30.83 | 0.594 | 1.945 |
| | Apr-98 | 9 | 0.879 | 33.95 | 0.459 | 1.685 |
| | May-98 | 3 | 0.293 | 58.09 | 0.101 | 0.847 |
| | Jun-98 | 9 | 0.879 | 33.95 | 0.459 | 1.685 |
| | Jul-98 | 10 | 0.977 | 32.27 | 0.526 | 1.816 |
| | Aug-98 | 3 | 0.293 | 58.09 | 0.101 | 0.847 |
| | Sep-98 | 6 | 0.586 | 41.33 | 0.268 | 1.281 |
| (d) IB | Apr-97 | 46 | 6.864 | 15.56 | 5.057 | 9.317 |
| | May-97 | 15 | 2.238 | 26.30 | 1.343 | 3.730 |
| | Jun-97 | 37 | 5.521 | 17.18 | 3.943 | 7.732 |
| | Jul-97 | 23 | 3.432 | 21.44 | 2.258 | 5.216 |
| | Aug-97 | 29 | 4.327 | 19.23 | 2.971 | 6.304 |
| | Sep-97 | 14 | 2.089 | 27.19 | 1.233 | 3.540 |

Table 3.4 continued

| | Month | No. of nests | Density | %CV | 95% LCL | 95% UCL |
|---|---|---|---|---|---|---|
| (e) SM | Apr-97 | 61 | 10.596 | 13.43 | 8.145 | 13.783 |
| | May-97 | 22 | 3.821 | 21.70 | 2.506 | 5.828 |
| | Jun-97 | 14 | 2.432 | 27.03 | 1.442 | 4.100 |
| | Jul-97 | 20 | 3.474 | 22.72 | 2.234 | 5.402 |
| | Aug-97 | 13 | 2.258 | 28.03 | 1.315 | 3.879 |
| | Sep-97 | 15 | 2.606 | 26.14 | 1.571 | 4.320 |
| | Oct-97 | 18 | 3.127 | 23.92 | 1.966 | 4.972 |
| | Nov-97 | 11 | 1.911 | 30.42 | 1.064 | 3.431 |
| | Dec-97 | 19 | 3.300 | 23.30 | 2.100 | 5.188 |
| | Jan-98 | 30 | 5.211 | 18.70 | 3.618 | 7.505 |
| | Feb-98 | 19 | 3.300 | 23.30 | 2.100 | 5.188 |
| | Mar-98 | 7 | 1.216 | 38.01 | 0.590 | 2.505 |
| | Apr-98 | 4 | 0.695 | 50.16 | 0.274 | 1.765 |
| | May-98 | 2 | 0.347 | 70.83 | 0.099 | 1.218 |
| | Jun-98 | 22 | 3.821 | 21.70 | 2.506 | 5.828 |
| | Jul-98 | 28 | 4.864 | 19.33 | 3.337 | 7.089 |
| | Aug-98 | 17 | 2.953 | 24.59 | 1.833 | 4.756 |
| | Sep-98 | 10 | 1.737 | 31.88 | 0.942 | 3.203 |
| (f) X | Apr-97 | 16 | 3.775 | 25.57 | 2.299 | 6.197 |
| | May-97 | 15 | 3.539 | 26.37 | 2.123 | 5.898 |
| | Jun-97 | 10 | 2.359 | 32.08 | 1.274 | 4.370 |
| | Jul-97 | 11 | 2.595 | 30.63 | 1.439 | 4.681 |
| | Aug-97 | 24 | 5.662 | 21.11 | 3.753 | 8.543 |
| | Sep-97 | 20 | 4.719 | 23.00 | 3.017 | 7.380 |
| | Oct-97 | 23 | 5.426 | 21.53 | 3.568 | 8.254 |
| | Nov-97 | 17 | 4.011 | 24.84 | 2.477 | 6.495 |
| | Dec-97 | 12 | 2.831 | 29.36 | 1.607 | 4.989 |
| | Jan-98 | 9 | 2.123 | 33.76 | 1.112 | 4.056 |
| | Feb-98 | 10 | 2.359 | 32.08 | 1.274 | 4.370 |
| | Mar-98 | 10 | 2.359 | 32.08 | 1.274 | 4.370 |
| | Apr-98 | 9 | 2.123 | 33.76 | 1.112 | 4.056 |
| | May-98 | 4 | 0.944 | 50.29 | 0.370 | 2.405 |
| | Jun-98 | 3 | 0.708 | 57.99 | 0.245 | 2.044 |
| | Jul-98 | 26 | 6.134 | 20.34 | 4.126 | 9.119 |
| | Aug-98 | 9 | 2.123 | 33.76 | 1.112 | 4.056 |
| | Sep-98 | 16 | 3.775 | 25.57 | 2.299 | 6.197 |

**Table 3.5**: Densities (individuals $\text{km}^{-2}$) estimated using new nests, over all months pooled for each transect.

| Transect | number of months | Density | %CV | 95%LCL | 95%UCL |
|---|---|---|---|---|---|
| GB | 13 | 2.69 | 18.81 | 1.81 | 4.02 |
| HJPLX | 18 | 2.62 | 10.93 | 2.10 | 3.27 |
| HILL | 18 | 1.45 | 22.68 | 0.91 | 2.32 |
| IB | 6 | 4.08 | 19.46 | 2.54 | 6.54 |
| SM | 18 | 3.20 | 17.08 | 2.25 | 4.57 |
| X | 18 | 3.20 | 12.62 | 2.47 | 4.14 |

**Table 3.6**: Models chosen by DISTANCE and estimated strip widths (ESW, in metres), using new nests.

| Transect | Model | ESW (m) | %CV | 95%LCL | 95%UCL |
|---|---|---|---|---|---|
| GB | Hazard rate and cosine | 33.27 | 5.32 | 29.96 | 36.94 |
| HJPLX | Hazard rate and cosine | 27.77 | 5.27 | 25.03 | 30.81 |
| HILL | Uniform and simple polynomial | 31.90 | 6.44 | 28.10 | 36.20 |
| IB | Hazard rate and cosine | 32.67 | 4.98 | 29.61 | 36.04 |
| SM | Hazard rate and cosine | 28.31 | 4.05 | 26.14 | 30.66 |
| X | Hazard rate and cosine | 30.52 | 5.38 | 27.46 | 33.93 |

#### 3.3.2.2.2. *All nests*

As the inclusion of nests that were already known from previous months was considered a potential source of bias (through artificially enhancing detectability), densities could only be estimated using all nests for the first month of monitoring, and hence only for GB, IB and SM. This is because all of the other transects had been continuously monitored for several years, and hence many nests along these transects were already known and identified. Again DISTANCE was allowed to select the best fitting model from those provided using minimum AIC but unlike the new nests method, using all nests to estimate densities requires the additional parameter $t$ (the duration of nest visibility). Results are given in Tables 3.7 and 3.8. Comparing Table 3.7 with Table 3.5 shows that the rank of each of the three transects with respect to the others remains the same as with new nests, whilst actual density estimates are slightly lower using all nests at SM, slightly higher at GB and distinctly higher at IB. This is more clearly illustrated in Figure 3.6. It must be remembered, however, that the estimates using new nests (Table 3.5) represent several months of monitoring for each transect, whilst those using all nests (Table 3.7) are estimated only for very first month of monitoring. Therefore differences between the two methods are expected, since they reflect different time periods and densities clearly fluctuate at transect level between months. Although the lower coefficients of variation of the estimates for GB and IB using all nests might suggest greater precision with this method, this is not the case at SM, for which all nests produced a slightly higher coefficient. In addition, the resulting estimated strip widths are also lower for all of the transects when using all nests. This is quite marked for the SM and IB transects at around 20 metres for both using the all nest method as opposed to 28.31 m and 32.67 m respectively using new nests. At GB the difference is less marked but still distinctly lower using the all nest method (28.17 m using all nests versus 33.27 m using new nests).

**Figure 3.3**: Monthly densities estimated by DISTANCE using minimum AIC and new nests, and pooling transects HJPLX, X and SM each month. Upper and lower 95 % confidence limits shown by the dotted lines.

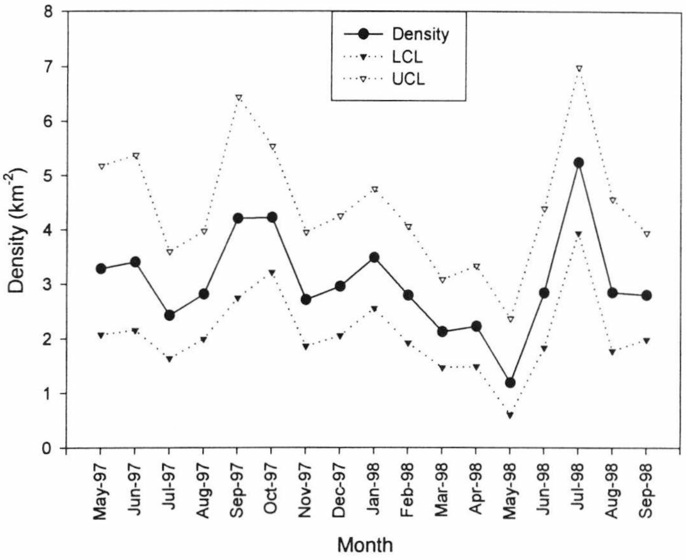


**Figure 3.4**: Distribution of perpendicular distances (m) of new nests in all plots and all months combined, using classes 0-4 m, 5-9 m, 10-14 m etc., inclusive.

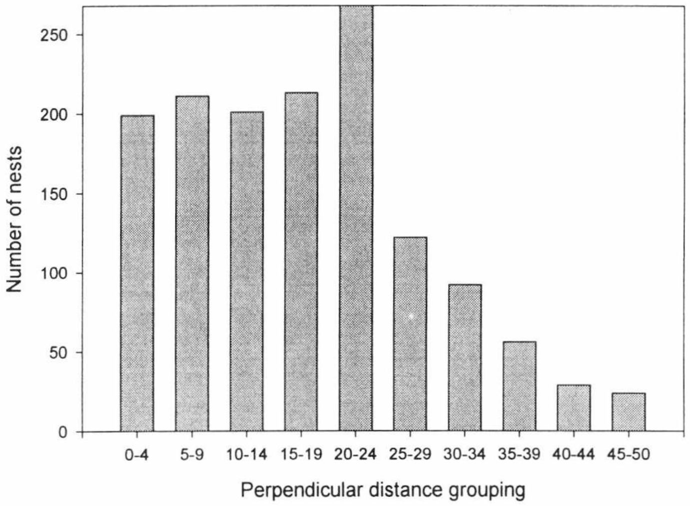


**Table 3.7**: Estimated densities (ind.km$^{-2}$) for plots GB, SM and IB, using all nests during initial month's census only. Associated nest densities also given (Nests km$^{-2}$) before use of multipliers.

| Transect | No. of nests | Nest density (nests km$^{-2}$) | Density (Ind. km$^{-2}$) | %CV | 95%LCL | 95%UCL |
|---|---|---|---|---|---|---|
| GB | 117 | 1113.6 | 2.86 | 9.84 | 2.35 | 3.47 |
| IB | 187 | 2348.6 | 6.02 | 9.26 | 5.02 | 7.22 |
| SM | 98 | 1212.4 | 3.11 | 18.58 | 2.16 | 4.48 |

**Table 3.8**: Models chosen by DISTANCE and estimated strip widths (ESW, in metres) using all nests, during initial month's census only.

| Transect | Model | ESW (m) | %CV | 95%LCL | 95%UCL |
|---|---|---|---|---|---|
| GB | Uniform and simple polynomial | 28.17 | 3.36 | 26.36 | 30.10 |
| IB | Uniform and cosine | 20.19 | 5.67 | 18.05 | 22.58 |
| SM | Half normal and hermite | 20.67 | 15.59 | 15.20 | 28.12 |

**Figure 3.5**: Density estimates for each transect using new nests only, and 'all nests' during the first month of monitoring (GB, IB and SM), arranged north-south (Hill imposed first).

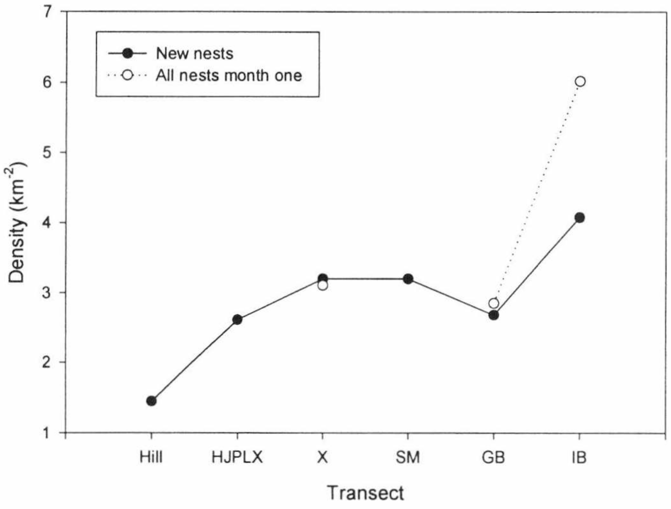
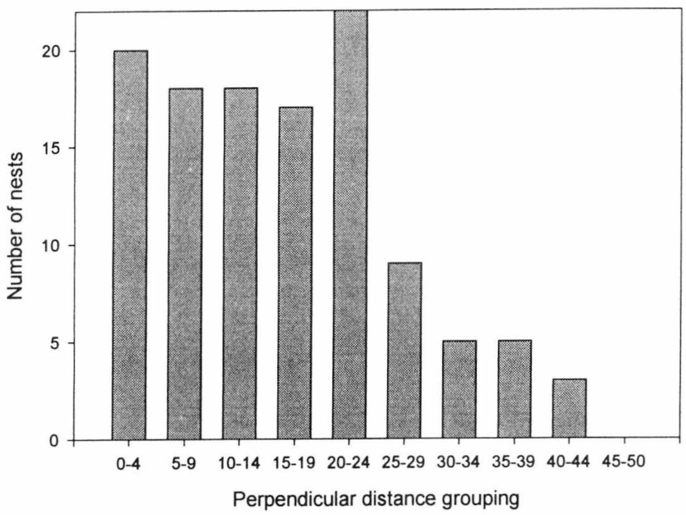
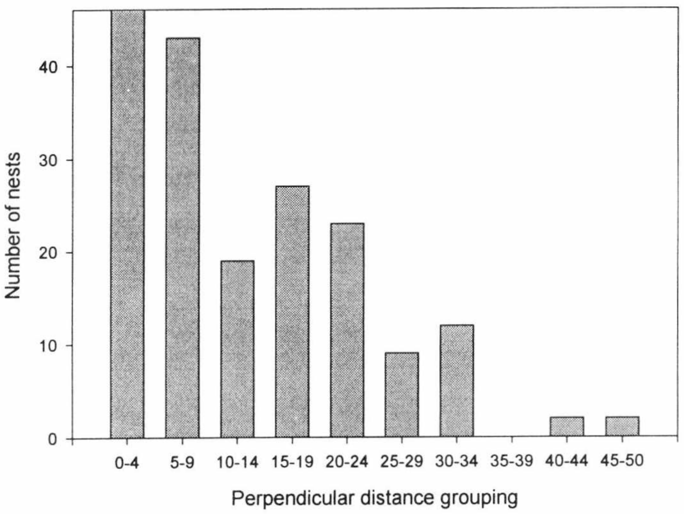


**Figure 3.6**: Distribution of perpendicular distances of 'all nests' for (a) GB in August 1997, (b) IB in March 1997 and (c) SM in March 1997.

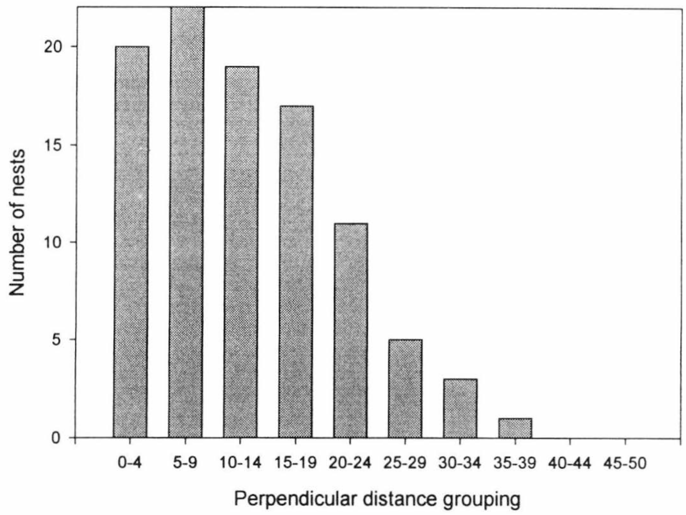
(a) GB



(b) IB



(c) SM



As when using new nests, the frequency distributions of the perpendicular distances of all nests were again plotted to attempt to identify any problems with the data (Figure 3.6). Again evidence of heaping perpendicular distances in the 20-24 m category was found, but not at all transects. A peak is clearly visible for GB (Figure 3.6a), but not for the other two.

## 3.4. DISCUSSION

The most striking result here is a large discrepancy between the density estimates produced, and those produced earlier by van Schaik *et al.* (1995b) of 6.9 km$^{-2}$, even though one of the same transects (X), estimated here using new nests to give a density of around 3.2 km$^{-2}$, was used in both studies. This estimate is also much lower than the perceived density of orangutans in the study area during fieldwork. The impression gained in the field was certainly that densities in the Suaq Balimbing area were noticeably higher than at Ketambe, which lies on an alluvial floodplain at the centre of the Leuser ecosystem. Previous estimates from Ketambe using line transect methods in conjunction with almost 30 years of continuous fieldwork, are all around 5 km$^{-2}$ (see Rijksen 1978; van Schaik *et al.* 1995b; Rijksen and Meijaard 1999). Several researchers (including myself) have visited both locations and all seem to agree that orangutans are more numerous at Suaq Balimbing. Thus it is strongly suspected that most, if not all, of the density estimates produced here, at least using nests, are in fact underestimates of absolute densities at Suaq Balimbing. Reference should also be made to the estimates produced using direct sightings of individuals. Although the methods were rather crude, and combined with the fact that some individuals close to the trail will almost certainly have been missed, these figures suggest that the true density of orangutans in the area around SM and GB is probably closer to 5.5 km$^{-2}$, than to the estimates using nests of between 2.69 km$^{-2}$ and 3.2 km$^{-2}$. In turn, assuming that the relative proportions between densities at the various transects are similar to those given in Table 3.5, this would imply that densities around the X transect are probably also closer in reality to 5.5 km$^{-2}$, and hence also to van Schaik *et al.*'s estimate.

These observations together with the discrepancies between density and strip width estimates produced using the two nest methods, and the evidence of heaping of perpendicular distances in the 20-24 m category, clearly also suggest that some problems exist with the methods. Thus all potential sources of error must be explored to evaluate their possible impact on density estimates, and hence to infer what absolute densities might be.

### 3.4.1. ASSUMPTIONS

Four basic assumptions are critical to achieving reliable estimates of animal densities when using line transect techniques (Buckland *et al.* 1993):

1) Objects are detected at their initial location.
2) All objects at zero distance from the transect (i.e. on or above the trail), are detected.
3) Distances are measured accurately.
4) Transects are located randomly in respect to the terrain, and hence the distribution of animals (or sign).

The first of these is clearly met since nests do not move. The remaining assumptions must, however, be addressed.

#### 3.4.1.1. *Detecting nests on or near the trail*

Figure 3.4 shows the observed distribution of perpendicular distances of new nests, in all transects combined, and over all months combined. As noted earlier a clear peak in the 20-24 m class is apparent. If this peak reflects the true number of nests at the 20-24 m from the trail, it would indicate that some nests between 0 m and 20 m, and hence probably some on or above the transect were missed. Interestingly, however, examination of the distribution of perpendicular distances of all nests (in month one of monitoring) at plots GB, IB and SM (Figure 3.6) shows less evidence for such a peak at both IB and SM, whilst a similar phenomenon is also apparent at GB. Under-recording of nests on or above the transect line therefore remains a possibility and cannot be discounted. That this feature is less marked for all nests at IB and SM, however, suggests that this assumption may have been met at some transects, at least in some months, though where it has not been met, estimates will be biased low as a result (Buckland *et al.* 1993).

#### 3.4.1.2. *Estimating distance from the trail*

All perpendicular distances were estimated by the observer as accurate measurements would have been prohibitively time consuming in the field, and in hindsight, there probably was a tendency of the observer to round distances to the nearest 5 m. This does not explain, however, why so many nests should be assigned to the 20-24m class.

An explanation might be provided by inaccuracies in estimating perpendicular distances i.e. underestimating distances that were greater than 24 m, or over-estimating those that were less than 20 m, and incorrectly assigning them to this distance class. Closer examination of the graphs does indeed reveal a clear drop in Figure 3.4, after the 20-24 m class to a much lower number of nests in the following 25-29 m class. Thus the peak could indeed be a result of a tendency of the observer to erroneously assign some nests from the latter category as falling within the former, and equally some nests from less than 20 m, could also have been erroneously assigned to the 20-24 m category. Buckland *et al.* (1993) state that ideally, recorded distances are exact, or for grouped data, detected objects are assumed to be correctly assigned. However, they also state that reliable estimates of density are still possible even if this assumption is violated.

Two alternative explanations exist for the anomalous peak in nests at some distance away from the trail. Firstly, in dense forests even an experienced observer might be expected to see more nests at a given distance from the trail since the nature of forests would suggest that there probably does exist a real distance at which the line of sight is least obstructed by foliage. Looking directly up from the trail the line of sight is impeded by the lower branches of trees meaning that some nests, especially higher ones, would be obscured from view, whilst at distance, nests lower down would be hidden. Indeed beyond 30 m from the trail no nests were recorded below 10 m in height. Thus no matter how well perpendicular distances are estimated, some nests within a certain distance of the trail, or beyond a certain distance, are likely to be missed. Secondly, orangutans may actively avoid nesting near forest trails, especially if they are very familiar with the area and know precisely where they are located. The disadvantages of nesting in more open areas, which may be more exposed to the weather and also make them more vulnerable to disturbance by other animals using the trails for travel e.g. bears, tigers and researchers would appear obvious. Also the density of small trees that are often selected by orangutans may be reduced immediately on or adjacent to some long established trails. However, the majority of trails in the area are not so clearly defined due to the abundance of ground vegetation, and even relatively small trees were retained during trail clearance. Orangutans were also frequently observed to nest above trails during focal animal follows.

It is therefore considered that a combination of: (1) missing some nests close to the trail, and (2) some degree of heaping distance estimates at around 20 m, will have created the observed peaks in the distributions. Together these facts will almost certainly have led to overestimates of strip widths and hence underestimates of densities, particularly if the heaping of distances is a result of overestimating distances as is suspected.

#### 3.4.1.3. *Random location of transects*

A further assumption of line transect sampling is that transects are located randomly with respect to the distribution of objects. In hilly terrain this may produce seriously distorted estimates if orangutans show a preference for, or avoidance of, nesting close to ridges, and transects do not adequately cover a variety of slopes and aspects. To take account of this the HILL transect was located by van Schaik (pers. comm.) to cover both the ridges and bottoms of slopes and also ascending and descending slopes. Trail location was considered a less important factor in the flat, more homogenous, swamps and transects there generally follow straight lines, forming crosses in the south (see Chapter 2).

In addition to these four basic assumptions, it is also true that observers may vary widely in their ability to detect nests (Payne 1987; Rijksen 1978; van Schaik *et al.* 1995b). This need not lead to large differences in density estimates, however, since lower nest counts should be compensated by lower estimated strip widths (Buckland *et al.* 1993; Burnham *et al.* 1984). Despite this, to negate any potential for bias the same observer was used for all censuses though it must be recognised that a single observer may still vary in his or her ability to detect nests due to fatigue, weather conditions etc., so potential for error inevitably remains. Furthermore, there are several further potential sources of bias that must also be addressed.

### 3.4.2. MINIMUM TRANSECT LENGTH REQUIRED

Mackinnon (1974), Rijksen (1978) and Payne (1987) all showed evidence of clumping of orangutan nests, and so the additional assumption, that transects are sufficiently long to give a realistic estimate of density in an area must also be examined. The encounter rates of all nests at SM and of new nests at both SM and IB did level out after around 1500 m, suggesting that the adopted transect lengths of circa 2000 m were adequate, and are probably also adequate for most swamp based transects. However, the marked increase in the cumulative number of all nests per 100 m at IB that occurred with the inclusion of the SJ trail, suggests this assumption may not have been met there. Adopting the IB and FR trails at this site was nevertheless considered likely to give the most accurate picture of the area that was realistically possible, since these trails fell between the two extremes. In any case monitoring at IB ceased after just 7 months as the distance from the base camp made continuing impractical. These points must be borne in mind, however, when examining the results obtained at IB, as they constitute clear evidence that at least in the far south, considerable variation may occur in orangutan densities within a relatively localised area. As the hills tend to support fewer orangutans, a longer transect of some 3000 m was adopted there by van Schaik.

Clearly there is evidence that some basic assumptions may not have been adequately met. It is also difficult to determine precisely in which direction estimates will be biased as a result, nor by how much. As the resultant density estimates were already considered unrealistically low, however, it is most likely that a combination of the above problems has resulted in overestimates of strip widths.

Tables 3.6 and 3.8 show that for the GB, IB and SM transects the estimated strip width was lower with the all nest method then with the new nest method, despite the fact that the density estimates are roughly comparable with both. In fact the different strip width estimates produced by the two method at IB and SM are actually quite large, whilst being less marked but still distinct at GB. The coefficients of variation of these estimates, however, are lowest for IB and SM when using new nests, but for GB when using all nests.

A problem therefore exists here. The density estimates produced using new nests and using all nests are fairly comparable, whilst estimated strip widths are consistently lower with the all nest method, markedly so for IB and SM. There is therefore a need to come up with an explanation of why the all nest method still produces density estimates that are too low, whilst estimated strip widths, at least for IB and SM, are probably close to accurate, or perhaps even underestimates. For this reason the parameters r, p and t, but particularly the latter since it constitutes the most fundamental difference between the two methods, must also be examined.

### 3.4.3. ESTIMATING THE PARAMETERS *r*, *p*, *t*.

Bias is expected, since all parameters will undoubtedly show true spatial and temporal variation. The proportion of the population that builds nests $p$, however, appears to be more or less consistent across all major studies, at around 90% (i.e. $p = 0.9$), and the greatest potential errors are more likely to come from estimates of $r$, for both the new nest and all nest methods, and $t$ for the all nest method.

#### 3.4.3.1. *Estimating nest-building rate 'r'*

The rate at which orangutans build nests was found to be 1.9 nests per individual per day. Rijksen (1978) gave a figure of 1.8 for $r$, based on 36 orangutan days at Ketambe and Mitrasetia (cited in van Schaik *et al.* 1995b), also at Ketambe, arrived at $r = 1.7$, based on 437 orangutan days. Van Schaik *et al.* (1995b), using some of the same data examined here, arrived at 1.6 for $r$ based on 134 days, but opted to use the mean of the three estimates, at 1.7 when producing their estimate for orangutan densities at the X transect of 6.9 $km^{-2}$. This is therefore at least one reason why their estimates are higher than those produced here though as can be seen from Table 3.10, adopting this lower value here would only increase density estimates by 0.7 of an orangutan or less with the all nest method. Both of the latter studies made some attempt to include a weighting for population composition when arriving at these figures (van Schaik *et al.* 1995b; see Table 3.9). It appears, however, that in each case, simply the mean of the sample means for each class was taken and no attempt made to weight these values according to the relative proportions of each class within the population as a whole.

Using the same methods for this study produces a value of 1.99 as the overall mean, slightly higher than the adopted value. The most likely explanation of this variation in estimates is temporal (ignoring potential cultural differences between sites). Van Schaik *et al.*'s estimated 1.6 implies that for some reason the orangutans at Suaq Balimbing built fewer nests per day before 1995 than more recently. Indeed, the impression gained during preliminary examination of the data was that this may well be the case. Females and subadult males in particular appeared to build more nests during periods when a receptive female was being followed by several subadult males, and also often the dominant adult male, during 1995 when several infants were conceived. This was often due to females being harassed by subadult males, and therefore leaving one nest only to construct another one nearby. The subadult males would frequently also construct nests whilst seeming to wait for the females. This behaviour can sometimes result in 6 or more nests being constructed in a single day by one individual. Temporal variation in the rate of nest building therefore represents an uncontrollable bias and should always be taken into consideration when evaluating densities estimated using nests, as the age of offspring and hence reproductive status of females, can affect the number of nests they build. One way to overcome this might be to use averages over periods greater than the inter-birth interval (assumed to be around 8 years; Leighton *et al.* 1995), though in the majority of cases this would be impractical. Also, since the timing of the census within this 'cycle' would be unknown $r$ is still likely to be inaccurate to some degree and furthermore, the majority of 'extra' nests built would most probably be flimsy day nests, that would disappear more quickly or go undetected. Hence there may be justification for using more conservative estimates of $r$, rather than to risk overestimating it, though as already noted small changes in $r$ do not affect the resulting density estimates by a great deal.

**Table 3.9**: Variation in nest production rates (nests/ind./day) among age/sex classes for two Sumatran sites (supporting data from van Schaik *et al.* 1995b).

| Age/sex class | Ketambe[1]<br>437 days | Suaq Balimbing[2]<br>134 days | Present study<br>660 days[3] |
|---|---|---|---|
| Adult males | 1.2 | 1.4 | 1.651 |
| Adult females with infants | 2.0 | 1.5 | 1.846 |
| Subadult males | 1.9 | 2.1 | 2.466 |
| Subadult/nulliparous females | - | 1.4 | 2.000 |
| Juveniles | - | - | - |
| Overall mean | 1.7 | 1.6 | 1.991 |

[1] data from Ketambe made available by T. Mitrasetia.

[2] data from van Schaik *et al.* (1995b).

[3] includes the 134 days of van Schaik *et al.*'s (1995b) study.

### 3.4.3.2. *Estimating proportion of population building nests 'p'*

As stated there is general agreement between this study (using data from the WCS study area) and those of MacKinnon (1974) and van Schaik *et al.* (1995b) that individuals of pre-nest building age (i.e. infants and young juveniles) tend to comprise around 10% of orangutan populations. Naturally this figure will fluctuate over time at any location, but in the absence of more detailed information for transect locations outside the WCS study area the proportion of the population that builds nests was assumed to be close to 0.9 and unlikely to vary markedly between sites.

### 3.4.3.3. *Estimating duration of nest visibility 't'*

As the density estimates for transects GB, IB and SM are roughly similar using both the nest methods, whilst the estimated strip widths are not, the most likely explanation of this discrepancy would seem to lie with the estimated decay rate of nests *t*, as this is only required for the all nest method.

The mean decay rates of nests were found to be 7.5 months (approximately 228 days) in the swamp habitats and 10.5 months (approximately 319 days) in the hills, thus illustrating variability between forest types. Previous studies estimates of *t* also highlight considerable variation. For Ketambe, Rijksen (1978) estimated a median value for *t* of 81 days based on a sample of 30 nests, whereas Djodjosudharmo (unpubl.) found a mean value of 3 months (90 days) based on a larger sample for the same location - both clearly very different from the estimates obtained in this study. Indeed of all the parameters used in density calculations it is *t* that is likely to vary most as nest decay rates will be highly dependent on climatic factors (e.g. temperature, humidity, wind etc.), the timber qualities of the tree species concerned, altitude, aspect, time of construction etc.

The reason for construction is also likely to affect a nests decay rate as day nests can sometimes be quite flimsy in comparison to others. In fact, Figure 3.2 clearly shows a high number of nests in the swamps that disappeared after only one month, which suggests they may well have been day nests. As a result, however, it is to be expected that some nests may disappear in less than a month and hence go undetected during monthly censuses, leading to underestimates of true densities. This would also lead to slightly overestimating the mean duration of nest visibility, which again would result in underestimates of densities. Why nests do not seem to disappear so rapidly in the hills is unclear, but a possible explanation would be that orangutans using the hills might build fewer, more flimsy day nests, perhaps if they preferred to descend to the more sheltered nearby swamps to rest.

What is clear is that the estimates of $t$ are much greater than those reported from other areas although sample sizes are favourable i.e. 100 nests (55 for the combined swamp transects and 45 in the hills), so greater precision is expected here. This then suggests a distinct difference between the Ketambe and Suaq Balimbing sites with respect to nest decay, which could occur due to any of the factors mentioned above. Perhaps surprisingly, the estimates of $t$ from this study are also much higher than those estimated by van Schaik *et al.* (1995b) for the same area. However, van Schaik *et al.* derived their estimate with more abstract statistical methods (i.e. transition matrices and Markov chains) and as the estimates produced here are the result of monitoring a large sample of nests over a long period, again greater precision is expected here.

It should also be noted that all of the above parameters $r$, $p$ and $t$, were estimated using data from focal animal follows primarily within the WCS study area. Thus whilst it is considered unlikely that major differences will occur to the south, this remains a possibility, and should be borne in mind when interpreting results from outside the WCS study area.

### 3.4.4. DENSITY ESTIMATES

Given that some nests immediately above the trail may well have been missed, and that some errors may have occurred in estimating perpendicular distances, it is highly likely that the density estimates presented are to some degree imprecise. As stated, missing nests above the trail would result in underestimates of density, whilst underestimating or overestimating some perpendicular distances would produce overestimates and underestimates of density respectively.

As mentioned, van Schaik *et al.* (1995b), using the Fourier series method estimated densities in the same area, though specifically at X, as 6.9 km$^{-2}$. This was with an estimated strip width for all swamp based transects of 22.6 m. Also, van Schaik *et al.* (1995b) found no evidence that nests above the trail had been missed during their surveys, nor of heaping of distance estimates. Furthermore, they evaluated the accuracy of their methods by comparing estimates produced by line transect sampling at other sites with estimates produced by researchers working in the field, based on encounters of individual orangutans, and found them to be highly comparable. For these reasons I suggest that 6.9 $km^{-2}$ is probably closer to the true density of orangutans, at least for the X transect, than the 3.2 $km^{-2}$ result of the new nest method for this transect.

To compare the other results obtained here with theirs, the densities for all nests using only month one were again re-calculated using their estimated strip width (Table 3.10). This produced density estimates for GB that are slightly higher than previously, and for IB and SM that are both slightly lower than previously, but all are still lower than 6.9 $km^{-2}$. Comparison between these three transects and those of van Schaik *et al.* should be made cautiously, however, as they all lie further south than the X transect and the estimates produced here do suggest quite distinct local variations in densities. Nevertheless it is still considered that the densities estimated here are predominantly underestimates.

A further point that must be addressed is that the estimated decay rate of nests was much higher in the present study at 7.5 months (approximately 228 days) for the swamps than van Schaik *et al.*'s 92 days. Van Schaik *et al.*, also reduced their 92 day estimate even further by use of a 'correction factor' to give 69.9 days. This was to take account of the discrepancy between the results of Markov chain estimates and those from monitoring nests directly at Ketambe (the latter from Rijksen 1978), which produced estimates of 118 and 90 days respectively. Hence the correction factor applied at Suaq Balimbing was 90/118 or 0.76. This then is an additional reason why density estimates produced here are lower than theirs. In fact, the densities given in Table 3.7 were once again estimated using $t$ = 69.9 days, and naturally were much higher (Table 3.10). Thus the duration of visibility of nests has a large influence on overall density estimates.

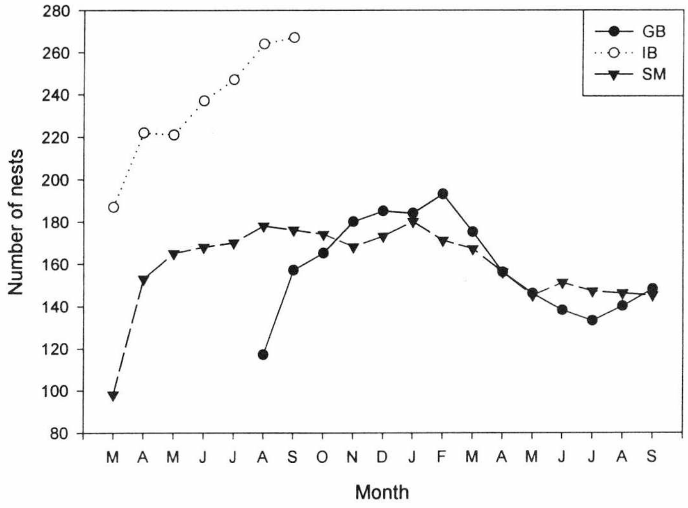
Furthermore, using van Schaik *et al.*'s estimated strip width and $t$ together produces density estimates that are distinctly higher than theirs for the WCS study area (specifically transect X) which strongly implies that densities at IB at least, probably really are noticeably higher than elsewhere. In addition, using the full estimate of mean time to total disappearance of nests for $t$ assumes that nests at a very advanced stage of decay are equally as likely to be detected during censuses as more complete nests. During long term monitoring this may in fact be the case but in one-off surveys, such as when using only the first month of monitoring, it is unlikely. Therefore, estimates using only nests in the first month's census, in conjunction with $t$ = 7.5 months, will almost certainly be lower than absolute densities, as many nests at advanced stages of decay will not be detected, despite being accounted for in the estimated decay rate. Thus whilst under-recording equally nests of each age class should be compensated by lower estimates of strip width, bias in the detection rate in favour of newer nests and against older nests, when using a decay rate estimated with the inclusion of older nests will produce serious underestimates of density. That older nests are missed during one-off censuses is clearly illustrated in Figure 3.7. It shows that a lot of nests went undetected during the first month of monitoring despite almost certainly being present, and a large proportion of these are highly likely to have been older nests.

**Table 3.10**: Orangutan densities estimated by DISTANCE using all nests in month one, at the transects GB, IB and SM, compared with estimates produced using the estimated strip widths and $r$ and $t$ values used by van Schaik *et al.* (1995b), also at Suaq Balimbing. All densities are km$^{-2}$. * data from Table 3.7.

| Transect | No. of nests | Nest density from this study* | Orangutan density from this study* | Orangutan density if $r$ = 1.7 | Orangutan density if ESW = 22.6 | Orangutan density if $t$ = 69.9 | Orangutan density if ESW = 22.6 and $t$ = 69.9 |
|---|---|---|---|---|---|---|---|
| GB | 117 | 1113.6 | 2.86 | 3.19 | 3.56 | 9.32 | 11.61 |
| IB | 187 | 2348.6 | 6.02 | 6.73 | 5.38 | 19.65 | 17.55 |
| SM | 98 | 1212.4 | 3.11 | 3.47 | 2.84 | 10.14 | 9.28 |

Using only new nests to estimate densities should circumvent these problems as the duration of visibility is not required in the calculations. However, only the estimate for IB is markedly different when using new nests as opposed to all nests. In fact estimates for both GB and SM are within only 0.2 of each other, despite higher estimated strip widths for the new nest estimates. Thus, if it can be concluded that the all nest method, using only the first month of monitoring and a decay rate of 7.5 months must underestimate absolute densities, then it can also be concluded that using new nests alone underestimates densities, since the two methods produced similar results. The precise reason why using new nests produces underestimates is unclear, but would seem to be at least partly due to some effect that lower sample sizes have on detecting nests above the trail and estimating perpendicular distances, to produce overestimates of strip widths. Despite these problems, the new nest method does produce density estimates that are proportional to the absolute number of new nests each month. They also rank the three GB, IB and SM transects in the same order with respect to the density estimates as the all nest method (see Figure 3.6). Furthermore, that nest densities provide a reliable indicator of relative densities between sites or over time has been shown by Blouch (1997), who found a significant positive correlation between nest densities (using all nests), and the number of orangutans sighted per kilometre of transect surveyed at 10 transect sites in Sarawak, Malaysia. For these reasons it is considered that new nests also provide a reliable indicator of relative densities between sites and over time and were therefore still used in Chapter 5.

**Figure 3.7**: Number of nests (of all age classes) each month at each of the transects GB, IB and SM, from March 1997 to September 1998.



As a measure of absolute densities, however, using all nests is likely to offer greater accuracy since sample sizes are always much larger, but only if transects are searched rigorously for older nests, or nest decay rates are weighted for reduced detection rates of older nests. That the use of all nests can reliably estimate absolute densities is supported by the findings of van Schaik *et al.* (1995b), as they found close agreement between estimates using these methods and densities estimated by researchers in the field at Ketambe. It should also be noted that any bias resulting from the use of multipliers (i.e. the parameters $r$, $p$ and $t$) in estimating densities is reduced if sample sizes of nests are very large relative to the resulting estimate of animal density (i.e. if the multipliers reduce the numbers by a large factor), as a large error in nest density estimates becomes only a small error in animal density, perhaps only 0.01 of an orangutan or less.

In summary, I strongly suspect that the combination of potential biases discussed above have resulted in estimates that are biased low for both the new nest and the all nest methods. Thus I suggest that the true densities are probably closer to 5.5 km$^{-2}$ in the main WCS study area, and the area around SM to the south (both in transitional swamps), and slightly lower in the GB area (nearer the backswamps). Given the very low numbers of orangutans generally found in the Hills, except during a masting event that began in May 1997, absolute densities there are considered likely to be close to those estimated here, at between 1 km$^{-2}$ and 1.5 km$^{-2}$.

Of particular interest are the estimates for the IB transect, further to the south, which were already high, reaching 4.08 km$^{-2}$ using new nests and 6.02 km$^{-2}$ with all nests. If these are also underestimates, as has been inferred for the other transects, then it could also be inferred that the ratio between estimates from line transects of nests at IB to those that would be expected using direct sightings there may be the same as at other transects (e.g. 3.20/5.34 for new nests at SM and 3.11/5.34 for all nests). If this is assumed then an estimate of the probable results of a line transect of direct sightings at IB can be obtained by multiplying 4.08 and 6.02 by these ratios. This procedure suggests that absolute densities at IB should in fact be nearer to 6.8 km$^{-2}$ if the new nest method is the most reliable, and 10.1 km$^{-2}$ if all nests is the most reliable. This location may therefore support the highest densities of orangutans yet recorded anywhere in the wild.

### 3.4.5. TEMPORAL VARIATION IN DENSITIES

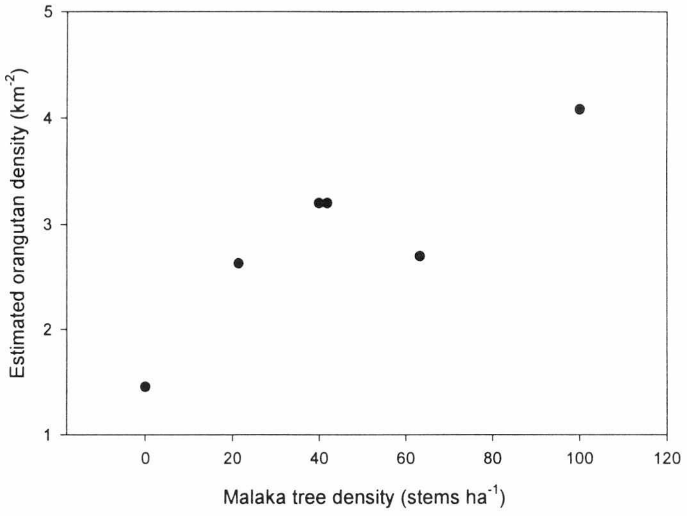
Figure 3.3 suggests that densities vary over time, when looking at the area covered by the three HJPLX, X and SM transects, though it should be noted that fluctuations involve only relatively small numbers of individuals. It should also be realised that the transects are widely scattered and therefore large expanses of forest where no monitoring occurred lie between them. Thus any attempts to identify temporal movements in this way must be tentative. Nevertheless, some movement of orangutans is implied and shall be examined in more detail in Chapter 5.

### 3.4.6. SPATIAL VARIATION IN DENSITIES

Figure 3.6 clearly demonstrates variability between the transect sites with respect to density estimates. Those using new nests show very low densities in the Hills, an increase through HJPLX to a plateau around X and SM and then a slight dip at GB, followed by a marked increase at IB, the southernmost of the transects. These trends are reflected by the pattern shown by densities estimated using all nests at the GB, SM and IB transects. Thus it seems reasonable to conclude that whilst the methods may underestimate absolute densities, these trends are probably real. This therefore suggests that densities in the transitional swamps (X and SM) are slightly higher than in the backswamps (HJPLX and GB), and that they are even higher still in the southernmost IB area.

The most obvious explanation for this might be the distribution of staple food resources. Malaka (*Tetramerista glabra*) is the single most utilised fruit species of the orangutans at Suaq Balimbing, comprising a mean of 39.9% (SD = 25.274, n = 17 months) of the fruit part of the diet (see Appendix 4). The observed density of malaka trees (>30 cm circumference at breast height), at each transect was therefore plotted against the density estimates produced using new nests at each location (Figure 3.8).

**Figure 3.8**: Estimated orangutan densities (km$^{-2}$), using the overall density estimated with new nests for each transect, against the density of malaka (*Tetramerista glabra*) stems (>30 cm cbh) per hectare, in each corresponding phenology plot.



The plot closely resembles the pattern of densities given using new nests (Figure 3.6), and the position of the points do correspond in order with the previous Figure (i.e. from left to right the transects represented in Figure 3.8 are HILL, HJPLX, X, SM, GB and IB). The plot also suggests a strong relationship between orangutan densities and malaka densities and indeed the two patterns correlate well ($r = 0.866$; $p < 0.05$; $n = 6$; 2-tailed). Thus in the swamp based habitats the pattern of densities found between the different localities may well be a constant feature of the distribution of orangutans, as opposed to simply being a function of the study period, and is probably attributable, at least in part, to the spatial distribution of malaka trees. It could even be argued that the very low orangutan densities in the hills may be a direct result of the absence of malaka there, though the situation is likely to be more complex.

## 3.5. CONCLUSIONS

1) Using new nests underestimated absolute densities. This appears to be mostly due to overestimating strip widths, probably as a result of a combination of smaller sample sizes, missing nests on or near the trail, incorrect estimates of perpendicular distances, and possibly also the existence of a distance at which nests are more visible. If accurate estimates are required, every effort should be made to ensure that all nests on or above the transect are located and that all perpendicular measurements are measured accurately.
2) Using nests of all ages in 'one-off' surveys underestimated densities. This appears to have been largely due to under-detecting older nests, whilst using an estimated decay rate that was calculated with the inclusion of older nests. During one-off surveys using all nests, decay rates ought therefore to be reduced by an unknown factor, to account for nests at advanced stages of decay that will not be detected during the census. If this is not done density estimates will almost certainly be biased low.
3) Line transects of nests do, however, offer a relatively quick method of determining relative densities between locations and over time, especially if the parameters $r$, $p$ and $t$, can be assumed to be constant, and the same observer can be used. Thus using new nests it is possible to monitor fluctuations in densities over time. This also means that if estimates using nests at one location can be calibrated against ‘known’ densities, estimates of absolute densities could also be made for other locations

4) It can be implied from the data that absolute densities at Suaq Balimbing probably lie around 1-1.5 $km^{-2}$ in the hills, and range from 5.5 $km^{-2}$ to as high as 10 $km^{-2}$ or more in the swamp habitats. The data suggest that orangutan densities vary temporally, both at the transect level, and at the area-wide level, though by only low numbers of individuals in both cases.

5) The data also show that densities vary spatially, and that a strong relationship exists between the density of malaka trees and orangutan densities. Thus malaka appears to be a major determinant of spatial dispersal at least within the Suaq Balimbing population.

# CHAPTER 4

# RANGE SIZES AND RANGING BEHAVIOUR

## 4.1. INTRODUCTION

Research on the range use of orangutans is important for two main reasons. First, it gives an indication of the spatial needs of individuals and populations, and therefore, with information on the spatial patterns of genetic relatedness, provides essential tools for conservation management, particularly in determining suitable areas for protection. Secondly, in these rather solitary animals, it may be one of the best ways to identify the nature of their social organisation, since relationships between groups or individuals may only be detectable through movement and distribution patterns. Despite its importance, however, orangutan ranging behaviour remains poorly understood.

Table 4.1 compiles home range estimates provided thus far in the literature. It shows that estimates vary widely. Most studies propose relatively small female ranges in the order of 40-200 ha. Galdikas (1988), however, reported much larger ranges for females, at up to 600 ha. MacKinnon (1974) did not give actual size estimates for ranges, instead inferring that they exceeded his main 500 ha Segama study area in Borneo. All researchers have concluded that adult male ranges are larger than those of females, though some were reluctant to speculate by how much.

**Table 4.1**: Previous studies' estimates of range sizes (hectares): B = Borneo, S = Sumatra.

| Source | Study area size | Adult females | Adult males | Study site | Duration (approx) |
|---|---|---|---|---|---|
| Horr (1975, 1977) | 390 – 2070[2] | 65 | 520 | Lokan (B) | 25 months |
| Rodman (1988) | 300 | 40-60 | 60-120 | Mentoko (B) | 15 months |
| Mitani (1989) | 300 | >150 | Larger[1] | Mentoko (B) | 18 months |
| Suzuki (1992) | Unclear[3] | >150 | 500-700 | Mentoko (B) | Several visits[4] |
| Rijksen (1978) | 150 | 150-200 | Larger[1] | Ketambe (S) | 38 months |
| Galdikas (1988) | 3500 | 350-600 | Larger[1] | T. Puting (B) | 48 months |

[1] larger than female ranges

[2] Horr (1975) states that observations were concentrated within the smaller area, though some were also made in the larger area.

[3] Suzuki (1992) surveyed an area totalling 3000 ha, though it is not clear how he derived his range size estimates within this.

[4] Suzuki made several visits to his study area; Aug 1982-Mar 1984, Aug 1985-Mar 1986, Aug 1986-Oct 1986 and Sep 1988-Mar 1989.

All studies have also noted that female ranges overlap those of other females and some state that subadult male ranges overlap those of other subadult males (e.g. MacKinnon 1974; Horr 1977; Galdikas 1979). Some researchers did not state this clearly for subadult males, but it can be inferred from the literature that there is general agreement on this. With the exception of Rodman (1973a,b), all also agree that adult male ranges overlap those of other adult males. Rodman instead concluded that the adult males in his Mentoko study area had discrete ranges, which they maintained by use of the long call, though he later conceded that his sample of only two adult males was probably insufficient (Rodman 1973b).

Most researchers have also suggested variation in residence status (e.g. Rodman 1973a,b, 1988; MacKinnon 1974; Galdikas 1978; Rijksen 1978; Mitani 1985a,b; Sugardjito *et al.* 1987; te Boekhorst *et al.* 1990; Suzuki 1992). In addition to residents, other individuals may be commuters, entering and leaving a site on a regular basis (e.g. te Boekhorst *et al.*1990; Rijksen and Meijaard 1999), or truly transient, and simply passing through (e.g. Rodman 1973b; MacKinnon 1974; Mitani 1985; Suzuki 1992). Rijksen and Meijaard (1999) go further by stating that orangutans can be distinguished into three classes based on dispersal activity, namely residents, commuters and wanderers. Only Horr (1976) deduced that ranges of both sexes were stable at his Lokan site, and that although adult male ranges were larger than female ranges, they did not travel infinite distances, as shown by their periodic reappearance every few months in the same female's range. Despite this general consensus that there are both resident and non-resident or transient individuals within populations, some disagreement remains as to whether or not individuals of both sexes fall into each of these categories. For example, Galdikas (1978) observed that there were resident and non-resident adult males at Tanjung Puting, but did not observe this dichotomy amongst adult females, whilst MacKinnon (1974) and te Boekhorst *et al.* (1990) clearly state that there was no sexual bias amongst transients.

The most likely explanation for the different interpretations of orangutan movements need not necessarily be a result of differences between locations, but could equally be an artefact of study area size. It is certainly interesting to note that the largest range estimate also comes from the largest study area i.e. Tanjung Puting (Table 4.1). By default, study area size imposes restrictions on the number of individuals encountered and the frequency of encounters. For example, an individual whose range is centred on the centre of the study area is likely to be encountered relatively frequently, whilst an individual whose home range only slightly overlaps the study area will be encountered only infrequently. In fact, if individuals use their home ranges equally intensively throughout, the frequency of their visits should be directly proportional to the proportion of their range coincident with the study area. If, however, they use the periphery of their range less intensively than other parts (e.g. the centre) visits will be even less frequent. Thus simply stating that an individual was only rarely encountered and is therefore transient, would seem a little tenuous, as residents of the area immediately adjacent to the study area would appear as transients, whilst residents of the study area would similarly appear as transients in adjacent areas. For the same reasons, seasonal influxes of orangutans into a study area might reflect only nearby residents at the limits of their ranges, rather than large scale seasonal 'migrations' of individuals (as suggested in Chapter 5).

This chapter therefore aims to determine the range sizes of orangutans at Suaq Balimbing and examine evidence for either stable home ranges or transience among the various age and sex classes. The results will then be discussed with respect to their implications for the social organisation of the orangutans.

## 4.2. METHODS

Data on orangutan movements were amassed during focal animal follows between June 1994 and September 1998. These data were collected by several observers over the whole period, with myself and field assistants joining the ongoing WCS project in September 1996. Data therefore include those collected by myself and my assistants, by the WCS project, and by a previous researcher in the area, Beth Fox, of Duke University, USA.

Within the WCS study area the routes taken by focal individuals were plotted on maps of the trail system at frequent intervals during all follows, using a compass and distance estimates. Each time a trail was crossed the accuracy of these maps could be verified. During follows outside the WCS study area, similar data were plotted on a grid, with cells measuring 100 m x 100 m, and the orangutan's actual location recorded at sporadic intervals using a hand-held GPS (Global Positioning System), receiver. The GPS positions were then located on a map of the entire study area, and the approximate route taken between positions inserted from the grid maps produced in the field. Again, routes could be verified whenever some of the less frequent trails outside the main WCS study area where crossed and by plotting GPS positions on a 1:50,000 scale topographic map of the area. Using this procedure, routes plotted between GPS fixes were considered to be reasonably accurate.

As well as the overall route taken, every 30 minutes the time and position of the animal was also noted on all follow maps. In addition, the identity and location of any other individuals encountered within 50 m of the focal animal, along with times of approach and departure, were recorded.

All follow maps were subsequently stored in ARC/INFO GIS software, as both routes (lines), allowing distances and velocities to be measured, and as 30 minute points (i.e. every zero and 30 minutes past each hour, regardless of the time the follow began or ended). Subsequent examination of ranges used primarily the 30 minute point data. It was also possible using GIS, to assign the 30 minute point locations of focal individuals, to any other individuals that were known to be less than 50 m away at the corresponding times. Hence the total number of 30 minute point locations for an individual includes both data from when they were focal individuals, as well as data from when they were not the focal individual, but were within 50 m of a focal individual. Some individuals were also encountered during other work (i.e. as casual observations), and a small number of these records were included in the analysis, particularly if they were encountered at locations not previously known to lie within their range. With the data thus obtained, three different methods were used to estimate range sizes.

### 4.2.1. GRID SQUARES

Two grids were superimposed over the study area. The 'small' grid was located primarily over the WCS study area and adjacent environs, and comprised grids of 1 ha (100 m x 100 m). The 'large' grid comprised grid cells of 4 ha (200 m x 200 m) and overlay the entire study area. Using GIS it was then possible to calculate the number of 30 minute points for an individual that fell within each cell of the two grids. Thus, by counting the number of cells of known area, estimates of range sizes can be obtained. Similar methods have been used for a variety of primates (e.g. Fossey 1974, Vedder 1984, Watts 1998, for Mountain gorillas *Gorilla g. beringei*; Chapman and Wrangham 1993, for Chimpanzees *Pan troglodytes*; Bennett 1986, Müller 1995, Holenweg *et al.* 1996, Curtis and Zaramody 1998, Kirkpatrick *et al.* 1998, Ostro *et al.* 1999, for other species). This method will almost certainly produce underestimates of range sizes, however, since 'empty' cells (those with no records of an individual) that lie between 'entered' cells (those with records), were not added to the total count, despite the fact that some must have been traversed during travel between 'entered' cells.

### 4.2.2. POLYGONS

Plotting all the 30 minute points at which an individual was ever seen gives a sample of points known to be within the range of that individual. The peripheral points can then be linked using straight lines, to produce a 'minimum area polygon' (Kenward 1987), also called the 'minimum home range method' (Trevor-Deutsch and Hackett 1980), as used by Bearder and Martin (1980), Macdonald *et al.* (1980) and Chapman and Wrangham (1993). This method is very sensitive to movements near the periphery of an animal's home range, however, irrespective of the frequency with which that area is visited, and individuals of many species do occasionally travel to unusual places, perhaps on excursions from their normal range (Macdonald *et al.* 1980). Also, since the polygon is evaluated from the outermost points no measure of internal space usage is obtained (Worton 1987). Instead this method assumes that an individual is likely to enter areas within the polygon in which they may not yet have been recorded, simply because they are nearer to the center of the polygon than other points at which they have been recorded. Thus ranges estimated by including all peripheral points give maximum known usable areas, and may overestimate regular home ranges or core areas.

There is little guarantee, however, except in the case of continuous tracking that an animal did not move beyond these sample boundary points (Voigt and Tinline 1980), and hence range sizes may also be underestimated. Attempts to correct these problems have included restricting the length of lines joining boundary points, excluding areas by experience and adding a 'boundary strip', but the results from the different methods are not comparable (Voigt and Tinline 1980). For orangutans, previous authors have simply used either curved or straight lines to enclose sightings of individuals. Rodman (1973a,b) and Rijksen (1978), for example, drew smoothed boundaries around the area that included all definite observations of an individual, as did Yamagiwa *et al.* (1996) for gorillas and chimpanzees, though Rijksen was careful to suggest that the area enclosed represented an estimate of core area, rather than home range. Galdikas (1978) used both smoothed boundaries and straight sided polygons to estimate home ranges. In the present study only straight lines were adopted as it was considered that they would almost certainly still provide conservative estimates of true ranges. This is because it seems reasonable to assume that most areas between the known points for an individual are likely to be entered at least occasionally, and that some areas outside of the polygon are also likely to be used. This is especially the case as much of the area is relatively homogenous, and not typically characterised by marked topographical features or other obstructions to movement, except perhaps for the eastern hill areas.

### 4.2.3. CIRCLES

For each individual, the distance between the two most widely separated capture points (30 minute points) is taken to represent the diameter of a circular range, and the area of the consequent circle calculated. This was called the 'observed range length circle method' by Trevor-Deutsch and Hackett (1980). Naturally, ranges are not likely to be precisely circular, but even if ellipsoid or similar, the widest known points are unlikely to be across the actual widest point of the animal's range, especially if the individual concerned was still moving away from the centre of its range when the widest known points were recorded. I therefore suggest that if considered alongside information on the presence of an individual in or near the centre of their range, these circular estimates correspond to a potential range size over the long-term.

As mentioned, the traditional grid-cell method is likely to provide a serious underestimate for most individuals in this case as only relatively few, scattered observations were made outside of the WCS study area, although the error will be reduced for individuals whose ranges are centred within it. Thus the polygon, and circle methods, however crude, are likely to provide more realistic estimates of range sizes, with the former giving a best minimum estimate and the latter a potential range size over the long-term, for all individuals with a reasonable number of observations.

### 4.2.4. PRESENCE AND ABSENCE

To evaluate the likely accuracy of the various range estimates it was deemed necessary to attempt to assess the relative presence of individuals within the WCS study area. To facilitate this, daily lists of all individuals seen or followed within the WCS study area were kept, and individuals subsequently recorded as present for each month during which they were seen within it at least once. These data were then used to calculate a residence index ($P_j$) using the methods adopted by te Boekhorst *et al.* (1990). Following the same methodology, the presence of an individual j during the $n_j$ months it was seen within the WCS study area is defined as:

$$\sum_{i=1}^{nj} P_{ij}$$

where $P_{ij}$ takes on the values 1 (present in month i) or 0 (not seen in month i). Thus the sum of $P_{ij}$ is effectively, simply the number of months individual j was seen. At Ketambe, however, te Boekhorst *et al.* (1990) found that the number of orangutans encountered each month increased linearly with monthly observation time, and therefore concluded that monthly presence scores (i.e. 1 or 0) for an individual should be adjusted to account for this. The adjustment they used is based on the assumption that the probability of finding an individual is proportional to the total number of orangutans encountered, and thus increases with the amount of time observers spend in the field. If this is true then the expected number of orangutans likely to be found in a given month ($y_{exp}$) can be calculated by the regression equation of $y_i$ upon $x_i$, where $y_i$ = the number of orangutans seen in month i, and $x_i$ = the number of days units (a unit being one or more people operating as a group), were in the field during month i. Therefore, to correct for monthly observation time $P_{ij}$ each month can be multiplied by a weighting factor $w_i$ where:

$$w_i = \frac{y_{min}}{y_{exp}}$$

in which, from the regression equation:

$y_{exp}$ = the expected number of individuals in month i with observation time $x_i$,

$y_{min}$ = the expected number of individuals in the month with least observation time, $x_{min}$.

Thus multiplying $P_{ij}$ by $w_i$ each month gives a monthly proportion that reflects the amount of search effort, and hence the probability of finding an individual, rather than simply using 1 for present or 0 for absent. Therefore, by summing these values over all months for an individual a 'weighted' number of months present ($Z_j$) can then be calculated as:

$$Z_j = \sum_{i=1}^{n_j} w_i . P_{ij}$$

Subsequently dividing $Z_j$ by the sum of the monthly weighting factors i.e. $\sum w_i$ for $i = 0$ to 48, then gives a residence index ($P_j$) with a range between 0 (absent in all months) and 1 (present in all months).

For general purposes, throughout this study individual orangutans have normally been categorised according to several age and sex classes. These are infants, juveniles and adolescents of both sexes, adult females, and subadult and fully adult males. However, for the purposes of range analysis so called adolescent females were further sub-divided into true adolescents i.e. those that have only recently begun to wander away from their mothers and still have some years to go before full sexual maturity, and subadult females i.e. those that are approaching sexual maturity and are already sexually active but still nulliparous. This distinction was made as the two sub-groups were considered likely to range in different ways, the former being still 'mother' orientated and the latter being more 'potential mate' orientated. Thus it was anticipated that regarding all young, nulliparous females as one could conceal any patterns that might be more apparent if treating them as two separate groups.

## 4.3. RESULTS

### 4.3.1. PRESENCE AND ABSENCE

Linear regression between search effort ($x_i$) and the number of individuals encountered each month ($y_i$) found the relationship to be $y_i = 0.119x_i + 11.169$, but $R^2$, at only 0.147, means that only 14.7% of the variability in the number met can be explained by search effort alone. Thus the strength of this relationship was not found to be as strong as might be expected. This raises questions about the need to calculate $P_j$ using the method of te Boekhorst *et al.* (1990), rather than simply dividing the number of months an individual was encountered by the number of months of the study. However, results of both procedures were compared and were found to produce very similar presence indices, ranking all individuals in the same order. Hence for ease of comparison, te Boekhorst *et al.*'s method was adopted and results are presented in Table 4.2.

It can be seen that individual presence within the WCS study area varies considerably, from individuals that were seen only once, to others that clearly spend a great deal of their time there e.g. Ani, Abby, Arno etc. It should be noted, however, that an individual could actually spend the majority of its time outside the WCS study area and still have a presence index of 100% since it need only be recorded on one day during any month to be scored as present. Nonetheless, it is considered that these presence indices still give a reasonable indication of true presence.

Table 4.3 summarises the results for each age/sex class and shows that adult females have the highest mean presence index at 26.23%, and the largest range. Despite sometimes travelling independently, adolescents of both sexes were excluded from both as data pertaining to adolescents was only recorded after the birth of a younger sibling. Hence calculated $P_j$ indices underestimate true presence for this class. They can be assumed, however, to be similar to adult females since they still tend to follow their mothers around, even after a younger sibling is born. Of particular interest is the exceptionally high presence index for the dominant adult male, Arno, compared to the means for all adult males, both with or without Arno. Figure 4.1 shows the data more clearly as plots of the number of individuals against the number of months they were seen. Arno is striking in being seen during 40 months; twice as many as the next highest adult male (Figure 4.1b). A similar situation exists for subadult females (Figure 4.1c), of which the majority were seen during only relatively few months and mostly early on during the period. One subadult female, however, Becky, remained in the area producing an infant in mid-1997, and was subsequently classed as an adult female. Also of interest is the shape of the graph for subadult males (Figure 4.1d). Most were only occasional or rare visitors, with at least 11 seen during only one month, and presumably just passing through.

Table 4.4 explores these results further, showing the proportion of individuals of each age/sex class falling into the categories of rare ($P_j < 3\%$), occasional ($3\% =< P_j < 25\%$) and regular ($P_j >= 25\%$). Regular visitors are then further refined to show frequent visitors ($P_j > 50\%$). As can be seen, 48% of adult females can be regarded as regular visitors and 22% would be regarded as frequent visitors. That 26% of adult females appear to be rare visitors is perhaps misleading. It must be remembered when interpreting presence and absence data that the size of the WCS study area increased slightly during the course of the study until it reached its current size in mid-1997. These expansions have been mostly southwards and since 1994 have only involved the addition of a few hundred metres to the overall area.

**Table 4.2**: Presence index ($P_j$ expressed as a percentage) of individuals; October 1994 to September 1998 (48 months). NB: Tomi and Becky appear twice as both matured to a new class during the study. Their relative presence was assumed not to change dramatically because of this.

| Age/sex class | Rank | Name | $P_j$*100 | No.of months |
|---|---|---|---|---|
| Adult females | 1 | Ani | 89.511 | 43 |
| | 2 | Abby | 70.454 | 34 |
| | 3 | Beki | 69.526 | 34 |
| | 4 | Diana | 63.815 | 31 |
| | 5 | Mega | 62.317 | 30 |
| | 6 | Una | 54.556 | 26 |
| | 7 | Tevi | 41.894 | 20 |
| | 8 | Karen | 34.795 | 17 |
| | 9 | Pelet | 34.660 | 16 |
| | 10 | Hanes | 33.362 | 16 |
| | 11 | Butet | 32.922 | 16 |
| | 12 | Sela | 31.799 | 16 |
| | 13 | Novi | 26.036 | 13 |
| | 14 | Molly | 12.807 | 6 |
| | 15 | Sara | 10.075 | 5 |
| | 16 | Afrika | 7.396 | 4 |
| | 17 | Yinta | 6.084 | 3 |
| | 18 | Rini | 4.736 | 2 |
| | 19 | Ling-ling | 4.186 | 2 |
| | 20 | Lily | 3.613 | 2 |
| | 21 | # 49 | 2.134 | 1 |
| | 22 | Duck face | 2.134 | 1 |
| | 23 | Ita | 2.074 | 1 |
| | 24 | #75 | 1.977 | 1 |
| | 25 | Nicola | 1.901 | 1 |
| | 26 | Imar | 1.853 | 1 |
| | 27 | Darlene | 1.629 | 1 |
| Adult males | 1 | Arno | 82.666 | 40 |
| | 2 | Tomi | 35.282 | 18 |
| | 3 | Agus | 29.501 | 14 |
| | 4 | Mack | 23.995 | 12 |
| | 5 | Budi | 22.717 | 11 |
| | 6 | Luwi | 16.335 | 8 |
| | 7 | Ngon | 15.101 | 7 |
| | 8 | Hotma | 11.678 | 6 |
| | 9 | Caca | 10.612 | 5 |
| | 10 | William | 10.002 | 5 |
| | 11 | Mukson | 8.419 | 4 |
| | 12 | Binu | 6.282 | 3 |
| | 13 | David | 6.084 | 3 |
| | 14 | Olly | 4.049 | 2 |
| | 15 | #48 | 2.134 | 1 |
| Adolescent females | 1 | Andai | 54.716 | 26 |
| | 2 | Beti | 14.580 | 7 |
| | 3 | Hilda | 2.264 | 1 |
| | 4 | Jane | 1.853 | 1 |
| | 5 | Linda | 1.744 | 1 |
| Adolescent males | 1 | Meggy | 35.499 | 17 |
| | 2 | Herdi | 23.244 | 11 |
| | 3 | Uno | 21.923 | 10 |
| | 4 | Nata | 15.356 | 7 |

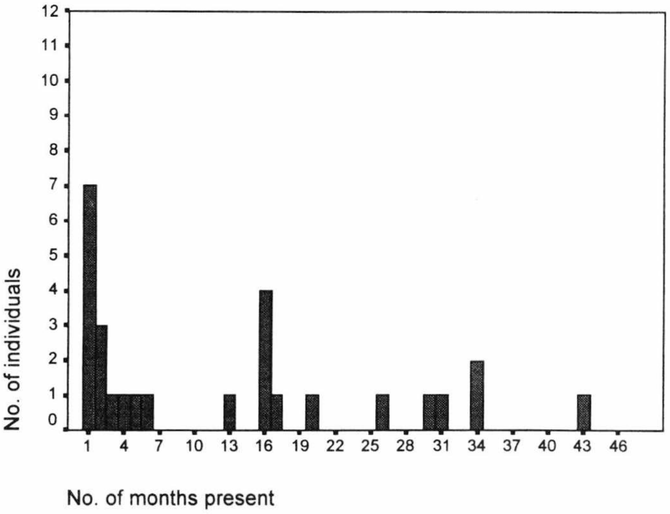
Table 4.2 continued.

| Age/sex class | Rank | Name | $P_j$*100 | No.of months |
|---|---|---|---|---|
| Subadult females | 1 | Beki | 69.526 | 34 |
| | 2 | Lena | 12.434 | 6 |
| | 3 | Tina | 11.446 | 6 |
| | 4 | Gama | 11.293 | 6 |
| | 5 | Helen | 9.750 | 5 |
| | 6 | Ros | 9.529 | 5 |
| | 7 | Barbara | 5.432 | 3 |
| | 8 | #77 | 4.353 | 2 |
| | 9 | #45 | 2.059 | 1 |
| | 10 | Eva | 2.004 | 1 |
| Subadult males | 1 | Lito | 65.122 | 32 |
| | 2 | Dio | 53.056 | 25 |
| | 3 | Koen | 43.254 | 21 |
| | 4 | Navi | 41.481 | 20 |
| | 5 | Syawal | 38.781 | 19 |
| | 6 | Tomi | 35.282 | 18 |
| | 7 | Musa | 33.833 | 16 |
| | 8 | Robert | 25.295 | 13 |
| | 9 | Ria | 23.629 | 12 |
| | 10 | Oloan | 19.798 | 10 |
| | 11 | Kris | 18.573 | 9 |
| | 12 | Fin | 17.254 | 8 |
| | 13 | Payung | 14.367 | 7 |
| | 14 | Joni | 8.870 | 5 |
| | 15 | Bestel | 8.233 | 4 |
| | 16 | #81 | 6.504 | 3 |
| | 17 | Brus | 6.412 | 3 |
| | 18 | Ryne | 4.085 | 2 |
| | 19 | #73 | 4.066 | 2 |
| | 20 | Zeus | 3.794 | 2 |
| | 21 | Tesi | 3.373 | 2 |
| | 22 | #78 | 2.264 | 1 |
| | 23 | Edi | 2.181 | 1 |
| | 24 | #86 | 2.134 | 1 |
| | 25 | Stan | 2.089 | 1 |
| | 26 | #67 | 2.074 | 1 |
| | 27 | #68 | 2.059 | 1 |
| | 28 | #69 | 2.059 | 1 |
| | 29 | #72 | 1.977 | 1 |
| | 30 | #76 | 1.977 | 1 |
| | 31 | #Z1 | 1.808 | 1 |
| | 32 | #83 | 1.714 | 1 |

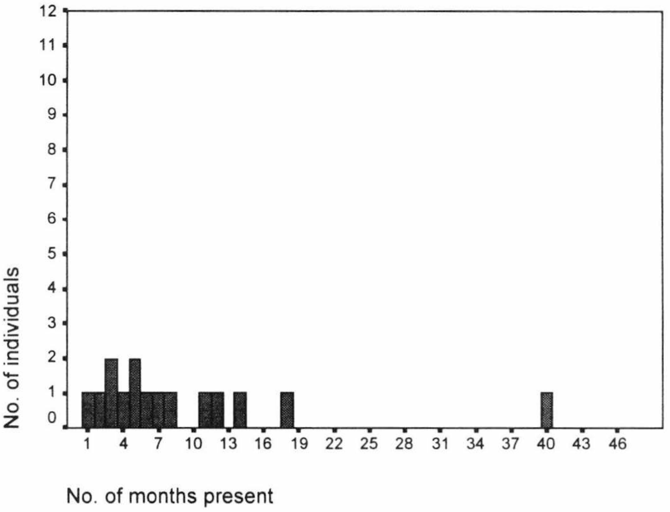
**Table 4.3**: Mean presence index ($P_j$), expressed as a percentage, for each age/sex class; October 1994 to September 1998.

| Class | No. of individuals | Range | Mean | SD |
|---|---|---|---|---|
| Adult females | 27 | 87.88 | 26.23 | 26.79 |
| Adult males | 15 | 80.53 | 18.99 | 20.08 |
| Subadult females | 10 | 67.52 | 13.78 | 19.97 |
| Subadult males | 32 | 63.41 | 15.54 | 17.58 |
| All orangutans | 93 | 87.88 | 19.35 | 21.37 |
| Adult males minus Arno | 14 | 33.15 | 14.44 | 10 |
| Arno | 1 | 0 | 82.67 | 0 |

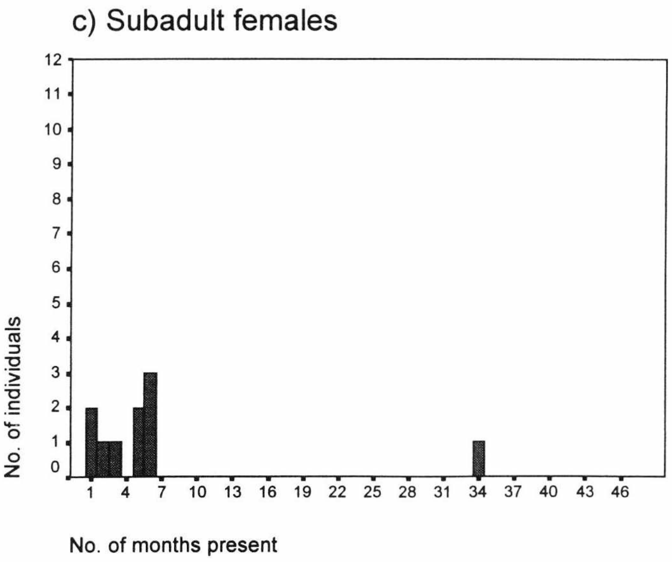
**Figure 4.1**: Monthly presence of individuals for a) adult females, b) adult males c) subadult females and d) subadult males (number of months seen in WCS study area versus number of individuals), between October 1994 and September 1998 (48 months). NB: Records for both Becky and Tomi pooled over both classes in which they occur and displayed under both classes.



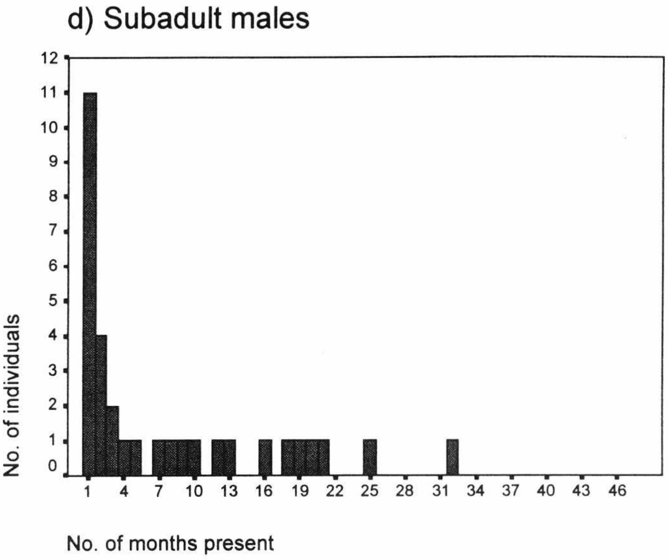
a) Adult females



b) Adult males



c) Subadult females



d) Subadult males

**Table 4.4**: Composition of age/sex classes according to $P_j$ (expressed as a percentage). $P_j < 3\%$ equates to being seen in only one month of the period. Note that individuals regarded as frequent are also included under regular.

| | All | Rare | $P_j<3$ | Occasional | $3=<P_j<25$ | Regular | $P_j>=25$ | Frequent | $P_j>=50$ |
|---|---|---|---|---|---|---|---|---|---|
| Age/sex class | N | n | % | n | % | n | % | n | % |
| Adult females | 27 | 7 | 25.9 | 7 | 25.9 | 13 | 48.2 | 6 | 22.2 |
| Adult males | 15 | 1 | 6.7 | 11 | 73.3 | 3 | 20.0 | 1 | 6.7 |
| Subadult males* | 32 | 11 | 34.4 | 13 | 40.6 | 8 | 25.0 | 2 | 6.3 |
| Subadult females | 10 | 2 | 20.0 | 7 | 70.0 | 1 | 10.0 | 1 | 10.0 |
| Adolescent females | 5 | 3 | 60.0 | 1 | 20.0 | 1 | 20.0 | 1 | 20.0 |
| Adolescent males | 4 | 0 | 0.0 | 3 | 75.0 | 1 | 25.0 | 0 | 0.0 |
| Total | 93 | 24 | 25.8 | 42 | 45.2 | 27 | 29.0 | 11 | 11.8 |

*Number of Subadult males with Pj < 3% likely to be underestimated as several went unidentified.

Due to this, however, some individuals were encountered for the first time only when the study area was extended into their ranges. In addition, search effort increased along the periphery of the study area as a result of this project, since individuals were actively sought leaving the area, and this will also have resulted in a few individuals being encountered for the first time and only very infrequently. These will therefore appear as rare visitors with low presence indices whilst in actual fact they are probably residents in areas immediately adjacent to, and only slightly overlapping the present study area. Hence in reality, it is considered that these females are probably mostly relatively frequent visitors that do not often venture far northwards.

Adult males tend to be mostly occasional visitors (73%) and subadult males appear to be mostly occasional (41%), or rare visitors (34%). However, it should be realised that these figures represent only those individuals that were observed and identified, and that of all the classes, it was subadult males that most often went unidentified. For this reason the proportion of subadult males falling in the rare category is almost certainly underestimated. Therefore rare visitors should probably constitute the largest proportion of individuals of this class. Subadult males also seemed to pass through the area most rapidly. To test for this the mean ratio of nest to nest distances divided by total day journey lengths was calculated for each individual of all age and sex classes (Appendix 2). A ratio of 1 would mean the animal travelled in a straight line, whilst increasingly smaller ratios indicate increasing deviation from a straight line. A one way ANOVA was then performed to check for differences between the different age/sex classes, but none were deleted ($F_{(5,44)} = 1.573$, $p = 0.188$), showing that no single age/sex class travelled significantly more directly than any other.

To examine whether or not the relative presence of age/sex classes changes over time the presence indices of individuals were re-calculated, first for the period October 1994 to September 1996, and again for the period October 1996 to September 1998. It was then possible to calculate the mean presence indices for each age/sex class, during each period, in the same manner as for Table 4.3. Thus with two values for each age/sex class representing periods I and II it was possible to calculate a value expressing the relative change between the two periods (i.e. the mean presence during period II as a percentage of the mean presence during period I), and thus detect if any of the age/sex classes tended to be more, or less, present during the second period (Table 4.5).

The results show that the mean presence index of adult females was virtually constant throughout the study as were all adult males (i.e. mean $P_j$ period II as a percentage of period I gives 101% and 102% respectively). Similarly orangutans on the whole were also constant (100%). Subadult females, however, were noticeably more absent during period II (48%), which may reflect them settling in areas nearby but outside the actual study area. Subadult males were also more scarce during period II (72%).

**Table 4.5**: Mean monthly presence indices of each age/sex class, period I (Oct 94-Sep 96) versus period II (Oct 96-Sep 98).

| Class | Period I Mean Pj(I) | Period II Mean Pj(II) | Period II as % of Period I |
|---|---|---|---|
| Adult females | 26.09 | 26.36 | 101.0118 |
| Adult males | 18.77 | 19.19 | 102.2275 |
| Subadult females | 18.9 | 9.04 | 47.8337 |
| Subadult males | 18.18 | 13.11 | 72.1037 |
| All orangutans | 19.3 | 19.39 | 100.472 |
| Adult males minus Arno | 13.64 | 15.18 | 111.2925 |
| Arno | 90.61 | 75.31 | 83.1192 |

Again the dominant adult male, Arno, is of particular interest. He clearly spent less time in the study area after September 1996 than he had during the previous two years (83%) reflecting a shift from almost constant presence ($P_j$ for period I = 90%) to only 75% presence. In contrast, adult males minus Arno appeared to do the reverse (111%) being more often encountered within the area during period II, when both Arno, and subadult males, were more often absent.

### 4.3.2. RANGE SIZES

In all, 1808 focal animal follows of 79 different individuals were amassed between February 1994 and September 1998, comprising a total follow duration of 14614 hours. Mean follow duration was 8 hours 48 mins (SD = 3 hours 25 mins, max = 13 hours 3 mins). The mean number of follows per individual was 22.89 (SD = 41.315, max. = 244). Additional follows were conducted during this time but were ignored if the individual was not clearly identified by the observer. A total of 90 different individuals were encountered within 50 m of the focal individual during follows. A summary of range estimates for some individuals, obtained using the different methods is presented in Table 4.6.

**Table 4.6**: Examples of range estimates (ha), with presence index, for adult females and adult and subadult males based on the above methods.

| Age-sex class | Identity | Pj* | Small grid | Large grid | Polygon method | Circle method |
|---|---|---|---|---|---|---|
| Adult Female | Ani | 0.895 | 323 | 488 | 608 | 1521 |
| Adult Female | Butet | 0.329 | 197 | 436 | 636 | 1437 |
| Adult Female | Mega | 0.623 | 296 | 520 | 853 | 1599 |
| Dominant Adult Male | Arno | 0.827 | 322 | 488 | 740 | 1990 |
| Adult Male | Mack | 0.240 | 127 | 328 | 1483 | 3913 |
| Adult Male | Caca | 0.106 | 52 | 140 | 505 | 1297 |
| Subadult Male | Fin | 0.173 | 65 | 176 | 462 | 1203 |
| Subadult Male | Navi | 0.415 | 161 | 296 | 612 | 2692 |
| Subadult Male | Robert | 0.253 | 121 | 212 | 353 | 1464 |

* Pj = presence index, after te Boekhorst *et al.* 1990.

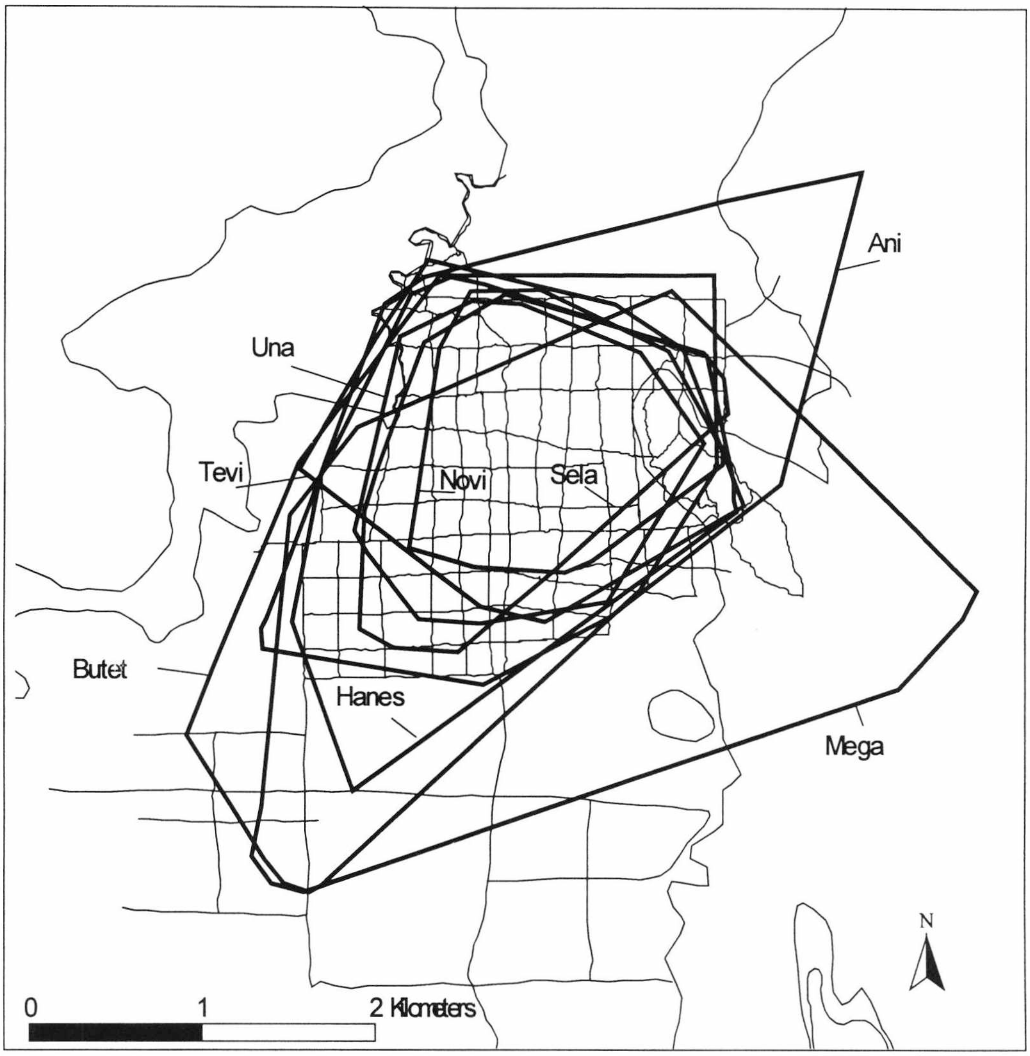
### 4.3.2.1. *Adult females*

What is immediately clear from range maps is the considerable amount of overlap of adult female ranges (Figure 4.2). For example, one of the 4 ha cells of the large grid, near the centre of the WCS study area, was used by at least 16 different adult females between October 1994 and September 1998.

Examination of the range of one of these, Ani (with young infant and older adolescent still often in association during 1998), who was the most frequently encountered and followed (number of half-hour points = 5291), shows 323 of the 1 hectare small grid cells which she is known to have entered (Figure 4.3a), whilst she was also observed outside the limits of the small grid. Likewise, there are 122 of the 4 ha large grid cells (= 488 ha, Figure 4.3b) in which she has been recorded. Given these observations along with the fact that Ani has been seen at some time in virtually the entire WCS study area (a total area of approx 460 ha), and that she also has the highest presence index of all, at 89.5%, it can be inferred that she spends the majority of her time within an area of around 500 ha.

Grid maps for a second female, Mega (also with young infant and older adolescent, often still nearby in 1998), show 296 small grid cells in which she has been seen, and 130 large grid cells (= 520 ha). Mega's presence data gives a $P_j$ of 62.3%. Thus Mega also appears to spend the majority of her time in an area of around 500 ha. Also of note is that Mega's ranging data suggest a tendency not to use the northern edge of the WCS study area, as she

**Figure 4.2**: Polygon ranges of those adult females known to use most or all of the WCS study area, showing high degree of range overlap.

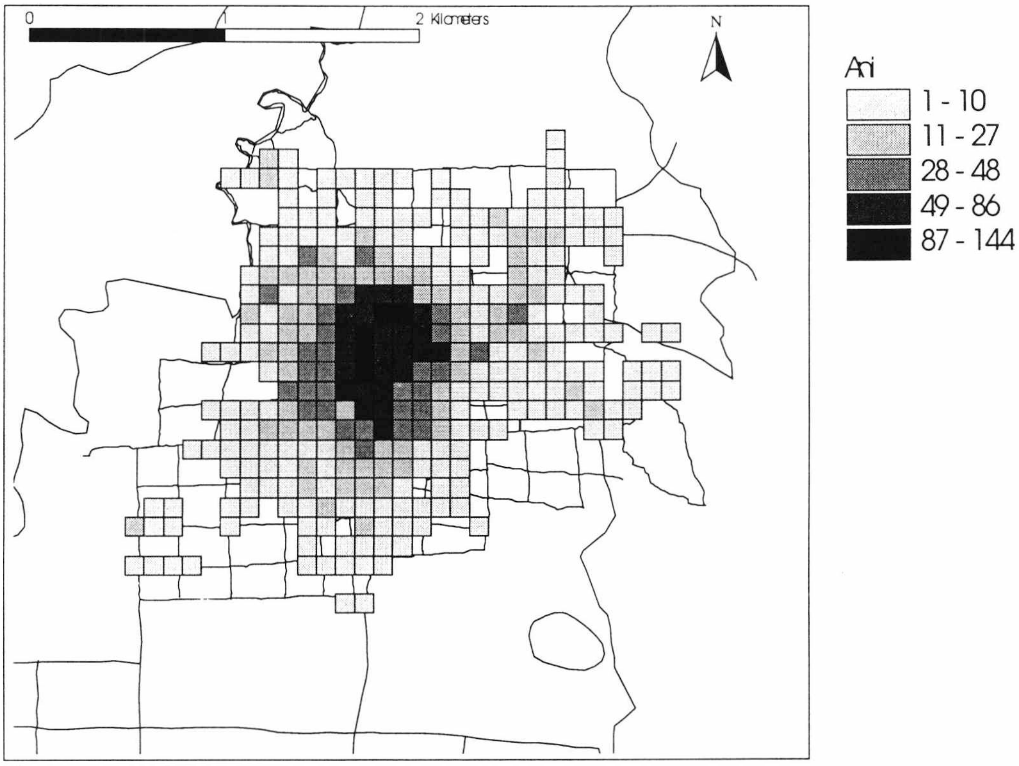


was only very rarely seen north of the LX trail, and hence that she may have some form of boundary within it (see Figure 4.5).

Despite these apparent core areas of around 500 ha, however, examination of polygon and circle range estimates suggests both are able to utilise much larger areas. In fact, the two most distant points of Ani's range would give a total range area of 1521 ha if it were circular (Figure 4.4). It should also be noted that Ani was still travelling away from her core area when she was followed to the most easterly of these points, and hence still extending the widest known point distance when the follow in question was abandoned. Using the polygon method a minimum range size of 608 ha is implied for Ani. Similarly, Mega's two most distant points produce a circular range estimate of 1599 ha whilst the

**Figure 4.3**: Grid cell ranges of adult female Ani using (a) small grid (cells = 1 ha), (b) large grid (cells = 4 ha). Numbers in the key represent the number of records per cell.

(a)



(b)

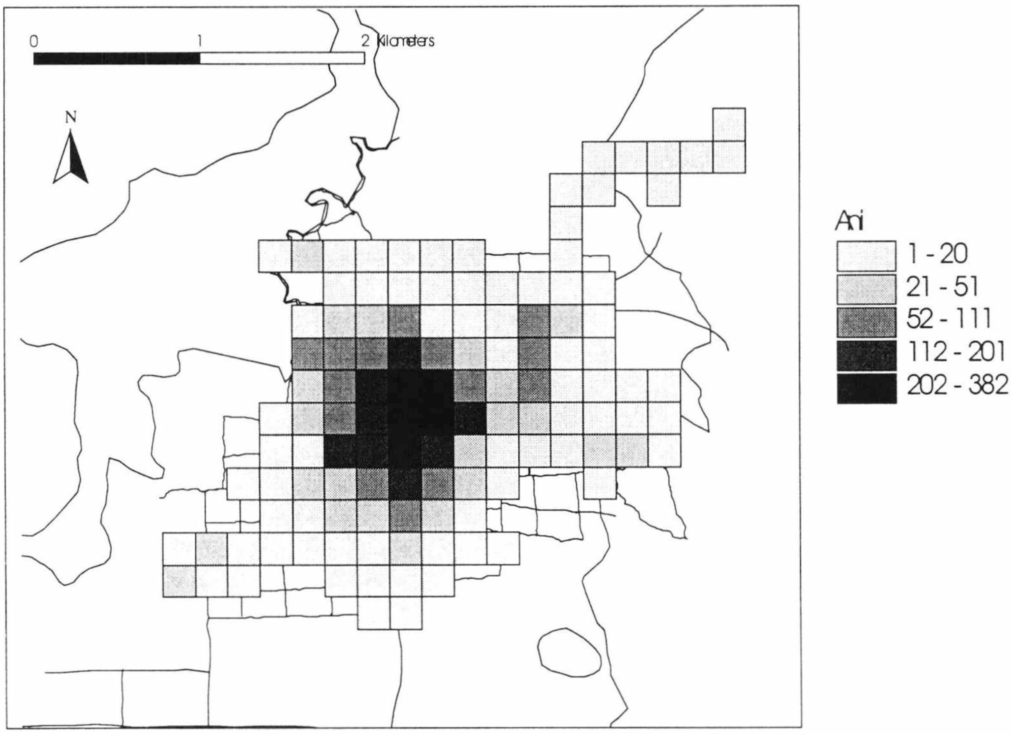
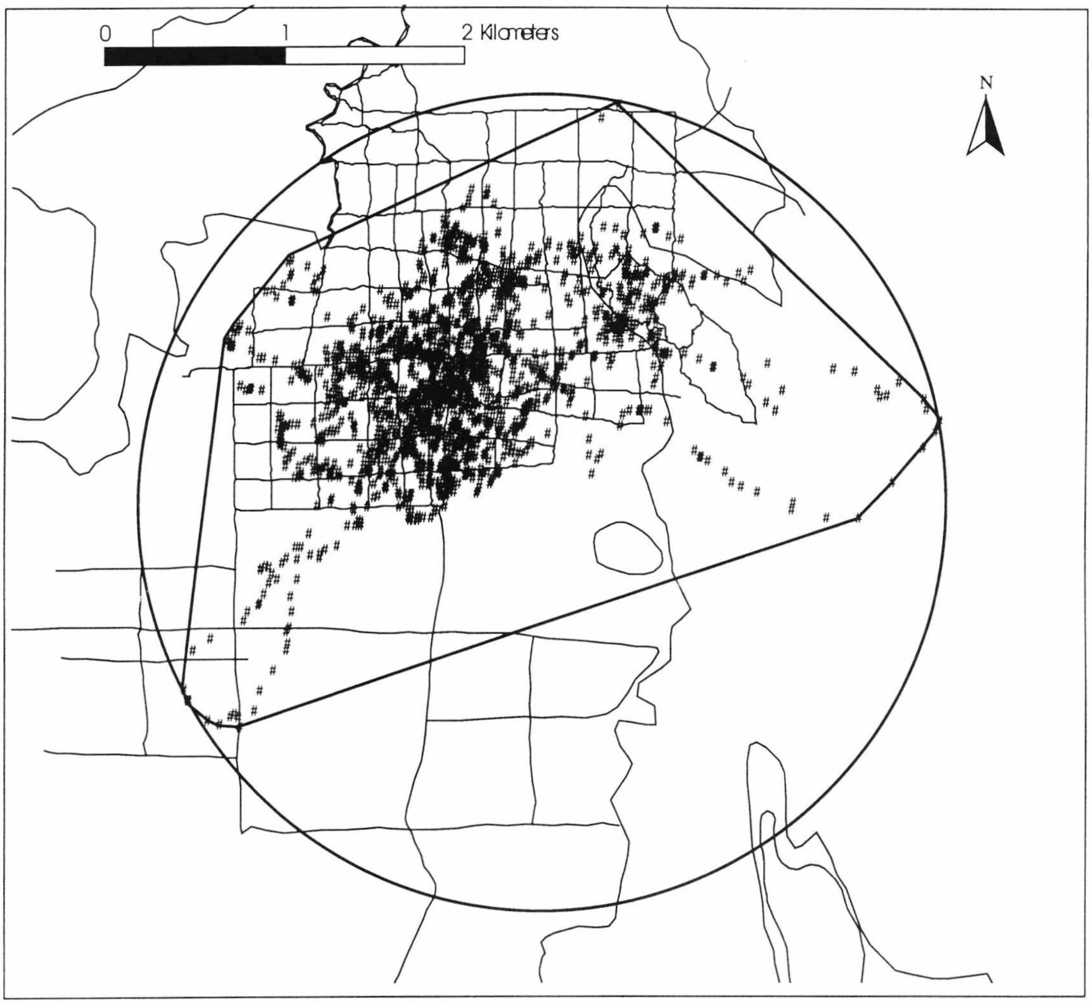


**Figure 4.4**: Polygon and circle range estimates for adult female Ani. Polygon = 608 ha, circle = 1521 ha (diameter = 4.4 km).

**Figure 4.5**: Polygon and circle range estimates for adult female Mega. Polygon = 853 ha, circle = 1599 ha (diameter = 4.5 km).



polygon method suggests a minimum of 853 ha (Figure 4.5).

Several of the adult female's ranges show apparently fixed boundaries within the WCS study area. For example, the three females Pelet, Diana and Becky, have with very few exceptions only ever been seen in the north and west of the trail system (Figure 4.6), whilst Abby and Karen, have only been seen in the north and east (Figure 4.7). These boundaries also appear to be consistent over time (Figures 4.8 and 4.9).

These results therefore suggest that adult females at Suaq Balimbing utilise a central zone, or core area in which they normally reside, of around 500 ha in extent, that has relatively fixed boundaries, is stable over time, and may overlap with as many as 15 other adult females. Around this central zone, however, exists a peripheral 'excursion zone' into which the females will occasionally venture on extended forays, perhaps when it contains abundant food resources.

**Figure 4.6**: Range limits for adult females Becky, Diana and Pelet; 1994 to 1998.

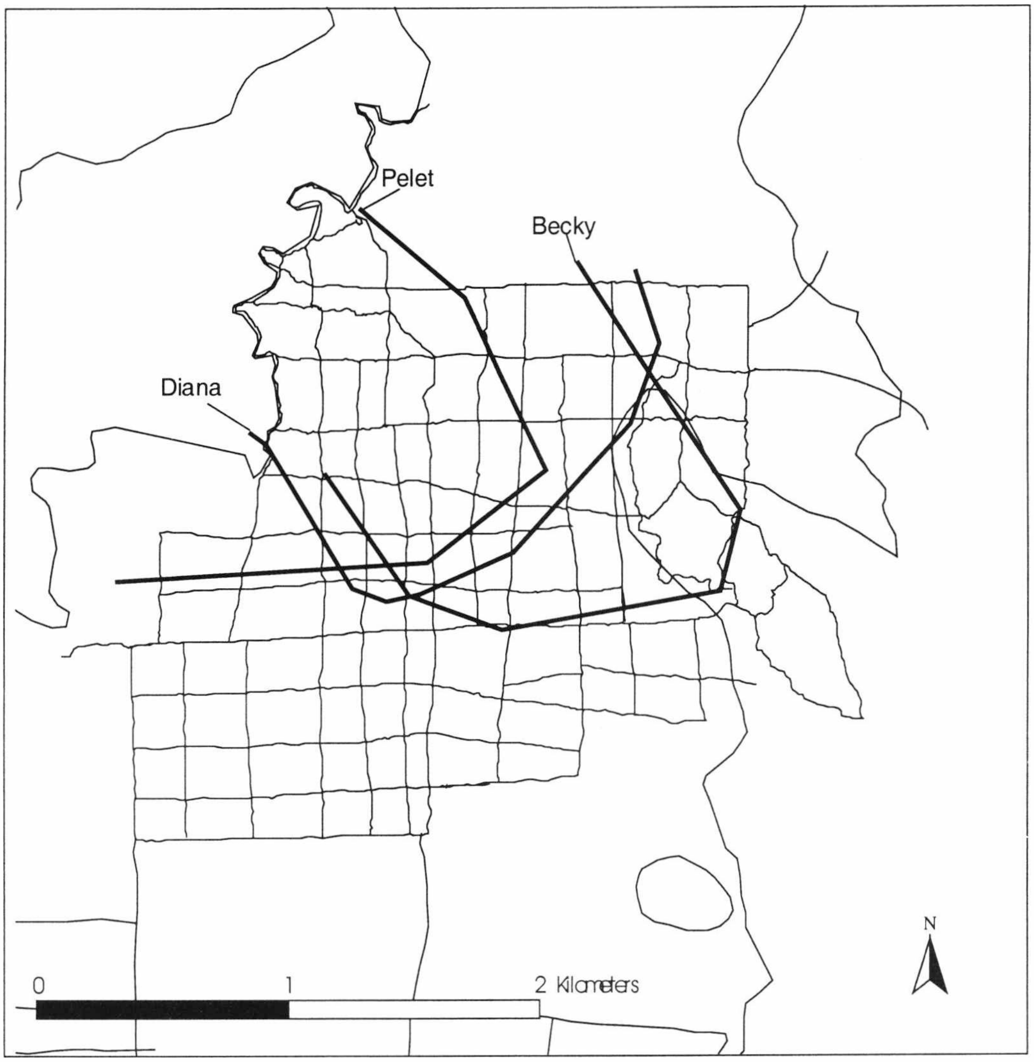


**Figure 4.7**: Range limits for adult females Abby and Karen; 1994 to 1998.

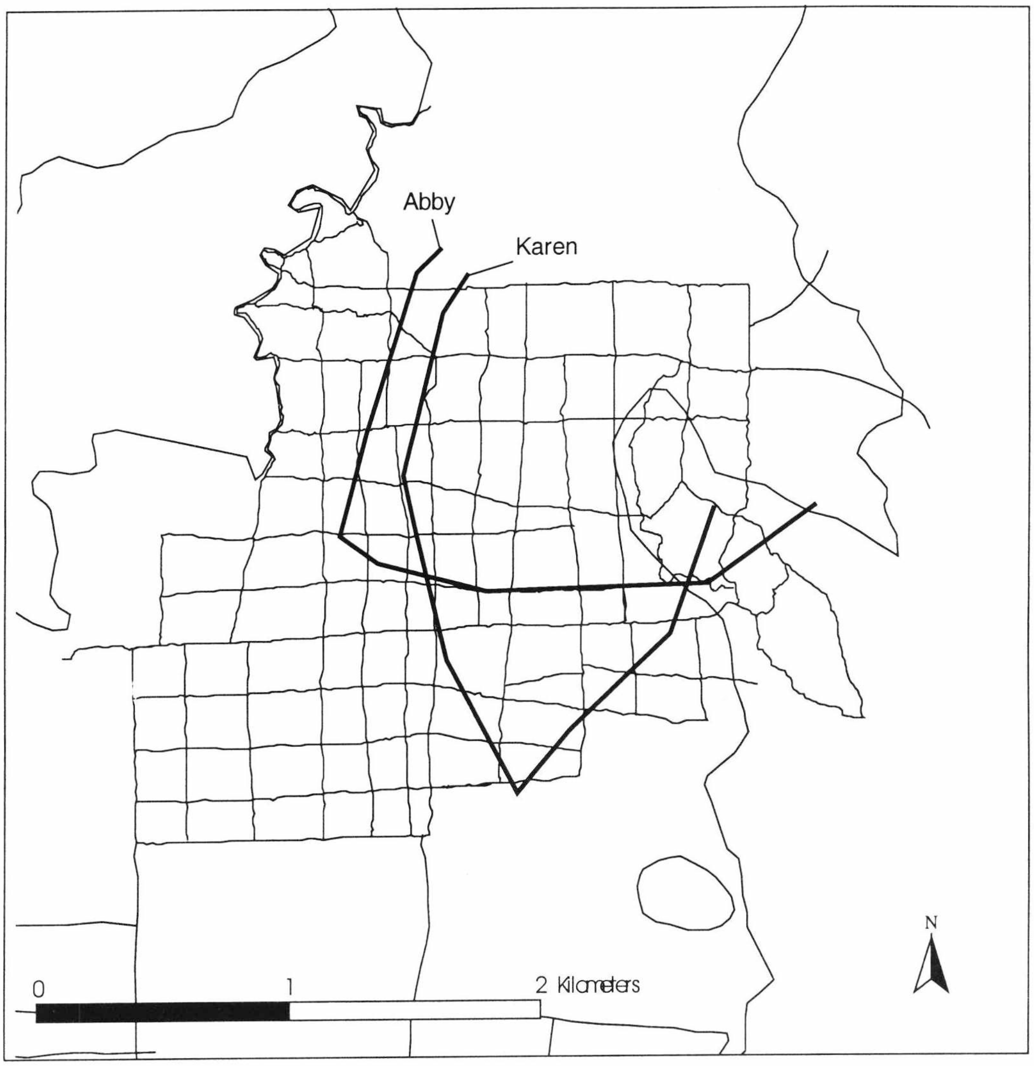


**Figure 4.8**: Yearly range boundaries for adult female Diana; 1994 to 1998.

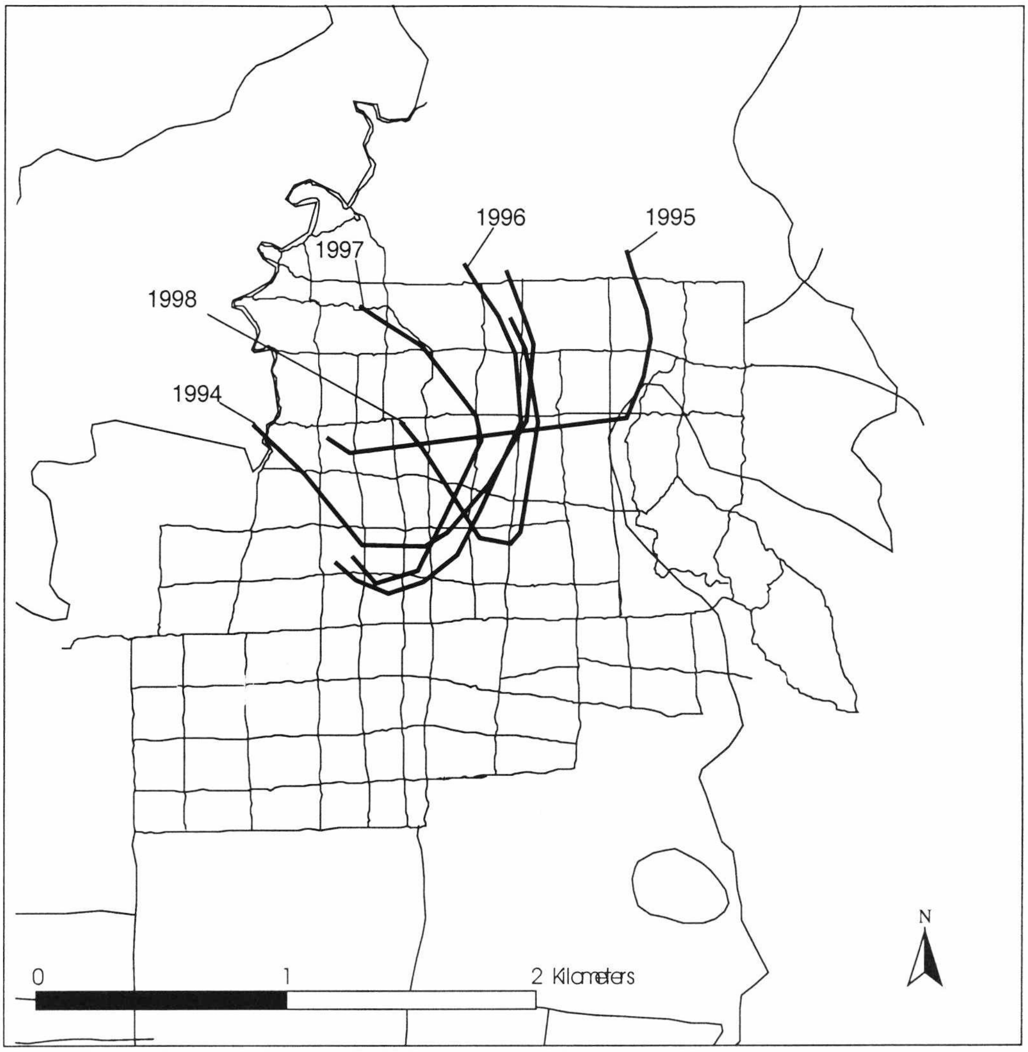
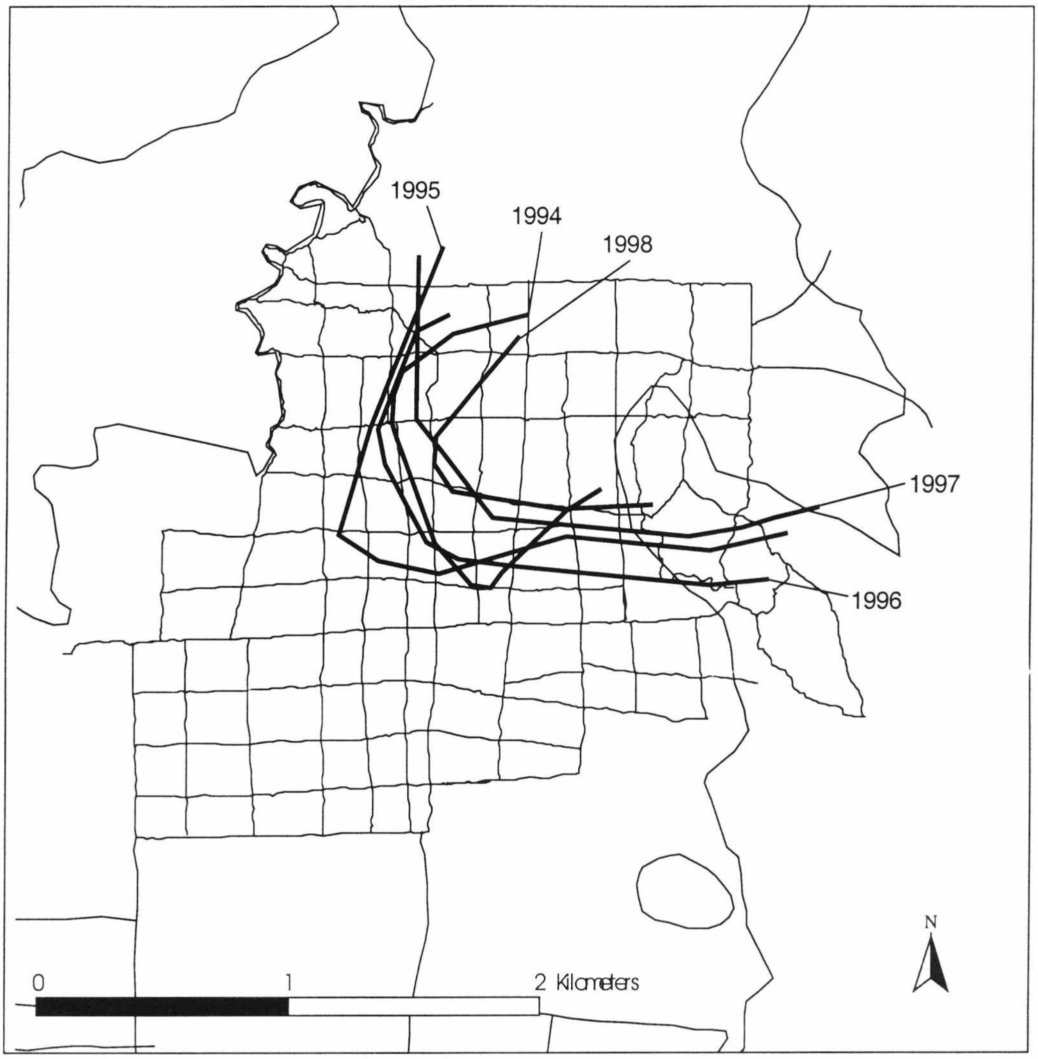


**Figure 4.9**: Yearly range boundaries for adult female Abby; 1994 to 1998.



4.3.2.2. *Adult males*

As reported by other studies, the ranges of adult males appear to be distinctly larger than those of females. For example, the adult male, Mack, has widest known points that would constitute a circular range of 3913 ha, although the polygon method provides a more conservative estimate of 1483 ha. The dominant adult male, Arno, is known to cover the entire study area and is often absent for periods. Due to the frequency of his returns ($P_j$ = 82.7%), however, it is suspected that Arno's range may be relatively limited in extent and that his ranging behaviour may not be typical of adult males in general (see also Figure 4.1b). Adult male ranges also show considerable overlap. At least 15 individual adult males are known to have entered the WCS study area, whilst the maximum number recorded within a single 4 ha cell of the large grid was 9. Furthermore, most adult males were seen in most parts of the WCS study area, or at least to exit most edges, suggesting they do not have fixed range boundaries within it. A few possible exceptions exist, however. William, was only first encountered in December 1997 and another two, Olly and David, in 1998, and by the end of the study all three had only been seen in small parts of the WCS study area. William, despite passing all the way through the study area from north to south, kept only to the western side, and David was only seen in the extreme west, at the edge of the trail system near the river. Olly had been briefly observed across near the foothills but was otherwise also seen only in the west. As these individuals were newly encountered and identified, it remains to be seen if they too will utilise the whole area or if their ranges do in fact have boundaries within it.

It is also of note that near the end of the study period (after June 1998) the trails extending to the south were searched several days per week to determine if any of the orangutans known from within the WCS study area could be found there. In fact, two additional adult males that had never been seen before were encountered, and similarly, another unidentified male was seen far into the hills during an excursion by the adult female Mega. Whether or not these individuals also use the WCS study area is not known and could only be determined with time.

### 4.3.2.3. *Subadult males*

Subadult male ranges are probably the most difficult to assess. Under field conditions individual subadult males can still be very difficult to identify unless there is some clear identifying feature (e.g. broken fingers, unusual beard shape etc.). Galdikas (1979) also reported difficulties with their identification. However, these difficulties may themselves suggest that they have very large ranges or are indeed transient, as recognition should be easier if individuals were more frequently encountered. Nonetheless, some were well known from within the WCS study area, and were also seen or followed at distance from it, so an attempt to estimate minimum range sizes can be made. Due to the large distances involved and the low number of observations for subadult males, however, linking up the known points of their ranges into straight sided polygons produces long narrow shapes that are considered unrealistic. For this reason, values for range sizes obtained in this way, whilst presented in Table 4.6, were subsequently ignored.

The circle method gives estimates of 1203 ha for Fin, and 2692 ha for Navi. It should also be noted that when Fin was followed to the most northerly known point of his range he was still travelling away from the WCS study area when abandoned, subsequently being absent for two months before returning briefly, and then absent again for nine months. This therefore suggests that his actual range is probably much larger than that observed, if indeed there are any limits to the ranges of this class. As with fully adult males, almost all subadult males recorded within the WCS study area, and for whom enough data was gathered, can be seen to use virtually the whole of the area, and to enter and exit from all sides. This then also implies that ranges are considerably larger than the WCS study area and that none have range boundaries within it, which is further supported by the low and erratic presence exhibited by subadult males (see Figure 4.3c), despite definite returns to the area by some.

Again there is considerable overlap of subadult male ranges, with at least 15 different individuals known to enter one of the large grid cells. But, a total of 31 individually recognised subadult males were recorded within the study area between October 1994 and September 1998 along with an undetermined number of unidentified subadult males, many only briefly seen and often afraid of the observer. That most of the well known individuals seem able to use the entire WCS study area, suggests that whilst some of the lesser known or unidentified individuals were not actually seen in the same large grid cell as the 15 above, all are likely to be able to enter it. Therefore, the true number of subadult males whose ranges overlap the centre of the WCS study area, is almost certainly higher than 15, probably at least 20, and more likely around 30 or more. Hence these figures are considered more realistic as estimates of range overlap and are perhaps still even underestimates.

Due to the identification difficulties mentioned, it is so far impossible to determine the true number of individuals that return to the study area, as opposed to being encountered only whilst passing through and not returning. That many are not known and afraid when encountered, however, suggests that at least some may be just passing through, though it still remains impossible to distinguish between true transience among subadult males, or simply very large ranges.

#### 4.3.2.4. *Subadult females*

The number of subadult females encountered within the study area (i.e. those females not yet with offspring but ranging independently of their mothers; see earlier), clearly varies between years. Between October 1994 and September 1998, a total of 10 were identified and recorded within the WCS study area. However, whilst 7 were seen between October 1994 and September 1995, only 3 were encountered between October 1997 and September 1998. Of these three, Becky gave birth in 1997 and was subsequently considered adult. That at least four were not seen in recent years suggests they may have been the offspring of adult females normally resident outside the WCS study area, and exploring the periphery of their natal ranges. Also, some of the 10 were newly encountered at the southern edge of the study area where the trail system was extended in 1997, and when search effort was increased there. As a result the true proportion that are now absent should be higher. Indeed, most of the early encounters with subadult females were close to the northern, rather than the southern edge of the study area, and presences were sporadic. It could therefore be inferred that subadult female ranges may be slightly larger than those of adult females, perhaps as they may be more adventurous at this age, but such an inference can be only tentative with such scant data.

### 4.3.2.5. *Adolescents and infants*

As has long been established by previous studies, this age group normally travels in close association with their mothers and hence share the same range. Adolescents of both sexes will often spend several days travelling alone but rejoin their mother after such periods

## 4.3.3. RANGE MODELLING

The observed degree of range overlap within age/sex classes allows an attempt to be made to model the effects of different range sizes on the density of each age and sex class. For example, if home ranges of adult females were 5 km$^2$ and the ranges of 10 individuals overlapped, then the density of adult females would be expected to be 5 divided by 10, or 0.5 km$^{-2}$. Once the expected density of each age/sex class for a given range size is determined it is then possible to determine what sex ratio of males to females would be expected with those range sizes (i.e. the density of males divided by the density of females).

Table 4.7 illustrates the process. It shows the number of individuals of each age/sex class that possess overlapping ranges, and substitutes different range sizes, to calculate the expected density of individuals of each class that would correspond to these parameters. Thus under model A, with the observed adult female range overlap of 16 individuals and an estimated mean size of regular home range (or core area) for females of 500 ha (5 km$^{-2}$), the resultant density of females is estimated as 16/5 or 3.2 $km^{-2}$. By carrying out the same procedure for each age/sex class it is then possible to add up the density estimates for each class to give an estimate of the overall density of all orangutans that would correspond to the range sizes and overlap measures adopted. These can then be compared with the estimates obtained in Chapter 3.

The resultant density estimate from the table that most closely approaches the minimum estimate for the WCS study area of 5.5 $km^{-2}$ (Chapter 3) is 6.374 $km^{-2}$, obtained under model D. In this model adult female ranges are 700 ha, Arno's range is 2000 ha, non-dominant adult male ranges are 7500 ha, subadult male ranges are 10000 ha and subadult female ranges are 950 ha. In all cases range sizes of adolescents and infants were assumed to be identical to adult females. This result is also close to van Schaik *et al.*'s (1995) estimate for the WCS study area of 6.9 $km^{-2}$. Thus if absolute densities in the area are indeed between 5.5 $km^{-2}$ and 6.9 $km^{-2}$ and the various measures of range overlap are reasonably accurate, it could be inferred that the range sizes under model D are close to reality as well.

However, as discussed in Chapter 3, a density of 5.5 $km^{-2}$ is considered likely to be a minimum for this area, and absolute densities to range between 5.5 $km^{-2}$ and 10 $km^{-2}$ in the swamp habitats. Therefore, the range sizes given under models B and D, where resultant densities are 7.251 $km^{-2}$ and 8.657 $km^{-2}$ may in fact be closer to reality. The results also suggest that the estimates of range sizes under model A in the table are likely to be underestimates, since they produce the highest density of 9.533 $km^{-2}$, although this is still less than maximum inferred for some parts of the study area as a whole. Thus it would seem reasonable to assume that true range sizes of orangutans at Suaq Balimbing probably lie within the minimum and maximum range estimates used in the table i.e. models A and D, with regular female home ranges of circa 700 ha, and those of both non-dominant adult males and subadult males lying somewhere between the extremes of 3000 ha and 10000 ha.

A possible source of error, as discussed earlier, arises from the somewhat speculative estimate of range overlap for subadult males. However, this does not have a large influence as even substituting a more conservative estimate of 20 reduces the overall density estimates only slightly (e.g. from 6.374 $km^{-2}$ to 6.274 $km^{-2}$ under model D).

**Table 4.7**: Model using varying estimates of range sizes to estimate overall density (km$^{-2}$)and population composition. * all adult females carried infants except two (whose infants died < 1year).

| | | Model A | | Model B | | Model C | | Model D | |
|---|---|---|---|---|---|---|---|---|---|
| Age/sex class | No. with overlapping ranges | **Minimum range estimates** | Density (km$^{-2}$) | **Female ranges larger** | Density (km$^{-2}$) | **Male ranges larger** | Density (km$^{-2}$) | **All ranges larger** | Density (km$^{-2}$) |
| Adult females | 16 | 500 | 3.200 | 700 | 2.286 | 500 | 3.200 | 700 | 2.286 |
| Subadult females | 6 | 750 | 0.800 | 950 | 0.632 | 750 | 0.800 | 950 | 0.632 |
| Adoles. females | 3 | 500 | 0.600 | 700 | 0.429 | 500 | 0.600 | 700 | 0.429 |
| Adult males (-Arno) | 8 | 3000 | 0.267 | 3000 | 0.267 | 7500 | 0.107 | 7500 | 0.107 |
| Arno | 1 | 1500 | 0.067 | 1500 | 0.067 | 2000 | 0.050 | 2000 | 0.050 |
| Subadult males | 30 | 3000 | 1.000 | 3000 | 1.000 | 10000 | 0.300 | 10000 | 0.300 |
| Adoles. males | 4 | 500 | 0.800 | 700 | 0.571 | 500 | 0.800 | 700 | 0.571 |
| Infants* | 14 | 500 | 2.800 | 700 | 2.000 | 500 | 2.800 | 700 | 2.000 |
| Total | 82 | | | | | | | | |
| **Overall density:** | | | **9.533** | | **7.251** | | **8.657** | | **6.374** |
| Ratio of males to females; full adults: | | | 0.104 | | 0.146 | | 0.049 | | 0.069 |
| Ratio of males to females; sexually active: | | | 0.333 | | 0.457 | | 0.114 | | 0.157 |

Of particular interest as a result of the modelling procedure are the estimates of sex ratios obtained (i.e. the density of males divided by the density of females). As an example, under model D the density of adult females was estimated to be 2.286 $km^{-2}$ and those of fully adult males were 0.107 $km^{-2}$ (excluding Arno) and 0.050 $km^{-2}$ (for Arno alone). Thus the ratio of fully adult males to adult females under model D is estimated as: (0.107 + 0.050) / 2.286 = 0.069. For the same model the ratio among all sexually active individuals (which includes subadults and full adults of both sexes, that will engage in sexual activity whether or not they are capable of conception) is 0.122. In fact all estimates of the sex ratio of fully adult orangutans lie between 0.049 (model B) and 0.146 (model B), and those of all sexually active or mature individuals between 0.114 (model C) and 0.457 (model B). Using the lower range overlap estimate for subadult males of 20 reduces these ratios even further for all sexually active individuals but of course does not affect full adults. Thus under all of the models the maximum ratio of fully adult males to females is 0.146 and that of sexually active or mature individuals is 0.457. The expected value, however, at least among all sexually active individuals would be around 1.0, if the ratio at birth was roughly 50:50. This therefore suggests a net loss of males from the Suaq Balimbing population as the population matures. In addition, that sex ratios are also much smaller among fully adult individuals supports previous reports that males may remain subadult for much longer periods than would be the case if the acquisition of secondary sexual characteristics was purely age related.

## 4.4. DISCUSSION

### 4.4.1. PRESENCE AND ABSENCE

Whilst the presence index $P_j$ gives an indication of the frequency of returns to the area by an individual, and the amount of time spent there, it is clearly open to bias. As stated, an individual need be seen only once in a given month to obtain the maximum presence score for that month, and whether the individual passes straight through the area in a single day or spends the whole month in the area is unaccounted for. Observations in the field suggest that this is most likely to overestimate the presence of adult and subadult males, as they can move fairly rapidly through the area, sometimes in just a few days. There remains the possibility, however, that the presence of some females at least may also be overestimated in this way. These facts must therefore be borne in mind when appraising the data.

The presence results show that adult females tend to be predominantly regular or frequent visitors, adult males predominantly occasional visitors and subadult males mostly occasional or rare visitors. It should be remembered though that majority of the latter are almost certainly rare visitors, as this group was considered to be underestimated. They also suggest that whilst overall numbers of orangutans appear constant over time, the composition of the male component of the population changes. The dominant adult male, Arno, and subadult males, were all more often present between 1994 and 1996 when non-dominant males were more often absent. Conversely, afterwards the situation was reversed. It could also be noted that an earlier paper using June 1994 to May 1996 as period I and June 1996 to May 1998 as period II showed this phenomenon even more clearly, Arno's presence in period II being 78% of period I, subadult males being 83%, and non-dominant males being 181% (Singleton and van Schaik in press). These results correspond with observations in the field, as during 1995 and early 1996 Arno was frequently encountered within the WCS study area and found to be consorting with several receptive females. These females also tended to be those with the highest presence indices and all subsequently gave birth around mid-late 1996. Such consortships often involved several subadult males as well, who would follow Arno and the females for several days (see also van Schaik 1999). During much of 1997 and 1998, however, Arno disappeared several times, sometimes for some months before returning, and subadult males were less apparent, presumably due to the reduced number or absence of receptive females. As a consequence, non-dominant males began to appear more often. Thus it seems that the dominant male, along with subadult males, is attracted to an area when the females there are receptive, but non-dominant males appear avoid the area at such times, presumably in avoidance of the dominant male.

The presence results therefore support the contention that if transience exists it is most likely to involve males, particularly subadult males, as these were predominantly only occasional or rare visitors to the WCS study area. They also suggest that the dominant adult male may range in a markedly different manner to other fully mature, but non-dominant adult males, and furthermore, that the composition of the male population changes as a result of the reproductive status of females. Females on the other hand tend to be mostly regular or frequent visitors implying that they are not transient.

### 4.4.2. RANGE SIZES

#### 4.4.2.1. *Adult females*

Adult females at Suaq Balimbing clearly have large ranges, that overlap with several others, and seem to be consistent over time. Ranges appear to consist of a core area of around 500 ha in which the individual is normally to be found, surrounded by a larger zone, potentially as large as 1500 ha or more, into which they make occasional extended forays or 'excursions'.

Total home range estimates for adult females at Suaq Balimbing are distinctly larger than those reported from all other studies. It might appear, however, that those from Tanjung Puting (Table 4.1) are similar, though it should be noted that these refer to total home range size and not just to core areas. Galdikas (1978) in fact stated that the core areas of adult females there were in the region of 200 ha to 300 ha. Thus adult females at Suaq Balimbing with core areas of circa 500 ha, and total home ranges of between 900 ha and 1500 ha, almost certainly do possess much larger ranges than even the estimates from Tanjung Puting. However, both these sites contain predominantly swamp forests, whilst most other studies were conducted in dryland forests. Therefore, it could be inferred that females in swamp forest habitats have larger ranges than those in drier forests. A further research site, at Gunung Palung in Borneo contains both swamp forests and drier forests but information on range size there is not yet available.

Whittaker (1965, 1972, 1975; cited in Kent and Coker 1992) made a distinction between two types of vegetation diversity; namely alpha diversity (the number of species within a given area or community), and beta diversity (the difference in species diversity between areas or communities). Thus it would follow that a habitat with low alpha and beta diversity might offer less food availability to a species such as the orangutan, and consequently require a larger foraging area than habitats with high alpha and beta diversity. Galdikas (1988) distinguished between peat swamp forests and mixed deciduous forests at Tanjung Puting. At Suaq Balimbing, each of the forest types present tend to be fairly homogenous in species content and abundance and relatively poor in species diversity (see Chapter 2), compared to dryland forests which can contain many micro-habitats (e.g. stream valleys, boggy areas, ridges, sunny slopes, sheltered slopes etc.), within a relatively small area. Hence both Suaq Balimbing and Tanjung Puting might be regarded as coarse- grained habitats with low alpha and beta diversity, and the dryland forests as fine-grained habitats, with higher alpha and beta diversity. It might therefore be expected that at least female orangutans, for whom food is likely to be the most important single factor influencing range sizes, would require larger ranges in coarse grained habitats, in order to encompass a sufficiently varied food resource to counter periods of shortage.

The influence of food availability on female ranging also helps to explain the occurrence of their observed excursions away from core areas. Daily energy demands are more easily met by fruit consumption (Leighton and Leighton 1983), so long forays might be more feasible at times of fruit abundance at the destination, as opposed to scarcity at the source. Furthermore, a female could freely enter an area with little or no risk of hunger due to unfamiliarity with the area if fruit was abundant there. It would also seem reasonable to expect a reduced risk of conflict with females whose core areas lie at the destination, as they are likely to possess greater tolerance during such times, and are probably at least familiar with the arrivals due to previous excursions by both individuals into each others core areas. Indeed it is true that both Ani and Mega's furthest observed forays into the eastern hills occurred during a mast fruiting event there and as such, long excursions into the hills may be relatively infrequent i.e. only every few years or so. However, both females also made forays to the south west of the study area during a period when a preferred fruit species, Puwin (*Sandoricum beccarianum*) appeared abundant there, but was not yet fruiting in similar quantities within the main WCS study area. Furthermore, the results of Chapter 5 confirm that forest areas of circa 3 km apart are out of phase by one or two months. Thus it is suspected that excursions within swamp areas may be more common than those into the hills, taking place several times per year, as more spatial and temporal variation in the distribution of fruit is likely than is typically found in the hill forests.

An alternative explanation for the smaller range estimates from other sites is that they are in fact underestimates, perhaps as an artefact of study area size. Indeed MacKinnon (1989) did conclude that Rodman underestimated the range sizes of orangutans during his study, pointing out that his estimates were based on very little data, and that there was a discrepancy between low encounter rates and the small ranges he derived. If an individual is frequently found within an area of known size, it might seem reasonable to assume that its range is approximately the same size as the area in question. However, follows of individuals leaving the WCS study area, show clearly that this is not necessarily the case.

Perhaps the best example is the adult female Ani, who clearly uses an area much greater than that of the WCS study area, despite being frequently found within it ($P_j = 89.5\%$).

Of further note regarding 'excursions' is that both Ani and Mega appeared to follow topographical features during their furthest forays into the hills, Ani adhering to a strip approximately 50 m either side of a stream, and Mega crossing the apex of ridges. A possible explanation for this would be unfamiliarity with the area, and therefore the use of such features for navigation. It would also enable a rapid retreat to more familiar areas should this be necessary.

Hence it seems that at Suaq Balimbing, adult females are sedentary, occupying large but restricted ranges, that contain a smaller, more densely utilised core area. This concurs with the findings of Galdikas (1979) who also found that female ranges seemed stable and had definite boundaries, with all individually identified females remaining in the same general area in which they were first encountered. Reports by previous studies of transient or migratory females are not supported by this study. Indeed it is possible to infer that females regarded as transient at other field sites, are simply individuals from adjacent areas, whose core areas lay outside but who occasionally venture inside the study areas on 'excursions', particularly when fruit is abundant there.

#### 4.4.2.2. *Adult males*

Adult males also exhibit considerable range overlap, and appear to possess much larger ranges than adult females, as reported from other studies. Ranges appear to be a minimum of 1500 ha, but probably lie in excess of 3000 ha and are possibly much larger. On a few occasions, adult males that had not been seen within the study area for some time, were encountered only a few kilometres outside, during searches or follows there. This did not seem to happen as often as it might be expected, however, supporting the idea that they range more widely.

Presence data shows that the majority of individuals could be regarded as occasional visitors. Whilst it is true that adult males can be absent from the study area for long and irregular intervals, almost all do return, implying large but limited ranges as opposed to true transience. Only two possible exceptions to this were recorded. Both of these, Binu and Hotma were observed in 1994 and 1995 but disappeared in early 1996. It is considered that both may have died, however, as one was physically handicapped (i.e. blind in one eye) and the other appeared to be in poor physical condition (e.g. old and emaciated). It is conceivable that these individuals could have been transient but their condition suggests death as an equally plausible explanation for their absence.

Despite the fact that adult males at Suaq Balimbing do not appear to be truly transient, transience remains a possibility in other areas. It is not inconceivable that the forests in and around Suaq Balimbing are in fact already isolated from the rest of the Leuser population. On the north-west, south-west and south-east sides the forest is discontinuous, either due to degradation or the coast. Therefore, the only real dispersal route would seem to be via the north-east, but this area has also experienced some forest destruction in recent years. Thus it is possible that adult males in this area must occasionally return as they cannot exit this closed system. They would then appear to circle around within it. However, on some expeditions outside of the WCS study area, a number of unknown adult males were encountered, that had never been recorded within it. Therefore, it is suspected that adult males probably do have range boundaries though only long-term fieldwork would show if unknown adult males continue to arrive in the area or not.

Presence data also suggest that the ranging habits of the dominant adult male, Arno, may be different from those of other adult males, he being the only one that can be regarded as a frequent visitor ($P_j > 50\%$), and also as there is evidence that non-dominant adult males may actively avoid him. As noted, $P_j$ can overestimate presence but observations in the field agreed that Arno was certainly far more often within the WCS study area than any other adult males. As a result it seems reasonable to infer that his regular home range may be somewhat smaller than those of other, non-dominant adult males. Thus Arno's regular home range might be considered to be in the order of 1500 ha or so, since range estimates for him were at least 740 ha with the polygon method, up to 1990 ha with the circle method. It is considered highly likely that he would be capable of covering a greater area, however, when and if required.

If Arno does indeed possess a more limited range than other adult males, it is possible to speculate that the maintenance of an effective monopoly over access to the maximum number of reproductive opportunities may be the major determinant of range size for dominant adult males. In fact, Galdikas (1985) also noted that adult males appeared to have relatively restricted ranges during periods of 'residence' (and presumably dominance too) at Tanjung Puting. From all of the behavioural data since 1994 it is clear that Arno does have almost exclusive breeding rights among fully adult males in the WCS study area, as only one other fully adult male was ever seen to mate with an adult female, and even then only once (pers. obs.; van Schaik unpubl.). Furthermore, whilst subadult males regularly mate with adult females at Suaq Balimbing, it is most often during periods when the females are clearly not receptive (e.g. carrying very young infants), and such copulations are usually forced (van Schaik 1999). It therefore seems logical to expect the dominant male to be reluctant to venture too far from the area in which he is dominant, due to the possibility of being absent during receptive periods amongst the females there, and also the potential risks incurred, such as injury or loss of status, were he to come into conflict with other powerful males.

Given that Arno's range should provide sufficient food, and appears to afford virtually exclusive access to all receptive females, the question must then be asked as to what determines the range sizes of non-dominant adult males. Three options seem likely; food, potential mates, and avoidance of the dominant adult male. Presumably, non-dominant adult males are able to range more widely than adult females as they do not have dependent offspring, and can therefore tolerate food stress more easily. Also, given the dominance of males such as Arno, they would have much to gain from searching for unguarded receptive females, since these would seem to present their only opportunity to reproduce. The results further suggest that non-dominant adult males may actively seek to avoid the dominant adult male. Thus it seems that when several females in a given area are receptive, the dominant male moves into that area, often along with a number of subadult males, but non-dominant adult males tend to avoid the area. If therefore, non-dominant adult males must range over large areas to stand any chance of reproducing, and must at the same time avoid dominant adult males who posses ranges of at least 1500 ha, their ranges would be expected to be considerably larger than this.

#### 4.4.2.3. *Subadult males*

From the presence data, it is clear that all but perhaps a few subadult males spend considerable periods of absence, but also that at least some do return from time to time. Observations of a few individuals outside the study area imply very large ranges, probably of several thousand hectares, though any attempt to estimate their true extent can be only speculation. The presence data also suggest that they are more often within the WCS study area when there are receptive females. Field observations supported this as several subadult males were often in close proximity when the dominant male was consorting with females (pers. obs; van Schaik, 1999). As previously mentioned data pertaining to subadult males is the most difficult to analyse due to the number of unidentified individuals observed, so true transience, very large ranges, or indeed both, remain possibilities.

### 4.4.2.4. *Subadult females*

Observations of adolescent females (which would include subadults as defined here), with known mothers at Tanjung Puting indicated that daughters travelled mostly within their mother's ranges (Galdikas 1988, 1995a). It has also been suggested that on maturation adolescent females settle in stable home ranges within or adjacent to those of their mothers (Galdikas 1988, 1995a; Rodman 1973b). The results of this study are consistent with these views. One subadult female Becky, did indeed appear to settle in the same area that she had frequented for several years previously after giving birth to her first infant. Before giving birth, however, there is evidence that she may have temporarily ranged over a larger area but given that adult female ranges appear to include an 'excursion' zone, this larger area may simply correspond to that. Such behaviour is also supported by the encounters during the early part of the study, but not in subsequent years, with several subadult females along the northern edge of the WCS study area. Their disappearance did not coincide with the appearance of any new adult females in that area, as should have occurred if they had simply matured. It is therefore suspected that these young females may have simply been exploring the periphery of their natal ranges, and slightly further afield. Ranging more widely would seem advantages to a maturing female as it would presumably be in her interests to explore the area and consolidate relationships with her potential neighbours, and also to increase her association time with potential mates. By ranging more widely she may be able to achieve both of these objectives. For these reasons a tentative range size estimate for subadult females would be slightly larger than the core areas of their mothers, probably in the region of 700 ha to 800 ha or so.

### 4.4.3. SEX RATIOS

At Ketambe, Rijksen (1978) estimated adult sex ratios as 0.5 (or 1 adult male to 2 adult females) and 1.2 (or 1.2 adult or subadult males to 1 adult female, which would be slightly lower if subadult females had also been included), both of which are considerably higher than those found here through range modelling. Rijksen made no allowances for range sizes, however, and simply estimated these values from the number of individuals of each age and sex encountered in his study area.

The values derived here are also all much lower than previously reported sex ratios at birth. For example Leighton *et al.* (1995) concluded that sex ratios at birth were around 50% to 55% (i.e. 1.0 to 1.1 male infants to every female infant using the terminology above). This was based on a large sample from Tanjung Puting (n approx. = 30). In addition, 53% of 98 individuals (ex-captive orangutans rather than births) brought to Bohorok in Sumatra during the 1970's were males (van Schaik and van Hooff 1996). Van Schaik and van Hooff (1996) also note two additional samples, one of wild births at Ketambe between 1989 and 1992 of which 7 of 9 births were males (though they pointed out that this was a small sample), and a sample of confiscated orangutans brought to a rehabilitation centre in East Kalimantan that was heavily skewed towards males. Thus the evidence suggests that the sex ratio at birth for orangutans on both islands is roughly equal (i.e. 1.0) or if not, that it is likely to be male biased (i.e. > 1.0), rather than female biased. This is further supported by the estimated sex ratio at birth for Suaq Balimbing. Of 9 infants born at Suaq between October 1994 and September 1998 (including two that subsequently disappeared), 4 were males, giving a sex ratio of 0.8 (i.e. that for every female infant born there were 0.8 male infants born, excluding the two presumed dead would give 0.75). Taking all offspring of known females (including older siblings of new infants) we find 14 males among 25 individuals, giving a ratio of 1.27. Either way it appears that the expected ratio in the population should be somewhere between 0.75 and 1.27, whilst all the estimates from Table 4.7 are noticeably lower, the highest being 0.457. These facts therefore imply a net loss of males from the Suaq Balimbing population as it matures.

That sex ratios are much lower among fully adult individuals also supports previous reports (see Chapter 1) that males may remain subadult for much longer periods than would be the case if the acquisition of secondary sexual characteristics was purely age related. If subadult males became fully adult at around the same age that females do the sex ratios should be approximately similar for both fully adult individuals and all sexually active individuals, but this was not found to be the case.

It should also be noted that the estimate for subadult male range overlap of 30 is based on impressions gained in the field but reducing this number, results in even lower estimated sex ratios. Even increasing subadult male overlap to 50, only increases the sex ratio to 0.686 adult or subadult males to one adult or subadult female (using the range sizes given under model B in Table 4.7). It might conceivably be argued that the measures of range overlap, which are based on all individuals known to have used the same grid cells over the period 1994 to 1998, could include some individuals that have since died, and could thus be too high. However, it is strongly suspected that deaths, particularly among mature individuals could only have accounted for very few losses over this time period, and there remains the possibility that any that may have occurred could have been either males or females and as such are unlikely to influence the results markedly. Hence it appears that the discrepancy in sex ratios between immature and mature orangutans is real.

Two possible explanations for this would be a net loss of males due to either emigration, or to higher male mortality. High male biased mortality would certainly account for such a reduction but there would appear to be a paucity of evidence for such a phenomenon. Some deaths of mature wild orangutans have been observed and recorded (e.g. Rijksen 1978; S. A. Wich pers. comm.; Knott 1998a) and the deaths of some adult males have been attributed to male conflicts (Knott 1998a; C. D. Knott pers. comm.). Some adult males also bear scars that are often attributed to fights (pers. obs.; Galdikas 1995b). However, whilst some deaths of males due to male conflict almost certainly will occur from time to time, the number so far observed remains too low to provide reliable evidence that this could account for all of the observed discrepancy.

It therefore remains possible that at least some males disperse through emigration, most likely during the subadult phase, from high density areas such as Suaq Balimbing (noting also that this type of habitat is increasingly rare in northern Sumatra), into other areas where densities may be lower. Leighton and Leighton (1983), also stated that peaks in local orangutan densities at their site were due to movements through the area by non-residents, particularly subadults and Galdikas (1988) reported that emigrants from Tanjung Puting were exclusively males.

If it was found that other areas contained a higher ratio of males to females than would be expected from range size and range overlap data, it might be inferred that there was indeed an influx of males in these areas. It could perhaps be argued that more marginal habitats, containing lower female densities, might make it more difficult for an adult male to maintain lengthy associations with receptive females and hence to monopolise more scattered reproductive opportunities. Such a situation might be exacerbated in hilly terrain, making such areas more profitable, and hence more attractive to subadult and non-dominant adult males searching for isolated, unguarded receptive females. This would therefore provide an incentive for males to migrate to such areas from habitats containing higher densities of orangutans, particularly females, in which the dominant adult males have almost exclusive access to receptive females, and where the prospect of finding unguarded females would be much reduced.

## 4.5. CONCLUSIONS

1. Adult females at Suaq Balimbing occupy fixed ranges comprising a core area of around 500 ha and a surrounding excursion zone giving a total usable home range in the order of 900 ha to 1500 ha. These ranges overlap considerably with up to 15 individuals sharing some areas. There does not appear to be any evidence to support the existence of transient adult females.
2. Changes in population composition occur over time as a result of the reproductive status of females. When females are receptive the dominant male is normally present along with a number of subadult males but when there are few or no receptive females the dominant male and subadult males are more often absent. Conversely non-dominant males appear to avoid the dominant male and are more often present when he is not.
3. Adult males range more widely and occupy large but probably fixed ranges of at least 2000 ha and more likely between 3000 and 10000 ha or more in extent. The dominant adult male is probably an exception to this and may have a more restricted range of around 1500 ha or so, at least during his period of dominance. Adult male ranges appear to be most heavily influenced by reproductive opportunities and not by food availability, as with females. Again there is considerable range overlap, and like females, it appears that transience is not a dominant phenomenon among adult males, if it exists at all.
4. Subadult male ranging remains the least understood. Ranges cover at least 1000 ha and as with adult males are probably between 3000 ha and 10000 ha or more. Many individuals certainly do return at irregular intervals suggesting very large ranges that are nevertheless, limited in extent, but the number of unidentified individuals encountered means that true transience may also occur among this group.
5. Orangutan ranges do not decrease as densities increase, an important fact to note for conservation management purposes.

6. There is compelling evidence that a significant loss of males from the population occurs as the population matures, possibly due to high male biased mortality, but also to excess male dispersal, perhaps over considerable distances. If real, the cause of this loss clearly warrants further investigation.
7. That sex ratios are less female biased amongst subadults and adults combined than amongst full adults only supports previous reports that males may remain subadult for much longer periods than would be the case if the acquisition of secondary sexual characteristics was purely age related.

# CHAPTER 5

# SEASONAL MOVEMENTS

## 5.1. INTRODUCTION

Tropical forests are seasonal habitats exhibiting complex rhythms of plant production (Daubenmire 1972; Leiberman 1982; Murali and Sukumar 1994). Even wet tropical forests exhibit fruiting seasonality (Frankie *et al.* 1974; Leighton and Leighton 1983; Longman and Jeník 1987; van Schaik *et al.* 1993; White 1994; Chapman *et al.* 1999). Furthermore, Rijksen and Meijaard (1999) report that in northern Sumatra the intra-population fruiting synchrony (or seasonality) of a particular tree species can 'move like a wave' over tens of kilometres, and at Ketambe, S. Orbons (unpubl., cited in te Boekhorst *et al.* 1990) found that fruit production at higher altitudes appears to peak about two months later than in lower areas (see also van Schaik 1986). In addition, several authors have noted that many frugivorous mammals in Sumatra and Borneo show large-scale seasonal movements (e.g. pigs, fruit bats and elephants), and have suggested that these movements occur as a result of fruiting asynchrony between areas (e.g. Leighton and Leighton 1983; Whitten *et al.* 1987; MacKinnon 1989).

It has also been proposed that seasonal movements are characteristic of orangutan populations. Both MacKinnon (1974) and Sugardjito *et al.* (1987) noted that orangutan numbers tend to increase during fruiting peaks and Leighton and Leighton (1983), found a positive correlation between peaks in local orangutan densities and the number of large patches of primate fruits (i.e. fleshy, pulpy fruits). Rijksen and Meijaard (1999) agree that under a regime of seasonal availability of food the frugivore is obliged to move, and speculate that a considerable proportion of orangutan populations may therefore be forced to move or migrate seasonally. However, they also point out that in some areas at least, several individuals appear to settle as residents, and furthermore, that most other frugivorous primates in the region (e.g. gibbons and long-tailed macaques), can live permanently in relatively small, fixed home ranges of less than 1 $km^{-2}$.

Several authors have indeed reported a clear distinction between resident and non-resident orangutans and also suggest that some individuals appear to be nomadic, or at least to emigrate during periods of fruit scarcity (e.g. MacKinnon 1974; Galdikas 1978; Rijksen 1978; Sugardjito *et al.* 1987; Rodman 1973a,b, 1988; Mitani 1985a,b; te Boekhorst *et al.* 1990; Suzuki 1992). Rijksen and Meijaard (1999) go further by stating that three categories of orangutans can be distinguished: (a) residents, who are frequently encountered, (b) commuters, who appear occasionally but normally return, and (c) wanderers, who are infrequently seen and may never return. MacKinnon (1974) even suggested that there were no sedentary residents at all in the immediate vicinity of his Ulu Segama basecamp, though he did later acknowledge that some may have been resident in the 'neighbourhood' and that his data were not incompatible with sedentary home ranges (MacKinnon 1989). Instead, however, MacKinnon (1974) described orangutan society as a community in which subgroups of larger travelling bands centre around an adult male and move in the same general direction; community members thus sharing a group range rather than occupying individual ranges. Thus there is considerable inconsistency in the literature as to whether all orangutans are residents, in that they remain within fixed ranges, or all are transients (e.g. migratory, nomadic), with no fixed ranges, or if populations contain both.

It has also been reported that sexual bias exists between residents and transients, and that it is predominantly males that are the most mobile, females tending to be mostly residents (Galdikas 1978; van Hooff 1995). Males rather than females are therefore often considered the wandering sex (Rodman 1973a,b; Galdikas 1979; Leighton and Leighton 1983; Mitani 1985a,b; Schurmann and van Hooff 1986). There is additional circumstantial evidence from rehabilitation projects that males are indeed the most mobile. At Ketambe during the early 1970s, individual males were often absent from regular 'feedings' for weeks or even months, sometimes never to reappear, whilst females remained more faithful visitors (van Schaik and van Hooff 1996). In contrast, however, neither te Boekhorst *et al.* (1990) nor MacKinnon (1974), found any sexual bias among non-residents or transients. Further inconsistency therefore exists as to whether only males, or individuals of both sexes are transient.

Clearly there is evidence of much temporal variation in orangutan abundance at field sites, but as acknowledged by MacKinnon (1989), different interpretations of these observations could be made. Leighton and Leighton (1983) suggest three possible scenarios. Firstly, small study areas could simply overlap only a portion of much larger, but fixed home ranges. Secondly, populations may be truly migratory, leaving an area on a cyclical basis but normally returning; and thirdly, populations may be truly nomadic, without necessarily ever returning. Each of these scenarios seems equally plausible as an explanation for the reported behaviour of individuals currently regarded as transient. It is important to point out, however, that the majority, if not all work on orangutan movements and range sizes, has been carried out in restricted areas, i.e. delineated study areas of limited extent, and so the first scenario remains a strong possibility. In itself, study area size imposes restrictions on the number of individuals that will be encountered, and the frequency of encounters. For example, an individual's home range may only slightly overlap the study area and such individuals are likely to be encountered only infrequently. In fact, if they use their home ranges with equal intensity throughout, the frequency of their visits to a study area would be directly proportional to the proportion of their range coincident with it. If, however, they use the periphery of their ranges less intensively than other parts (e.g. the centre) then visits would be even less frequent. Thus categorising an individual as transient, solely on the basis that it was seen only rarely, would seem a little tenuous, as orangutans that were in fact resident in the area immediately adjacent to the study area, would appear to be transients. For the same reasons, apparent seasonal influxes of orangutans into a study area might reflect only nearby residents at the limits of their ranges, rather than large scale seasonal 'migrations' of individuals.

In attempting to explain why males might be more transient than females it has been speculated that they are attracted to an area when the number of receptive local females increases (Galdikas 1979; Mitani, 1985a,b; Rodman and Mitani 1986). Te Boekhorst *et al.* (1990) explored this but found that although the observed influx of non-resident males into the Ketambe area did not correlate with the number of receptive resident females, a positive correlation did exist with the number of receptive non-resident females. From this they postulated that non-residents of both sexes are seasonally attracted to areas with increased fruit availability, supporting a food-attraction hypothesis. They were careful to point out, however, that their data did not categorically disprove a female-attraction hypothesis. In contrast, Utami *et al.* (2000b) did find that during at least a part of their study at Ketambe, there was a positive correlation between the number of fully adult (flanged) males and the number of potentially reproductive females. Given that there is therefore some evidence to support both a food-attraction hypothesis and a mate-attraction hypothesis, it is reasonable to expect that both will influence fluctuations in local orangutan densities, particularly as they are not mutually exclusive.

If large influxes of individuals into an area do occur, whether as a result of non-residents acting independently or as 'waves' of coordinated individuals as suggested by MacKinnon (1974), it should be possible to identify significant variation over time in the total abundance of individuals over a large area, such as the whole study area. If, however, individuals respond more locally, e.g. to regional variation in fruit availability, then more compensatory changes (negative correlations) with respect to densities should occur between sites that are relatively close together. Furthermore, if non-residents or transients constitute only a small component of the population, sites that are less distant than the diameter of home ranges should show stronger positive relationships with respect to densities than sites that are more distant.

The primary aims of this chapter are therefore to determine if seasonal movements of orangutans do indeed occur at Suaq Balimbing, and if so on what scale, i.e. if they are large scale 'wave'-type movements or smaller localised movements, representing only movement within relatively limited home ranges, or both? The influence of phenology, more specifically fruit availability, on orangutan movements will also be explored, to assess the degree to which movements can be explained by the food-attraction hypothesis. With this information it is then hoped that a subsequent examination of ranging patterns, based on direct observations of individuals, will allow a more thorough investigation of orangutan movements, their causes, which age and sex categories are most mobile, and whether or not there is real evidence of a dichotomy between residents and transients.

## 5.2. METHODS

Nest transects and phenology plots were established at six locations scattered over the whole study area (as described in Chapter 2), in order to monitor monthly fluctuations in orangutan densities and forest productivity in different parts.

### 5.2.1. DENSITY ESTIMATES

The density of orangutans was estimated monthly at each location, using the number of new nests built since the preceding month, and the program DISTANCE (see Chapter 3). The estimates thus obtained were considered to be underestimates of absolute densities but were still considered to reliably indicate changes in relative densities between transects and between months. They were also directly proportional to the actual number of nests each month. This being the case, the number of new nests per month was used directly to explore relationships between orangutan movements and phenology indices at the plot or transect level. To facilitate comparison at an area-wide level, however, the density estimates themselves were required to remove any bias from different forest types (e.g. different nest detection rates etc.) at each location.

### 5.2.2. PHENOLOGY METHODS

To assess the influence of phenology on fluctuations in densities, monthly phenology observations were carried out in the same areas as nest transects. Various methods may be used to evaluate food resource availability. These include fruit (litter) traps, fruit counts on forest trails and direct phenological observations within plots. However, Chapman *et al.* (1994) concluded that fruit traps had many limitations in determining resource availability for an animal community, and also found that the results they produced did not correlate well with results from direct phenological methods. Furthermore, frequent flooding of many of the trails at Suaq Balimbing precluded the use of fruit counts on trails, so for these reasons direct systematic phenological observations were conducted within plots.

#### 5.2.2.1. *Field procedure*

In each plot, all trees of 30 cm circumference at breast height (cbh) or more, and lianas of at least 20 cm cbh, with the base of their trunk (or stem) within 5 m of one side of the trail, were tagged and identified, initially using local names. To negate any error due to aspect, every 50 m the plot was switched to the alternate side of the trail. Plots were checked each month by the same observer, thus removing any effects of inter-observer variability. Using binoculars the observer first determined the presence or absence in each tree of young leaves, flowers and fruits and then estimated the abundance of each phenophase within the crown of each tree, using the following scales:

1) Young leaves: recorded in percentage classes i.e. none, <5%, <10%, <25%, <50%, <75%, <100%, of total leaf cover. Only young leaves were recorded as for most tree species these tend to be the ones eaten by orangutans. They are readily identified as they tend to be more opaque than mature leaves, or a different colour. Each score was then assigned a second score representing the midpoint of the range recorded, i.e. none = 0, <5% = 2, <10% = 7, <25% = 17, <50% = 37, <75% = 62, and <100% = 87. The mean

of these scores over all trees and lianas was then calculated as a monthly index of young leaf production in each plot.

2) Flowers: recorded on a four point scale:

    0 = flowers absent
    1 = only very few flowers present,
    2 = approximately half of the crown in flower,
    3 = crown almost full.

   The monthly proportion of trees with a score of 1 or greater was then calculated for each plot.

3) Fruit: recorded on a scale that increases by order of magnitude according to the number of fruits present (i.e. none, 1+, 10+, 100+, 1000+, etc.). Fruits were also identified as unripe, half-ripe, and fully ripe. From these data the monthly proportion of trees producing fruit of all stages of ripeness (i.e. unripe, half-ripe, and fully ripe) was calculated for each plot. A second index, representing only ripening fruit (half-ripe and fully ripe) was also calculated in the same manner.

These methods therefore produced four indices for each plot reflecting the monthly availability of:

- Fruit at all stages of ripeness ('all fruit'),
- Ripe and half-ripe fruit only ('ripening fruit'),
- Flowers,
- Young leaves.

### 5.2.3. DIET COMPOSITION

Naturally, orangutans are not expected to consume the fruit, leaves or flowers of all species available to them and indeed do show a strong preference for soft, pulpy fruits and fruits with arils or seed-walls around the seeds (Leighton and Leighton 1983; Djojosudharmo and van Schaik 1992; Leighton 1993). For this reason it was considered that simply using fruit of all species as an indicator of food availability might prove inadequate in detecting relationships. Hence several additional indices were also calculated, to reflect the contribution of fruit and other food types to the diet each month, and to reflect the availability of fruit of those species comprising a large proportion of orangutan diets.

To facilitate this the activity of focal individuals was recorded instantaneously at two minute intervals, during all focal individual follows of orangutans (see Chapter 2). If the focal individual was feeding, the food type being eaten was recorded (e.g. fruit, flowers, leaves, stem, bark, insects etc.), and the species identified using local names, if known. These data were then used to determine the percentage of total feeding time each month that was devoted to acquiring each of the various food types (Appendix 3). The monthly percentages were then converted to proportions and transformed using arcsines. As with the other indices, all were subsequently found to conform to the normal distribution, using the Kolmogorov-Smirnov one sample test and Shapiro-Wilks test. This procedure resulted in seven new indices representing the proportion of the diet made up each month of fruit, all non-fruit items combined, young leaves, flowers, insects, stems and bark. These were subsequently correlated with numbers of new nests each month to test whether orangutans move as a result of dietary shifts (i.e. switching from fruit to leaves or bark etc.). This procedure was expected to show if they move into some areas as a consequence of a general absence of fruit, for example, in search of other more ubiquitous food items.

A further four indices were also produced using the diet data, representing the percentage of the total time feeding on fruit, that was spent on each species each month. A list of species together with their percentage contribution to the diet each month was then created (Appendix 4). This list was then further refined to include only those species that represented at least 5% of the fruit portion of the diet in at least one month of the study. Unidentified species were removed along with 3 species that were not represented in any of the phenology plots (one of these is an Agavaceae-like species that is common in most of the plot areas but is not a tree or liana).

The first two of these 'diet-specific' indices, were calculated from the proportion of trees each month producing (a) all fruit or (b) ripening fruit, of only those species that were present in at least one of the plots, and constituted at least 5% of the fruit part of the diet, in one month or more. The second two, also for all fruit and for ripening fruit, were calculated in the same manner but using only those species that were the dominant species in the diet of orangutans during one or more months. This therefore resulted in the additional indices:

- 5% all fruit,
- 5% ripening fruit,
- dominant all fruit,
- dominant ripening fruit.

The raw monthly values of all eight phenological indices are presented in Appendix 5, for all plots. It should also be noted that virtually all of the data on orangutan diets were collected within the confines of the WCS study area. Therefore, it is possible that orangutans further south (in the SM, GB and IB areas) may have fed on different food species, or at different times, so there is some potential for error when attempting to assess the contributions of diet species to orangutan movements over this wider area. However, in view of the large floristic overlap between plots, however (see Chapter 2), any error is considered unlikely to be substantial.

All indices comprised of proportions were first transformed using arcsines and then examined using Pearson's correlations to determine if any relationships exist with either the number of new nests (at plot level), or estimated orangutan densities (at an area-wide level). Pearson's correlations were also performed using time-lags, in case some relationships involved delays between phenology indices and the orangutan's reactions to them. For example, a positive correlation coefficient for *a* with *b* under a time-lag of +1 indicates that variable *a* increases 1 month before variable *b*, whilst a time-lag of -1 would indicate that variable *a* increases 1 month later than variable *b*.

Where several correlations were performed on the same data set, significance levels were adjusted to allow for the experiment-wise error rate, using the sequential Bonferroni test for k comparisons, by the Dunn-Šidák method (Sokal and Rohlf 1995), in which:

$$\alpha' = 1 - (1 - \alpha)^{1/k}$$

and $\alpha = 0.05$. Sequential Bonferroni tests were not performed on any of the time-lag cross correlations.

## 5.3. RESULTS

### 5.3.1. ORANGUTAN DENSITIES

Figure 5.1 shows monthly orangutan densities estimated for each transect using new nests between April 1997 and September 1998 (from Table 3.4). The first month of monitoring at each site was excluded (i.e. March for most and August for GB) as all of the nests were effectively new. Despite this, it is immediately clear from the graph that density estimates were exceptionally high for some plots during the second month of monitoring as well (April for most, September for GB). These exceptionally high estimates are considered most likely to be a function of the observer recording some 'missed' nests for the first time during the second month, despite the fact that they were present in the previous month. For this reason, the second month of monitoring was also excluded from further analysis.

The graph shows that at each transect orangutan densities were not stable and therefore that some movement into and out of the transect areas did occur. For example, high estimated densities were recorded at X from August to October in 1997 and in July 1998, around SM in January 1998 and July 1998, and around HJPLX in October 1997 and April 1998. It also shows that orangutans were more abundant in the HILL area from May to July 1997 than at any other time, returning to more normal lower densities soon afterwards.

These facts, together with the results of correlations between transects with respect to the number of new nests each month, suggest that orangutan presence at each location was not in phase. None of the correlations was significant after Bonferroni corrections, without a time-lag. Time-lag cross correlations, however, found three significant relationships. These were between the HILL and X with a time-lag of +3 months ($r = 0.559$, $p<0.05$, $n = 17$ overlapping months; Figure 5.2), and between SM and HJPLX with a time-lag of -3 months ($r = 0.750$, $p<0.05$, $n = 17$ overlapping months), and again with a time-lag of +3 months ($r = 0.616$, $p<0.05$; Figure 5.3).

Instead of being in phase, the results suggest that there may be some trade off between transects, in particular between SM and HJPLX, and perhaps between X and the HILL. For example, the time-lag results for SM and HJPLX suggest the possibility that orangutans using both locations may be the same individuals. This is because fluctuations in the

**Figure 5.1**: Monthly orangutan densities ($km^{-2}$) estimated using new nests for each plot.

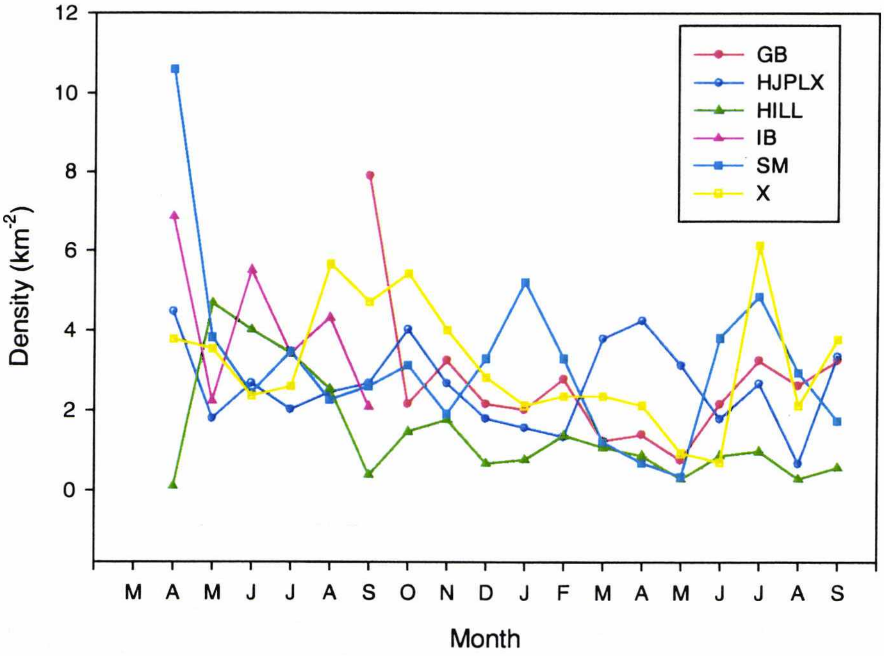


**Figure 5.2**: Time-lag cross correlation coefficients between transects HILL and X , using number of new nests. Confidence limits are 95%. Lag number on the X-axis represents months.

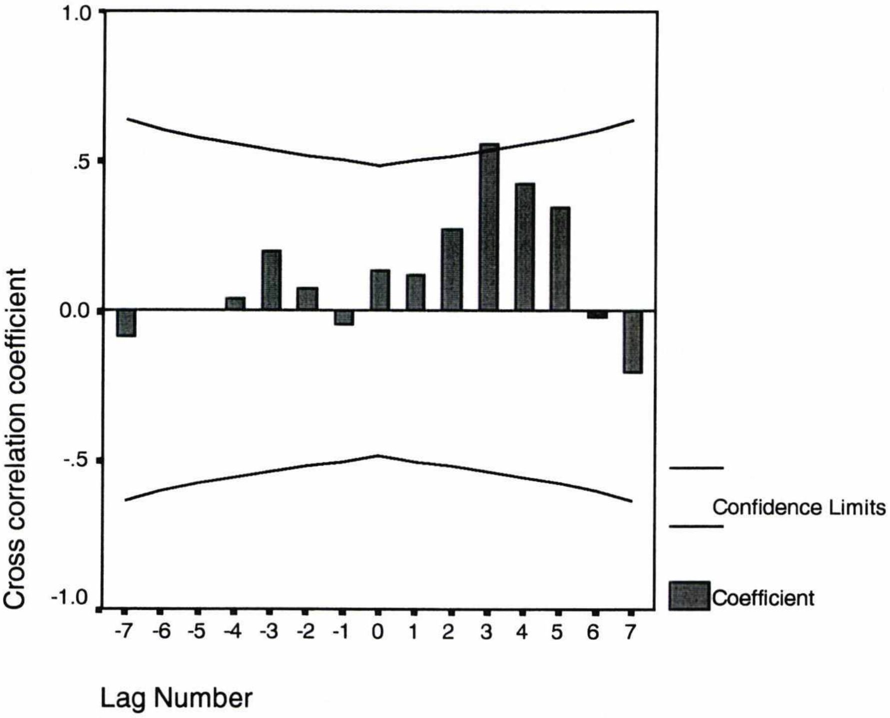
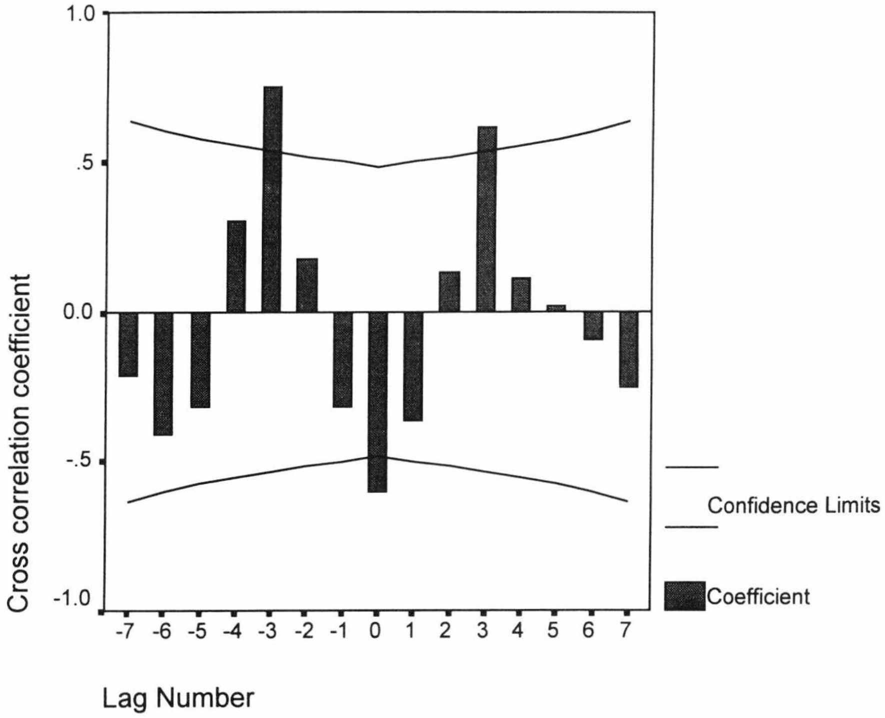


**Figure 5.3**: Time-lag cross correlation coefficients between transects SM and HJPLX , using number of new nests. Confidence limits are 95%. Lag number on the X-axis represents months.



number of new nests at SM appear to mirror fluctuations at HJPLX, both 3 months earlier and 3 months later, whilst with zero time-lag the relationship is significantly negative. Several possible interpretations of these findings could be made, however. It could be that there was movement between the two locations over a 6 month period, individuals travelling from the SM area to HJPLX and back again, so that when they were abundant at one they were scarce at the other, and vice versa. That individual orangutans do possess ranges large enough to do this is not in question as even some females, who possess the smallest ranges, have been seen further south than SM and further north than HJPLX (e.g. Mega and Butet) and are therefore likely to utilise all of the transect sites, with the exception of IB. Males on the other hand can probably reach IB as well. An alternative could be that two 'waves' passed through the area 6 months apart. In theory, however, both scenarios should be detected by relationships between both transects and X, since it lies between the two, but none were found. Thus it is impossible to draw any hard conclusions other than that movements between transects do occur, and perhaps that waves seem unlikely.

Reference to Figure 3.3 helps to explore this further. The graph represents the overall density estimated by pooling these three transects. It suggests movement of orangutans into and out of the area covered by them as a whole, as the overall density fluctuates on a monthly basis. It also shows two small peaks in densities around September and October 1997 and July 1998, which could be construed as supporting the idea of two waves of orangutans passing through, in this case roughly 9 months apart. However, despite these peaks, the overall density changes by only a few individuals over the entire period, i.e. 1.10 $km^{-2}$ to 3.58 $km^{-2}$, which does not support the wave hypothesis since only a few individuals are involved. It must also be realised that the large distances between some transects are such that large numbers of individuals would remain effectively hidden between them, and furthermore, it cannot be concluded that the densities at all transects changed, only that densities on at least one transect experienced some changes. Hence, large scale movement of individuals into the area, or waves, cannot be inferred from these data though movement of individuals is clear, on at least a local level.

## 5.3.2. PHENOLOGY

Appendix 5 shows the raw values of each of the phenology indices for each month in each plot. Raw values of the original four (non-diet-specific) indices are also presented graphically in Figures 5.4 to 5.7. After arcsine transformations of all proportions each of the indices was then tested for normality using the Kolmogorov-Smirnov one sample test and Shapiro-Wilks test and all were found to conform to the normal distribution.

### 5.3.2.1. *Fruit*

Figure 5.4 shows clearly a large peak in fruiting that occurred in the hills, relative to normal levels there, from March to June 1997. During this period all fruit scores for the HILL attained the 10% level for 4 months against a backdrop of relatively low fruit production at this plot. A second distinct, but much smaller peak in fruiting occurred in the HILL around July 1998. The much larger first peak therefore appears to represent a mast fruiting event (see Chapter 2) and also corresponds to the period of highest densities in the HILL as noted earlier. Peat swamp forests do not experience mast fruiting (Knott 1999). However, it is interesting to note that the highest peaks in fruiting observed at IB, HJPLX and X all occurred during the same months as the mast fruiting in the hills. Therefore despite the fact that mast fruiting is not known in peat swamp forests (Knott 1999), there is

**Figure 5.4**: Percentage of trees/lianas in each plot producing fruit at all stages of ripeness (all fruit), each month.

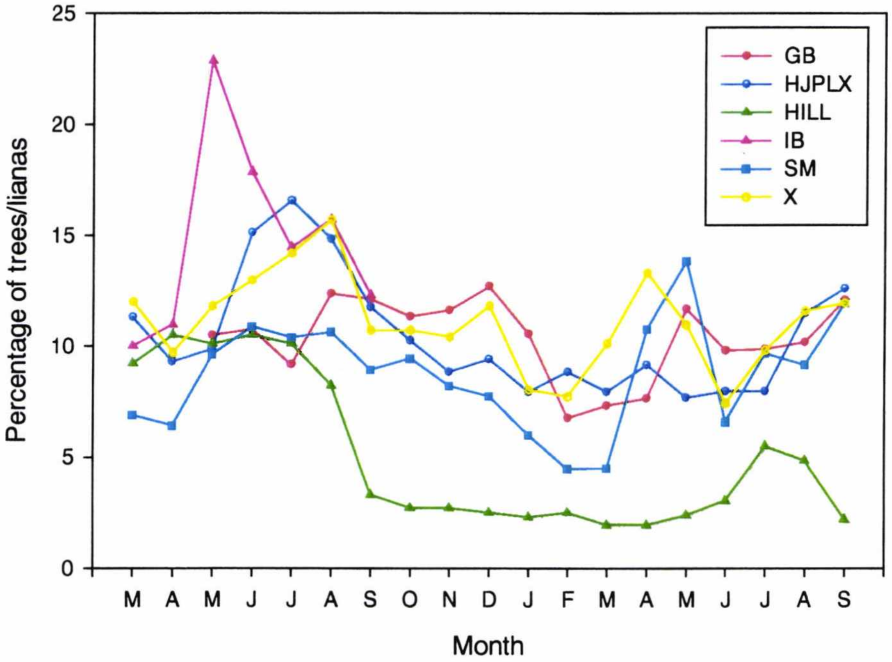


**Figure 5.5**: Percentage of trees/lianas in each plot producing ripening fruit, each month.

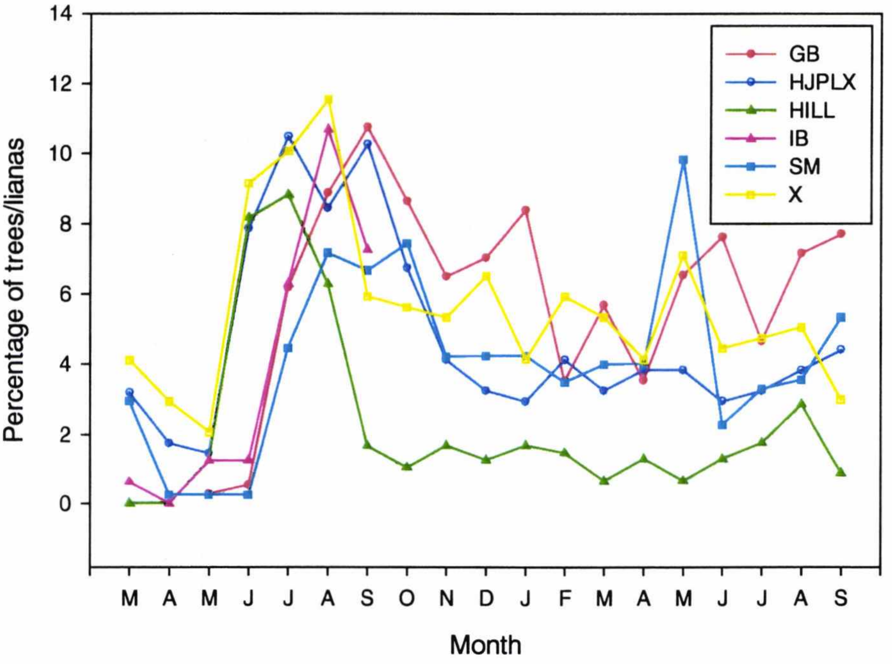


**Figure 5.6**: Percentage of trees/lianas in each plot producing flowers each month.

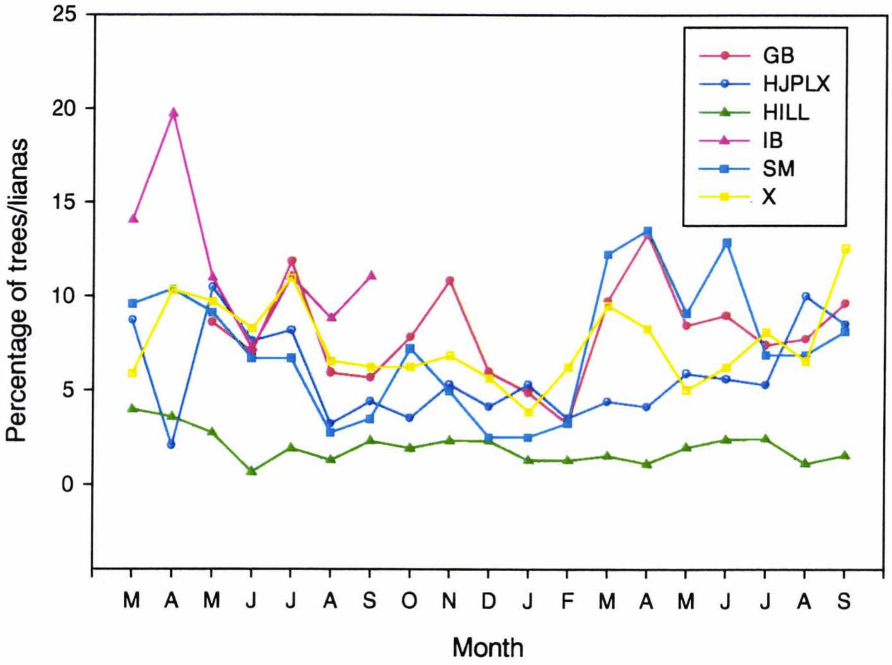
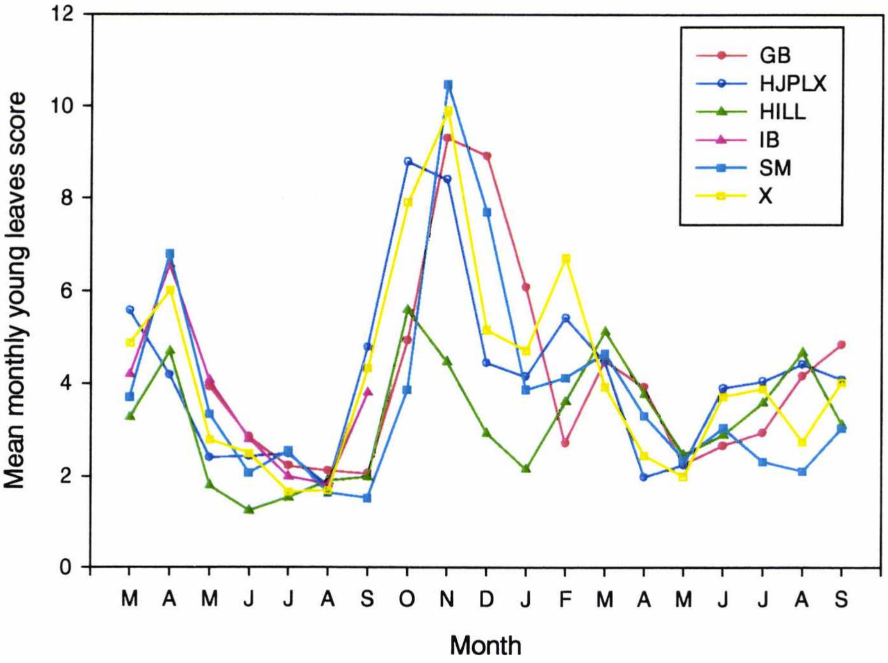


**Figure 5.7**: Mean monthly young leaves scores for each plot.



evidence that neighbouring swamps can experience high levels of fruiting at the same time. In addition, IB is notable due to the very high levels of all fruit production in April 1997, distinctly higher than at any other plot throughout the rest of the study. Figure 5.5, which is restricted to ripening fruit, clearly shows the masting in the hills, and confirms that many of the swamp plots were producing a lot of fruit at the same time.

The graphs also suggest that the plots are in phase to some degree with respect to fruiting, though not precisely, with peaks in all fruit production occurring around July 1997 and May 1998 in most plots, and in ripening fruit production in most around one month later. Pearson's correlations provide further evidence that plots exhibit some degree of synchrony but are not precisely in phase, with significant positive correlations between each plot and at least one other for ripening fruit, (Table 5.1). Fruit at all stages of ripeness suggests plots are not in phase, however, as only plots HJPLX and X produced a significant correlation ($r = 0.757$, $n = 19$; Bonferroni/Dunn-Šidák corrected level calculated using $\alpha = 0.05$, $k = 15$).

**Table 5.1**: Significant Pearson's correlation coefficients between plots for ripening fruit (variables arcsined, n = no. of months). Significance is at Bonferroni/Dunn-Šidák corrected level ($\alpha = 0.05$, $k = 15$).

| Plot | GB | n | HILL | n | HJPLX | n | IB | n | SM | n | X | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GB | | | | | | | | | 0.702 | 17 | | |
| HILL | | | | | 0.719 | 19 | | | | | 0.808 | 19 |
| HJPLX | | | | | | | | | | | 0.755 | 19 |
| IB | | | | | | | | | 0.919 | 7 | | |
| SM | | | | | | | | | | | | |
| X | | | | | | | | | | | | |

### 5.3.2.2. *Flowers*

Flower production is plotted in Figure 5.6 and shows less evidence of synchrony between plots. This is also reflected by the correlation coefficients, with only SM and GB showing a significant relationship ($r = 0.715$, $n = 17$; Bonferroni/Dunn-Šidák corrected level calculated using $\alpha = 0.05$, $k = 15$). Again IB is notable due to a very high initial peak in flower production in April 97, one month before the observed peak in fruit production there. In both cases the peaks are much higher than any observed in other plots during the study period.

### 5.3.2.3. *Young leaves*

Figure 5.7 suggests that the plots are most strongly in phase with respect to young leaf production, as clear peaks are visible in all around April 1997 and November 1997, the latter of which coincides with the month with the highest rainfall during the study (see Figure 2.2), and also follows just a few months after high fruiting levels in all the plots. Again correlation coefficients support this apparent synchrony, with significant positive correlations between all the plots and at least one other (Table 5.2).

**Table 5.2**: Significant Pearson's correlation coefficients between plots for young leaves (n = no. of months). Significance is at Bonferroni/Dunn-Šidák corrected level ($\alpha = 0.05$, k = 15).

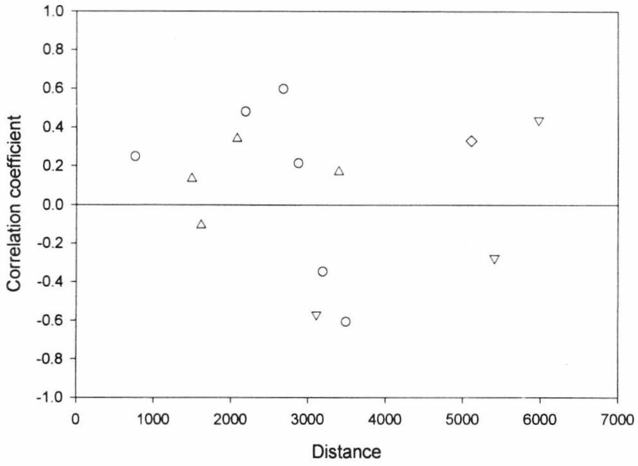
| Plot | GB | n | HILL | n | HJPLX | n | IB | n | SM | n | X | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GB | | | | | | | | | 0.897 | 17 | 0.651 | 17 |
| Hill | | | | | 0.656 | 19 | | | | | | |
| HJPLX | | | | | | | | | | | 0.916 | 19 |
| IB | | | | | | | | | | | 0.921 | 7 |
| SM | | | | | | | | | | | 0.756 | 19 |
| X | | | | | | | | | | | | |

## 5.3.3. RELATIONSHIPS BETWEEN SITES WITH RESPECT TO DISTANCE

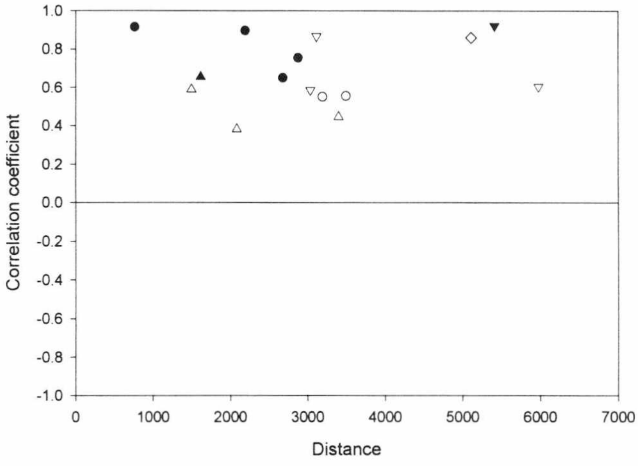
Figure 5.8 shows how the strength of correlation between plots, regarding numbers of new nests and the various phenological indices, varies with respect to the distance between them. At first glance the graphs do not appear to show any clear trends. However, it could be argued that for these purposes, correlations involving the HILL should be excluded as it represents a markedly different habitat type to all of the others, and was not generally used by the orangutans in large numbers except during the mast event in early 1997. If the HILL is excluded, it is possible to see that the strength of correlations between plots using some of the indices appears to decline around the 3000 m mark. For example, with respect to numbers of new nests, all correlations between plots are then positive up to 3000 m, and then some become negative (Figure 5.8a). The same also applies to all fruit (Figure 5.8d), to all fruit and ripening fruit of species that were the dominant part of the diet in at least one month (Figures 5.8f and 5.8g), and to all fruit of species that constituted at least 5% of the diet in at least one month (Figure 5.8h). This tendency to decline is even more apparent if only relationships denoted by circles are examined. It should be noted that correlations involving IB are based on only 7 months of data (only 5 for new nests). IB is also over 3 km from any other site and over 5 km from some, and is therefore unlikely to be accessible

**Figure 5.8**: Relationship between strength of correlation coefficient between plots, using numbers of new nests each month and various phenological indices, to distance between plots (metres) for (a) new nests, (b) young leaves, (c) flowers, (d) all fruit, (e) ripening fruit, (f) dominant all fruit, (g) dominant ripening fruit, (h) top 5% all fruit, and (i) top 5% ripening fruit; △ denotes correlations involving HILL plot, ▽ involving IB plot, ◇ involving both HILL and IB plots, and ○ denotes all others. Solid symbols indicate significance at Bonferroni/Dunn-Šidák corrected level ($\alpha = 0.05$, k = 14 for new nests, 15 for all others).

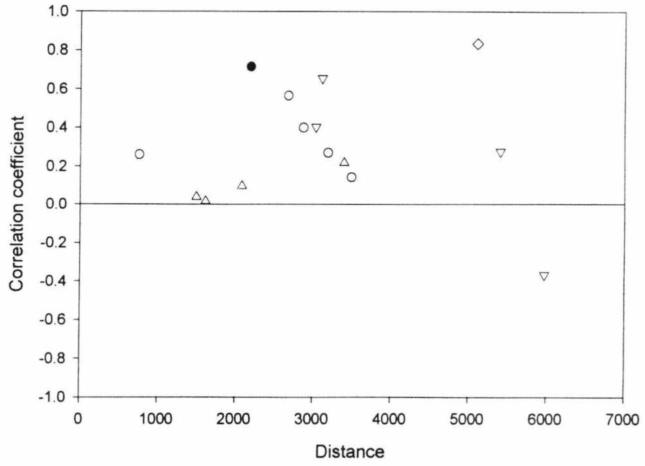
(a) Number of new nests



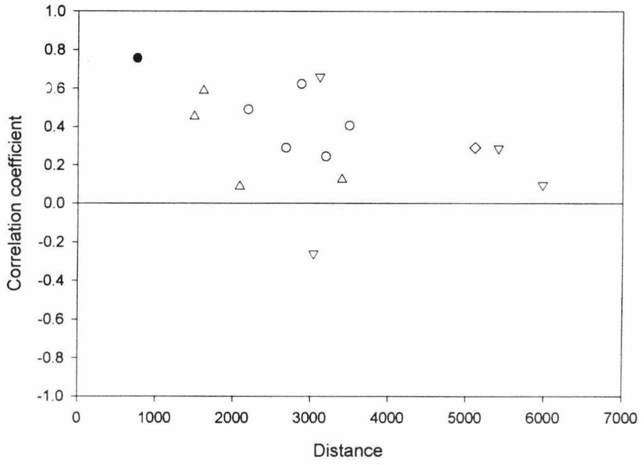
(b) Young leaves.



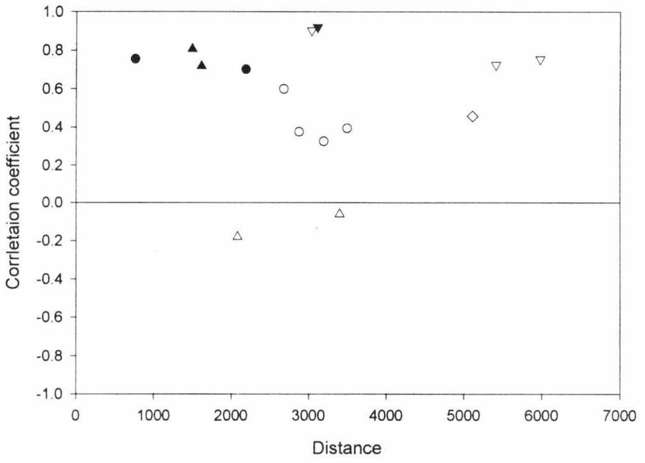
(c) Flowers



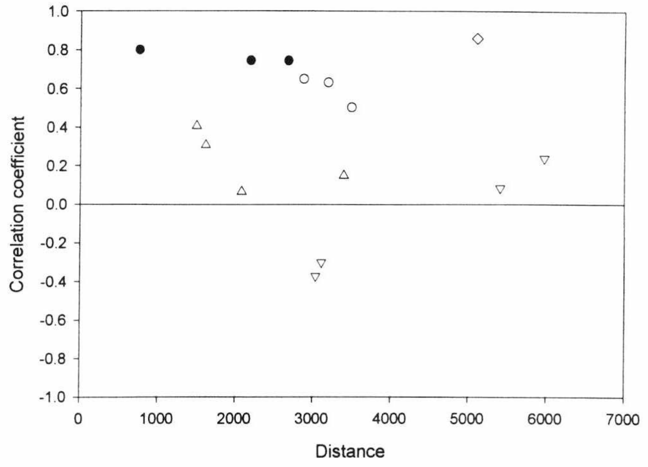
(d) All fruit



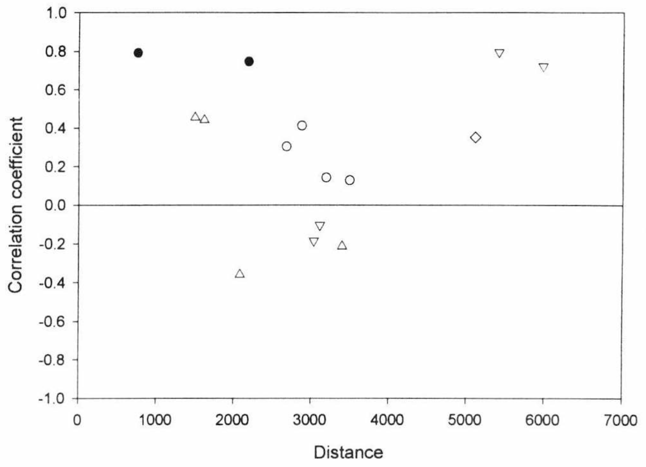
(e) Ripening fruit.



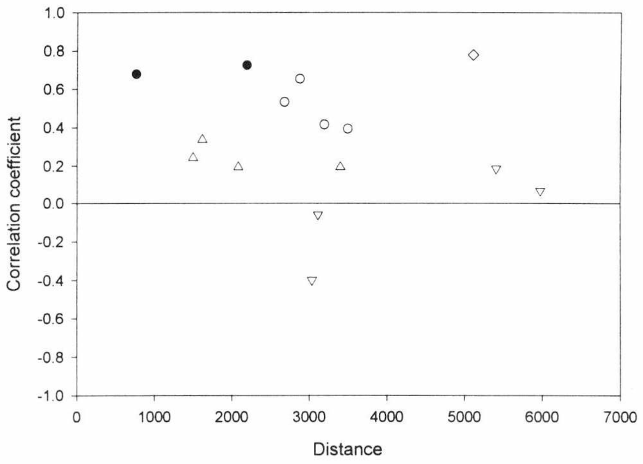
(f) Dominant; all fruit



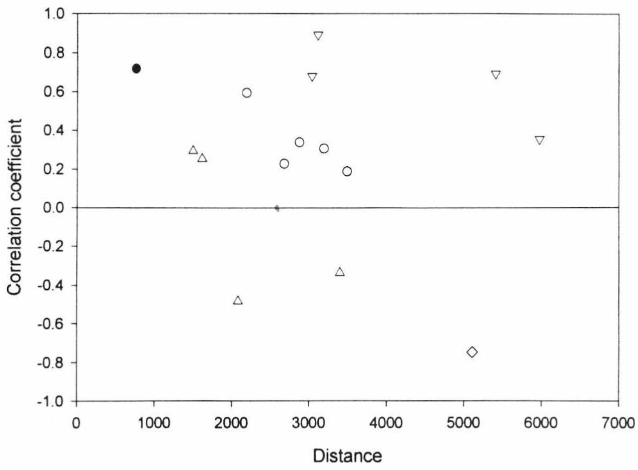
(g) Dominant; ripening fruits



(h) Top 5%; all fruit



(i) Top 5%; ripening fruit



to many of the orangutans that use the other areas. However, by including IB it can also be seen in each of the figures that the strength of correlation appears to rise again, so that plots that are circa 6000 m apart show positive relationships with respect to fruit.

Thus it can be seen that up to around 3000 m plots appear to be approximately in phase with respect to fruiting, then are negatively related, but show positive relationships again at around 6000 m. Fruiting therefore does show spatial effects, and in general, for each of the three fruit species criteria, the gradient of the decline in correlation coefficients and subsequent increase appears to be steeper for ripening fruit than for all fruit (e.g. Figures 5.8g and 5.8i). Thus there is evidence that fruit production is slightly out of phase between plots that are circa 3 km apart, particularly for ripening fruit, but not necessarily between plots that are 6 km apart. In contrast, young leaf production shows no spatial effects, and is presumably therefore more dependent than fruiting on macro-climatic variables (e.g. rainfall). Fruit production, and particularly ripening rates, on the other hand, may be more dependent on other ecological variables such as soil depth or acidity.

An additional means of assessing the effects of distance on the degree of synchrony between sites is to plot the distance between them against the time-lag giving the strongest positive correlation between them. The results of this procedure are presented in Figure 5.9. If the HILL is again excluded then with the exception of new nests (Figure 5.9a) and all fruit of dominant diet species (Figure 5.9f), all indices show a tendency to exhibit greater time-lags as the distance between plots increases, up to around 3000 to 4000 m apart. Again this is clearer if IB is also temporarily ignored. As with correlation coefficients, however, there is some indication, when including IB, that time-lags also decrease at circa 6000 m distance. As before this is most apparent with ripening fruit, of both dominant and the top 5% diet species categories (Figures 5.9g and 5.9i). For all fruits of dominant diet species, the distance between plots seems to have little effect on the time-lag (Figure 5.9f). For new nests, however, there appears to be a negative relationship between time-lag and distance, suggesting that plots further apart are in greater synchrony (Figure 5.9a).

The most interesting result of this procedure is that despite the fact that fruit at all stages of ripeness (all fruit) for all three of the species classes (i.e. all tree species, dominant species and top 5% diet species), show slight increases in time-lags with increasing distance (or no increase at all for dominant species, as noted above), followed by a decrease at greater distances these changes are much clearer for ripening fruit. Thus production of all fruit is slightly out of phase between plots that are circa 3 to 4 km apart, but when only ripening fruit is considered, the asynchrony is more pronounced. If relationships between plots did not strengthen again at around 6 km, the implication might be that fruiting passes through the area in some form of 'wave' as suggested by Rijksen and Meijaard (1999), particularly with respect to fruit ripening, but as they do seem to strengthen again at greater distances this can not be inferred.

## 5.3.4. RELATIONSHIP BETWEEN NESTS (DENSITIES) AND PHENOLOGY

### 5.3.4.1. *Plot-wise analysis*

Correlating numbers of new nests with each of the original four non-diet-specific indices directly each month (i.e. all fruit, ripening fruit, flowers and young leaves, with no time-lags), surprisingly produced only two significant relationships, both of which involved the HILL. Coefficients were found to be significant and positive there between new nests and all fruit ($r = 0.876$, $n = 17$; Bonferroni/Dunn-Šidák corrected level calculated using $\alpha = 0.05$, $k = 4$, for each plot/transect), and between new nests and ripening fruit ($r = 0.625$, $n = 17$; Bonferroni/Dunn-Šidák corrected level calculated using $\alpha = 0.05$, $k = 4$, for each location).

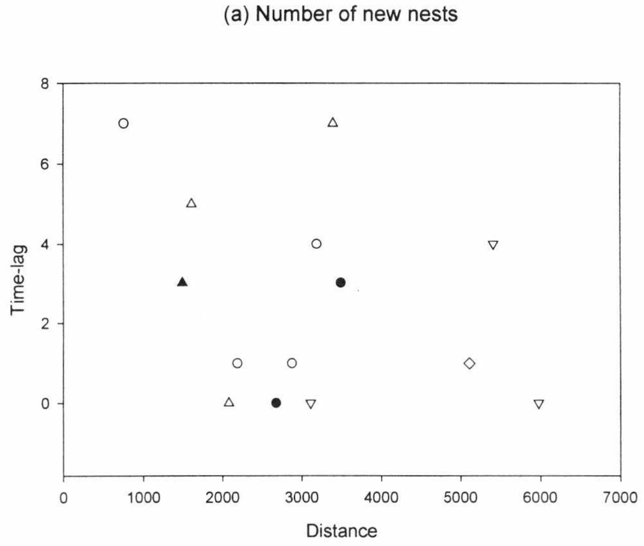
Despite this general absence of relationships, however, fruit production would still seem the most likely predictor of orangutan movements at all of the sites, since it normally comprises around 60% of orangutan diets (Rodman 1973; MacKinnon 1974; Rijksen 1978;

Galdikas 1988). The data were therefore re-examined with the addition of the diet-specific indices. Using all 8 indices, a stepwise multiple regression was performed, separately for each plot in an attempt to determine which index is the best predictor of numbers of new nests and hence orangutan densities. The results are shown in Table 5.3.

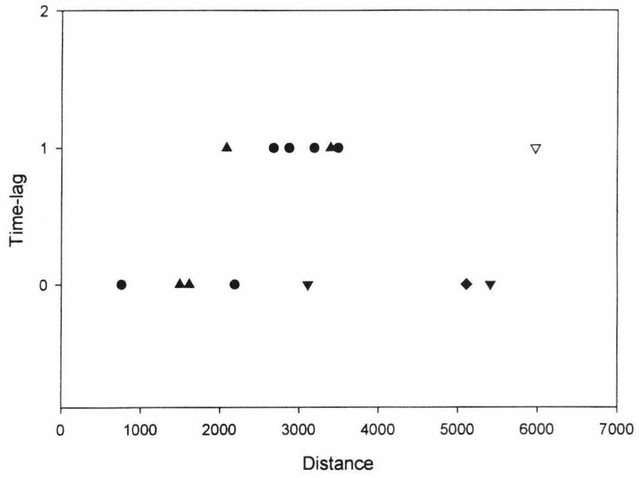
**Table 5.3**: results of stepwise multiple regression for each plot using number of new nests as the dependent variable, and all 8 phenology indices as predictors (Probability of F to enter <= 0.050, probability of F to remove >= 0.100).

| Plot | Predictor variable | $R^2$ | F | df | p | Constant | B | t | p |
|---|---|---|---|---|---|---|---|---|---|
| GB | None | | | | | | | | |
| HJPLX | None | | | | | | | | |
| HILL | 5% ripening fruit | 0.857 | 89.701 | 1,15 | 0.000 | 8.976 | 320.938 | 9.471 | 0.000 |
| IB | Flowers | 0.871 | 20.252 | 1,3 | 0.020 | 74.502 | -518.155 | -4.500 | 0.020 |
| SM | 5% ripening fruit | 0.260 | 5.271 | 1,15 | 0.037 | 19.209 | -88.117 | -2.296 | 0.037 |
| X | None | | | | | | | | |

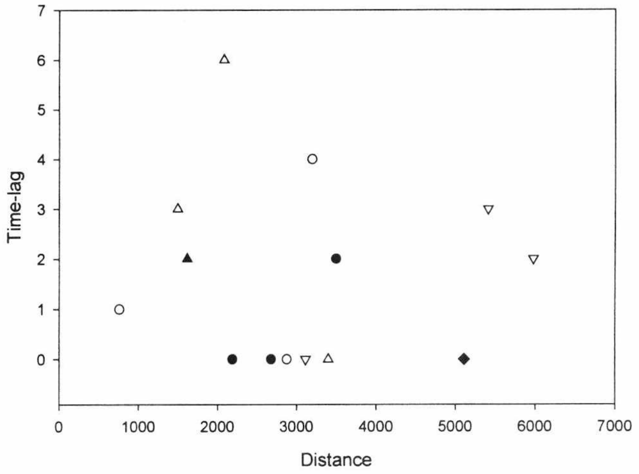
**Figure 5.9**: Time-lags giving the strongest positive correlation between plots for (a) new nests, (b) young leaves, (c) flowers, (d) all fruit, (e) ripening fruit, (f) dominant all fruit, (g) dominant ripening fruit, (h) top 5% all fruit, and (i) top 5% ripening fruit, plotted against distance between plots (in metres).; △ denotes correlations involving HILL plot, ▽ involving IB plot, ◇ involving both HILL and IB plots, and ○ denotes all others. Solid symbols are significant to within 95% confidence limits. No time-lag correlations were performed between GB and IB as monitoring periods overlapped only slightly.


(a) Number of new nests

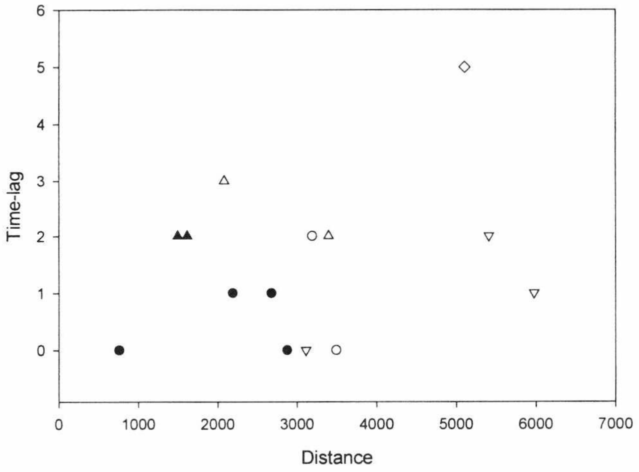
(b) Young leaves



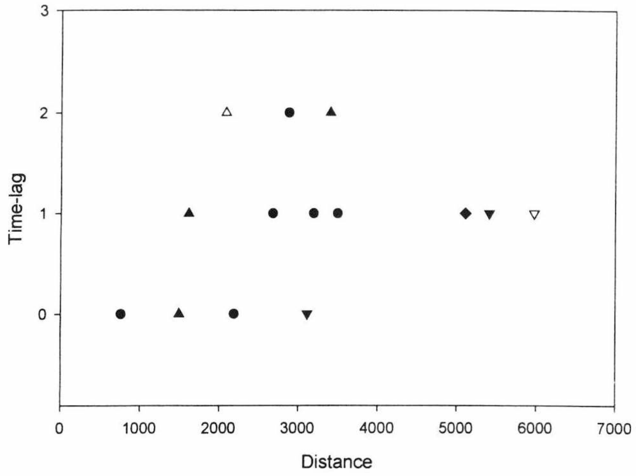
(c) Flowers



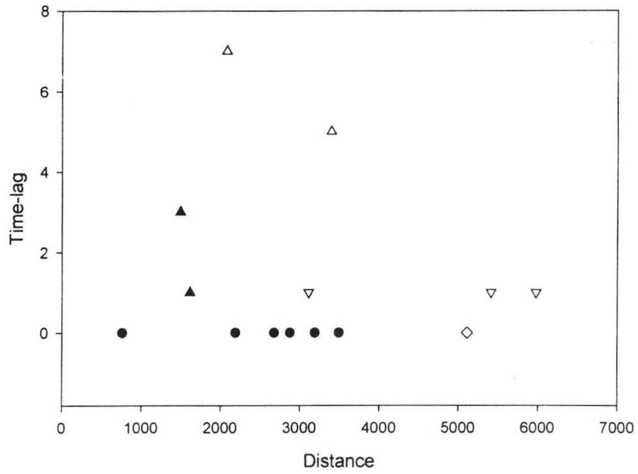
(d) All fruit



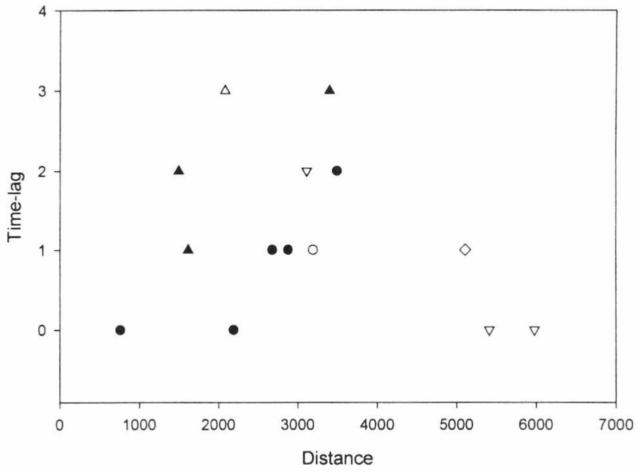
(e) Ripening fruit



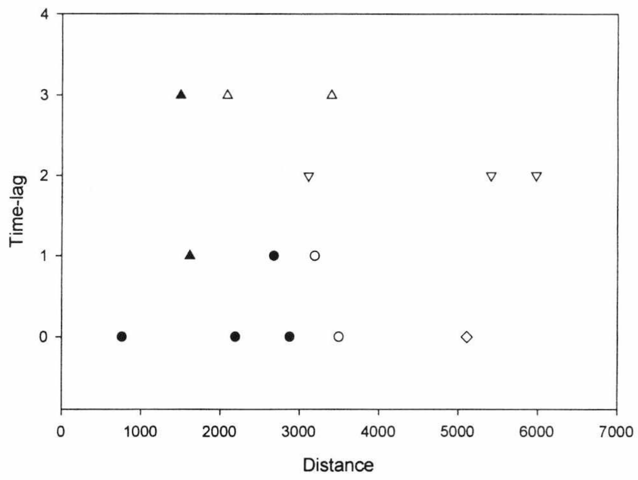
(f) Dominant; all fruit



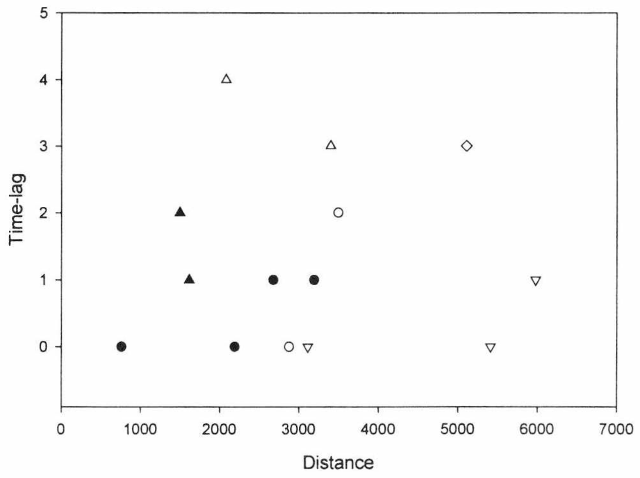
(g) Dominant; ripening fruit



(h) Top 5%; all fruit



(i) Top 5%; ripening



For three of the plots the regression also failed to identify any significant predictors of numbers of new nests. For the HILL, IB and SM plots, however, it identified the variables shown in the table as significant, and for both IB and SM the relationship is negative (as B is negative). All other variables failed to meet the selection criteria. Thus again, when no time-lags are taken into consideration, the only significant positive relationship between numbers of new nests and phenology occurs in the hills.

To examine this further time-lag correlations were then performed, again using all 8 indices and new nests. The results are shown in Table 5.4. Note that the table only shows coefficients that were significant to at least the p = 0.05 level, and that these are the maximum positive coefficients for each combination (i.e. in a few cases, significant correlations were also found at other time-lags, but these were ignored). As with the multiple regression, the results confirm that there is a strong relationship between fruit abundance and the number of new nests in the hills, and that it is strongest at a time-lag of zero with ripening fruit of both the 5% of diet and dominant species indices (r = 0.926 and r = 0.925 respectively). For clarity the former relationship is illustrated graphically in Figure 5.10.

Positive relationships also exist, however, at GB SM, and X if a time-lag is taken into consideration. The correlations are strongest for GB with ripening fruit (r = 0.776, time-lag = -1), for SM with all fruit (r = 0.616, time-lag = -2), and for X with ripening fruit of the 5% of diet species (r = 0.792, time-lag = -2). In fact, all of the relationships except the ones involving the HILL, involve negative time-lags of -1 to -3. Therefore the number of new nests, and hence of orangutans, tends to increase or decrease between 1 and 3 months after fruit abundance increases or decreases in these areas. This would be expected, however, particularly as half of the new nests appearing as a result of increased fruiting would only be apparent in the following months census. In the hills orangutans appear to respond more rapidly (several time-lags of zero), and even arrive before much of the fruit has ripened (time-lag of +1 for ripening fruit).

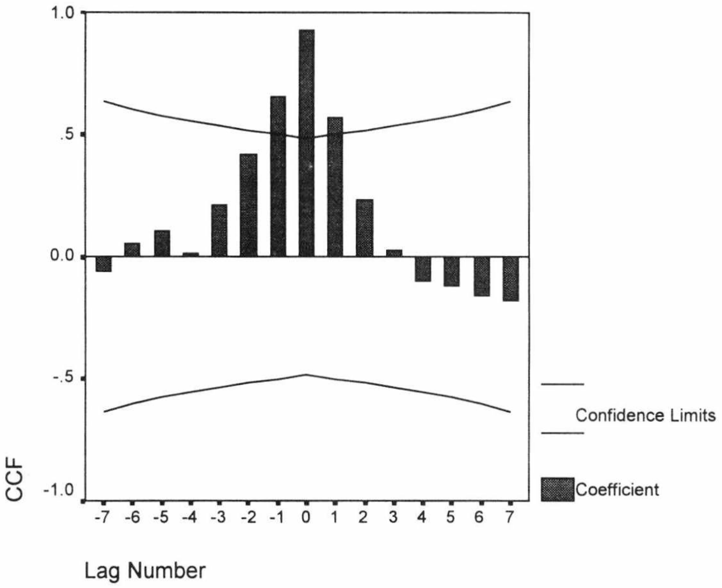
**Table 5.4**: Correlation coefficients produced by time-lag cross correlations between number of new nests and various aspects of fruiting phenology (arcsine transformed). Coefficients given are the strongest found in both positive and negative directions, significant to at least the 95% level.

| Index | Plot | Time-lag | Coefficient |
|---|---|---|---|
| All fruit | HILL | 0 | 0.876 |
| | SM | -2 | 0.616 |
| | X | -3 | 0.596 |
| Ripening fruit | GB | -1 | 0.776 |
| | HILL | 1 | 0.874 |
| | X | -2 | 0.661 |
| 5% all fruit | HILL | 0 | 0.738 |
| | SM | -2 | 0.529 |
| | X | -3 | 0.583 |
| 5% ripening fruit | GB | -1 | 0.637 |
| | HILL | 0 | 0.926 |
| | X | -2 | 0.792 |
| Dominant all fruit | HILL | 0 | 0.737 |
| Dominant ripening fruit | HILL | 0 | 0.925 |
| | X | -2 | 0.589 |

**Table 5.5**: Pearson's correlation coefficients between density estimated using new nests and indices of phenology over all plots pooled, therefore effective number of months, n = 85; 'p' refers to significance before Bonferroni corrections whilst * denotes significance at Bonferroni/Dunn-Šidák corrected level (α = 0.05, k = 8).

| Species included | Ripeness class | Coefficient | p |
|---|---|---|---|
| All species | Young leaves | 0.046 | 0.674 |
| | Flowers | 0.135 | 0.218 |
| | All fruit | 0.405* | 0.000 |
| | Ripening fruit | 0.218 | 0.045 |
| > 5% diet species | All fruit | 0.330* | 0.002 |
| | Ripening fruit | 0.207 | 0.057 |
| Dominant species | All fruit | 0.408* | 0.000 |
| | Ripening fruit | 0.315* | 0.003 |

**Figure 5.10**. Time-lag cross correlations at the HILL site, between numbers of new nests and top 5% diet species ripening fruit. CCF = Cross correlation coefficient. Confidence limits are 95%. Lag number on the X-axis represents months.



### 5.3.4.2. *Area-wide analysis*

The findings above demonstrate that orangutan movements are significantly related to at least some aspect of fruiting phenology at all sites except HJPLX and IB. In a further attempt to identify the most influential of the 8 indices on the movements of orangutans in the area as a whole, the plots were pooled together, thereby effectively giving one very long transect or plot. For this procedure orangutan densities were required (as estimated using new nests in Chapter 3) rather than simply the number of new nests. A stepwise multiple regression analysis (probability of F to enter $<= 0.050$; probability of F to remove $>= 0.100$) selected all fruit of the dominant species as the only significant predictor of densities, whilst all other variables failed to meet the selection criteria. It was found to be a good predictor of orangutan densities although a large amount of variability is still unexplained ($R^2 = 0.167$; $F_{(1,83)} = 16.598$, $p < 0.001$; Constant = 1.570, B = 6.621, SE = 1.625).

### 5.3.5. EFFECTS OF FRUIT SCARCITY

So far only weak relationships have been found between numbers of new nests and phenological indices at GB and no significant relationships at all have been found at HJPLX. Therefore, to test whether orangutans move into these areas for diet related reasons other than simple fruit abundance, correlations were also performed with other aspects of the diet. Using the data in Appendix 3 it was possible to correlate for each site, the number of new nests with the proportion of the diet made up of each of the various food types each month. Appendix 3 gives the percentages before conversion to proportions and arcsine transformation. Time-lag cross correlations were then performed for each plot, between the monthly number of new nests and each of these indices.

The indices therefore give the proportion of the diet each month made up of each of the main dietary items regularly consumed by orangutans. These were fruit, young leaves, flowers, insects, stems (usually lianas or rotan), and bark, and all non-fruit items combined. Other food items that orangutans were observed to eat included roots (which may in some cases include insects living in the roots of epiphytes), fungi, and also slow lorises (*Nycticebus coucang*), though these were infrequent and so were not included in the analysis. The overall mean percentage of the diet that was made up of fruit was 63.76% (±15.20, n = 17 months), similar to figures reported from other studies (Chapter 1).

The strongest coefficients, significant to at least the $p < 0.05$ level are summarised in Table 5.6. Perhaps surprisingly, only SM shows a positive relationship with the proportion of fruit in the diet. Despite this, X, SM and the HILL all show negative relationships with at least one non-fruit item; X with bark, the HILL with stems and young leaves, and SM with all non-fruit items combined. Conversely, the remaining three locations all show positive relationships with at least one non-fruit item: HJPLX with young leaves, IB with insects, and GB with insects, stems, and all non-fruit items combined. The latter is most striking as it naturally corresponds with a strong negative correlation with the amount of fruit in the diet. With the time-lag of -1 this shows that when fruit begins to form a smaller proportion of the diet, orangutans subsequently move into the GB area. Presumably this is in search of insects and stems, and they subsequently leave again when the proportion of fruit in the diet begins to increase. This may also be the case for HJPLX and IB due to their positive relationships with young leaves and insects respectively, but is less obvious.

**Table 5.6**: Pearson's correlation coefficients between numbers of new nests and the percentage of the diet of orangutans made up by various food types. All coefficients significant to the $p<0.05$ level.

| Plot | Item | Time-lag | Coefficient |
|---|---|---|---|
| X | Bark | 0 | -0.552 |
| GB | Fruit | -1 | -0.720 |
| SM | Fruit | 2 | 0.575 |
| GB | Insects | 0 | 0.688 |
| IB | Insects | 0 | 0.923 |
| GB | Non-Fruit | -1 | 0.688 |
| SM | Non-Fruit | 2 | -0.587 |
| GB | Stems | -2 | 0.754 |
| HILL | Stems | 0 | -0.574 |
| HILL | Young leaves | 0 | -0.550 |
| HJPLX | Young leaves | 3 | 0.586 |
| SM | Young leaves | 2 | -0.552 |

## 5.4. DISCUSSION

### 5.4.1. CAUSES OF MOVEMENTS

#### 5.4.1.1. *Fruit availability*

It is clear from the ranging data in Chapter 4, and from the range of monthly density estimates at both the transect level and at the level of the larger area covered by the plots HJPLX, X and SM (Figures 5.1 and 3.3), that individual orangutans are highly mobile, whether or not movements are large scale or relatively localised. Therefore, the factors that govern such movements need to be addressed if they are to be fully understood.

The proportion of trees producing fruit is implicated as a major attractant, at least in some habitat types. This is evident from the correlations between numbers of new nests and the various fruit indices at X, SM, GB, and especially at the HILL. Also, as might be expected the best overall predictor of densities was the availability of fruit of species that comprise a large proportion of the diet. Using new nests as an indicator of densities may produce errors, however, due to the standard deviation in nest building rates, but they are still considered a reasonable indicator of increases and decreases in orangutan numbers in a given area. In the hills the attractant effect was clearly observed in the field during May and June 1997 when many, but not all individuals known from other parts of the study area moved there in response to a mast fruiting event. They also moved there relatively quickly as shown by the strong correlations with zero time-lag. This period was also a time when some adult females known to spend a large proportion of their time within the swamp part of the WCS study area made long forays or 'excursions' outside their regular core areas and into the hills (see Chapter 4).

#### 5.4.1.2. *Orangutan response times*

The attractant effect of fruit in all of the areas showing positive relationships between new nests and fruit often involved a degree of delay between maximum fruit abundance and maximum densities, particularly in the swamp areas. This might be expected by default, however, as any increase in new nests would only be detected at the end of the month in which the increase occurred, but despite this some of the time-lags were greater than one month. This therefore suggests that the apparent delay between fruiting and the arrival of orangutans is real. Attempts to identify causal relationships between fruit abundance and densities or movements of orangutans may therefore be unable to detect relationships, or at least underestimate the strength of relationships, if variation in response times is not accounted for.

A possible explanation for the delay might be that orangutans respond only when fruits begin to ripen. This may have been the case at X and GB as new nests increased there at least one month later than ripening fruit increased. But at the HILL, densities increased one month before ripening fruit, and at SM, numbers of new nests were actually negatively correlated with ripe fruit of both diet-specific indices. This is not so surprising, however, as orangutans will eat the fruit of many species well before it is ripe (pers. obs.; Ungar 1993). Hence only a relatively small proportion of the fruit crops of some species may ever ripen fully. Perhaps orangutans responded more rapidly to fruiting in the hills than in the swamps as a greater proportion of the fruit species they were eating there are palatable before ripening. The preferred food species in the hills are very different from those in the swamps, and the influence of ripeness is likely to vary considerably between habitats with different tree species composition and abundance. For example, a single highly prized fruit species in an area might attract orangutans, but it would also attract greater numbers into areas where that species is most abundant. Thus it could be present, but at lower densities in other locations, without attracting orangutans there. Indeed, the very fact that it is there and visibly available, may result in orangutans leaving the area if they know it exists at higher densities elsewhere.

It is also possible that the 'novelty' value of some less frequently available fruit species may be enough to attract orangutans long before it ripens. A few novel or highly prized species could in fact have attracted the orangutans to the hills before the massive increase in fruiting due to the mast event even occurred. Under these circumstances densities would appear to increase coincident with the large increase in fruit, rather than show a delayed response. Conversely, fruit of relatively ubiquitous species (e.g. malaka in the swamps) would presumably result in slower response times. It should also be noted that at Suaq Balimbing, trees of *Tetramerista glabra* appeared to fruit at different times resulting in year round availability of these fruits, though in varying quantities. The ability of this species to fruit year round has also been noted by Soerianegara and Lemmens (1993; cited in Rijksen and Meijaard 1999). That plots were also slightly out phase over a distance of around 3 km would seem to confirm these findings as this indicates that fruit of a given species may well be more abundant even just a short distance away. Thus orangutans will move into areas in pursuit of fruits under some circumstances, which will vary according to the fruit species present, their stage of ripeness (for some species), and their density relative to other areas. The speed at which they respond also varies considerably.

#### 5.4.1.3. *Response to fruit scarcity*

What is less apparent from the initial correlations is the cause of movements into the deeper backswamp areas, namely HJPLX, and to some extent GB. These areas contain some of the staple food species of orangutans, but also some deeper swamp species not found in other, less deep areas. Correlations with the proportion of the diet made up by the various food types, however, show that orangutans tend to move into the GB area when fruit begins to constitute a smaller proportion of the diet. This suggests that they do so when fruit availability is generally poor throughout the area. It may be that they are attracted there by a perceived greater likelihood of maintaining adequate nutrition through other ubiquitous items such as stems, bark, palatable leaves and insects etc. However, given that these items are generally available year round, the arrival of orangutans at GB is unlikely to result from a "pull effect" of these food types, but rather from a "push effect" of a paucity of fruit generally. This would be more strongly supported had it also occurred in HJPLX, which contains both the highest tree density and tree species density of all the plots (see Chapter 2), as this would have supported the hypothesis that more varied habitats are more attractive when fruit is scarce. A tentative explanation for movement to GB when fruit is scarce might be the higher density of both stems and species of liana there, which may still offer a more varied diet to orangutans, despite GB having comparable tree stem and species densities to other plots. Thus fruit is implicated as at least a factor influencing orangutan movements, and in some habitats it exerts a "pull effect". It also seems that a paucity of fruit generally can exert a "push effect", making more varied habitats more attractive due to an abundance of consistently available food items.

All vertebrates that maintain fixed ranges or territories year-round, shift diets to some extent during times of fruit scarcity, consuming more of their less preferred fruit species and food types, and primates that eat primarily fleshy fruit shift to eating more animal prey and/or foliage, or more bark (Leighton and Leighton 1983). Orangutans have also been clearly shown to do this (Knott 1998b). The results here therefore concur with these observations as they too suggest that orangutans shift diets during periods when fruits are scarce, moving into subtly different but nearby habitats, rather than migrating over large distances. Clearly orangutan foraging decisions, and therefore movements can be seen to be highly complex, and not simply due to the "pull" effects of fruit. It is also not unreasonable to suggest that home ranges must encompass a sufficiently varied 'habitat matrix' (i.e. a minimum of two different habitat types that offer different food sources at different times), to sustain them through periods of fruit is scarcity.

#### *5.4.1.4. Other possible causes of movements*

No investigation has been carried out here into the possible effects of social organisation, more specifically the influence of female or male reproductive strategies on orangutan movements. As mentioned earlier there is conflicting evidence that males are attracted to areas by the presence of receptive females. For example te Boekhorst *et al.* (1990) found no significant relationships between numbers of males arriving in the Ketambe study area and the number of resident females there, whilst Utami (2000b) more recently did, for fully flanged adult males at least. Thus it remains likely that the reproductive status of females will have an effect, at least on male movements. This would unavoidably 'interfere' with any attempt to identify the relationships between movements and food availability, causing some relationships (if they exist) to remain hidden to some degree.

Despite this, clear relationships have been detected, and serve to reinforce the fact that fruit is probably the major determinant of orangutan ranging patterns, especially if females alone are considered. Furthermore, given that even receptive females must eat, fruit must also influence the movements of male orangutans, even if only indirectly, and whether or not they are primarily seeking females.

### 5.4.2. EVIDENCE FOR LARGE SCALE SEASONAL MOVEMENTS

Focal animal follows showed that at least some of the movements of individuals around the area involve travelling between plot locations, and hence compensatory movement between sites. For example, several individuals have been seen in many of the plot and transect locations (e.g. Figures 4.4 and 4.5). Compensatory movements were particularly evident during the mast fruiting in the hills in May and June of 1997, when densities there increased markedly, and the majority of the individuals encountered there were ones known to frequent other parts of the study area (e.g. HJPLX, X, and in some cases SM and GB as well). Such movements are to be expected though, since they do not involve great distances (SM being the furthest of these from the hill and still less than 3.5 km away), and even females can travel over 4 km in one direction (see Figures 4.4 and 4.5). Some individuals known from the rest of the study area were not encountered in the hills at that time, however, and in fact never have been (e.g. Pelet and Diana and some of the 'south-westerners'). Only those already known to have ranges that include the hills, appeared there during the mast fruiting. This strongly suggests that they are unable (or at very least reluctant) to leave their ranges, even if fruit is unusually abundant just a short distance away.

Within the swamps, whilst it is true that all plots correlated with at least one other in ripening fruit abundance, they do not all correlate with all others, and are thus not precisely in phase. This is illustrated in Figures 5.8 and 5.9, which show that there is spatial variation in fruit availability, such that swamp plots that are 3 to 4 km apart can be 1 or 2 months out of phase. However, they also suggest that waves of fruiting do not occur, at least on a local scale, since even at a distance of circa 6 km positive relationships between plots with respect to fruiting, and involving zero or only little time-lag can still be found. Instead these results indicate that variation in fruit availability in the swamps is still relatively localised, and probably results from varying soil conditions (e.g. acidity). Consequently by gradually crossing their ranges females may be able to exploit a particular crop for considerably longer than would be possible with smaller ranges. Female ranges of up to 4.5 km across (as indicated in Chapter 4), would indeed be large enough to include areas that are slightly out of phase (by one or two months). This then would encourage orangutans to move around considerably within their ranges in order to make optimum use of the available resources. It would not appear to be worth their while travelling much greater distances, however, at least within the swamp areas. This further supports the conclusion that females are not transient, and are restricted to finite ranges within which they move around according local variations in fruit availability (or absence), and do not make large-scale seasonal movements.

The results of Chapter 4 do not support the existence of large-scale seasonal movements either. All adult females, the majority if not all adult males, and possibly some subadult males, appear to have fixed range boundaries, albeit encompassing large home ranges. Of further note from Chapter 4 are the results of the presence data analysis. These indicate that the overall presence of orangutans does not fluctuate from year to year, even of males. Instead they suggest that the age (or class) composition of the male population shows temporal changes, as a result of female reproductive status. Non-dominant males avoid the dominant male, who appears to occupy an area when there are a number of receptive females, and is usually accompanied by many subadult males. When these are more absent absent, however, they are replaced by the non-dominant males. Hence the overall number of males remains relatively stable, as does the number of females. Thus the concept of large communities centred around a single dominant adult male, roaming over the landscape as a unit as suggested by MacKinnon (1974), is not supported here. Even adult females who have the smallest ranges, are able to utilise areas of at least 600 ha to 900 ha and possibly even as large as 1500 ha. Furthermore, adult female range overlap allows up to 16 adult females to converge on an area simultaneously. Thus if a given area contained a particularly prized food resource, at least 16 adult females could suddenly appear there, and would no doubt be accompanied by a number of fully adult and subadult males as well. Similarly they may also depart simultaneously, but in different directions according to the location of their core areas. This scenario would explain the apparent simultaneous arrival and departure of orangutans in a given area but does not require waves of orangutans travelling together as an explanation, nor even the existence of any transient individuals. Instead it relies only on the convergence of individuals on common resources within large ranges.

Despite these findings, seasonal movements could still occur. As mentioned some movement is indicated by the lack of correlation in the number of new nests between transects each month. However, as also noted this appears more likely to be due simply to small-scale compensatory movements. Also, despite the fact that densities do fluctuate temporally in a given area, these fluctuations are not large and tend to involve only a few individuals (see Figures 5.1 and 3.3). Furthermore, measuring fluctuations by combining transects (Figure 3.3) does not mean that all transects experience fluctuations, only that at least one does. If large numbers of orangutans moved into an area en masse, transects scattered widely over that area should show a degree of correlation with respect to orangutan densities, especially with time-lags, but this was not evident here. Van Schaik (unpubl.) on the other hand did find some correlations between densities among the three most northerly transects (HJPLX, X and HILL) over 29 months preceding this study, but this only implies that there may at times be some degree of synchrony in the arrival in, and departure from the WCS study area of a few individuals. Thus there is little evidence of the simultaneous arrival or departure of large numbers of orangutans, as would be expected if large-scale seasonal movements did take place. These observations cannot entirely disprove the idea of seasonal movements, but they do suggest that only limited numbers of individuals could be involved, and that if they do occur they would only be apparent in relatively small areas. A more likely explanation of the apparent seasonal movements reported elsewhere, could simply be that within small study areas, the convergence of several individuals with ranges that are much larger than the study area, would appear as a large simultaneous influx.

## 5.5. CONCLUSIONS

1. Large-scale seasonal movements or 'waves' of orangutans entering and exiting the area were not evident here. Transects show little evidence of being in phase with respect to orangutan densities, even if time-lags are accounted for. If large numbers of orangutans arrived and departed the area simultaneously, correlations between plots with respect to

densities would be expected to show stronger and more consistent relationships than were found.

2. Some degree of synchrony amongst plots is suggested with respect to ripe-fruit and young leaf production. However, plots located around 3 km apart were still slightly out of phase by one or two months with respect to fruiting in general. Thus female range sizes at Suaq Balimbing appear just large enough for them to benefit from longer fruiting periods than would be possible with smaller ranges.
3. Orangutan movements are positively correlated with at least some aspect of fruiting phenology in all plots except HJPLX and IB, when time-lags are taken into consideration. The results suggest that orangutans make at least three clear distinctions between habitat types at Suaq Balimbing and the food species they contain:-
   a) In the main transitional swamp habitats they move according to spatial variation in the timing and abundance of ubiquitous, 'staple' fruit species.
   b) They enter the hills at times of abundant, less common fruit, perhaps in some cases for particular favoured species. This probably takes the form of occasional forays (if for only one or two favoured species) or movement en masse in times of masting.
   c) They enter the deeper backswamp habitats at times when fruit is generally unavailable anywhere and rely on ubiquitous food items such as bark, stems, leaves, insects etc. Therefore in times of fruit scarcity they appear to shift diets rather than migrate large distances.
4. Due to the above I suggest that orangutans require home ranges that encompass a variety of habitats or 'habitat matrix' to sustain them over the long-term.
5. Reports of seasonal movements in other study areas could be explained by the simultaneous convergence on the area, of individuals whose ranges are much larger.
6. The location IB is enigmatic, showing exceptionally high orangutan densities and high levels of fruit and flower production. This therefore suggests that areas further south than the WCS study area may well contain even better quality orangutan habitat.

# CHAPTER 6

# FEMALE CLUSTERS

## 6.1. INTRODUCTION

Most diurnal primates form social groups, although these groups vary widely in size, and cohesiveness, and in age and sex composition (van Schaik 1999). The benefits to grouping are considered to arise from protection against predators, defence of resources, foraging efficiency and improved care-giving opportunities, due either to direct help or protection from harassment or infanticide (Dunbar 1988). Other potential benefits might include reduced radiative and conductive heat loss, reduced ecotoparasite loads (van Schaik 1999) and opportunities for social learning of valuable skills (e.g. tool use, perhaps most relevant in great apes). Naturally there are also costs to grouping. These come in two forms: (a) Direct costs as a result of intra-group competition for limited resources, and (b) Indirect costs as a result of being obliged to coordinate activities in order to remain together (Dunbar 1988).

Among the great apes, social systems are generally considered to vary from the semi-solitary orangutan, through the loosely associated multimale communities of the chimpanzee to the small but cohesive one-male groups of the gorilla (e.g. Dunbar 1988). However, all chimpanzee (and Bonobo; White 1996) populations are now considered to live in fission-fusion social systems (Boesch 1996). These are systems in which 'communities' include all individuals that are regularly seen over months in temporary sub-groups called 'parties' (Boesch 1996). Such systems have also been observed in eight other large bodied primate species, and are thought to allow greater flexibility in exploiting resource patches of different sizes, in species that are free from predation (Boesch 1996). Van Schaik (1999) distinguishes between two types of fission-fusion systems: group based fission-fusion, in which permanent social groups split into smaller parties, or lone individuals, that regularly re-group; and individual based fission-fusion, in which individuals are often solitary and social groups can only be recognised through analysis of association patterns. Social units within the latter system are much harder to recognise, but compiling ranging and association data of individuals shows the existence of spatially distinct communities in some species (e.g. spider monkeys: Terborgh and Janson 1986; Symington 1990; chimpanzees: Wrangham 1977; bonobos; White 1996). Given that chimpanzees are therefore considered a fission-fusion species it is interesting to note that in a comparison between female Sumatran orangutans at Ketambe and female chimpanzees, by Wich *et al.* (1999), the orangutans were found to be no more solitary than their African relatives. Indeed van Schaik (1999), proposes that female orangutans, at least at Suaq Balimbing, can be regarded as an example of an individual based fission-fusion system, in that they regularly form parties, but are also often solitary.

If orangutans can be regarded as a fission-fusion species then they are still puzzling, however, as it has so far not been possible to recognise any higher social units, or communities. As mentioned in Chapter 1, spatially distinct communities, as in spider monkeys or chimpanzees, certainly do not appear to exist in orangutan populations. In fact van Schaik and van Hooff (1996) stated that there is no indication of active female bonding through affiliation, grooming, agonistic support, or even some dispersed form of spatial association. However, they do note that there is evidence of convergent mate choice of receptive females which suggests the possibility of female-male relationships (that might also include relationships with subadult males), and hence some form of 'community', based on the premise that females may gain protection from harassment. In a later paper, van Schaik (1999) adds to this by showing that females at Suaq Balimbing also associate in parties far more than would be expected from null models. Thus there appears to be at least some evidence of a form of social organisation or community among orangutans.

Certain observations in the field during this study also suggested the possibility of communities at Suaq Balimbing, more specifically groupings or 'clusters' of females. For example, the ranges of some females appeared to share similar boundaries (e.g. Pelet, Diana and Becky in the north-west, and Abby and Karen in the north-east; Figures 4.6 and 4.7), and some of these individuals were also physically very similar in appearance, at least facially (e.g. Abby and Karen; Pelet and Diana; and also Molly and Rini in the south-east, and Butet and Hanes in the south-west). These observations are compatible with previous reports that as adolescent (or subadult) females mature into adults, they settle in ranges that are overlapping or adjacent to their natal range (e.g. Galdikas 1995a). As well as the above, it also appeared that many of the adult females sharing similar range boundaries had infants of approximately the same age, which suggests reproductive synchrony. Those in the north-west had infants around 5 to 6 years old (excluding the newly matured Becky), infants in the north-east were a year or so younger, and those in the south and south-east were roughly 6 or 7 years of age. The fact that several subadult females of approximately the same age were occasionally encountered along the northern edge of the WCS study area between 1994 and 1996, adds further evidence of reproductive synchrony within clusters, as they too were presumably born around the same time in approximately the same area.

Thus it is suspected that some degree of female social organisation may indeed exist at Suaq Balimbing, that involves females who may be related, who share ranges with similar boundaries and considerable overlap, and who are also synchronised reproductively. Naturally, the degree of reproductive synchrony is bound to vary as primiparous females may not yet be in synchrony, and as some infants will die, subsequent offspring then being born out of synchrony. However, in order to investigate the possibility of social 'units', the aim of this chapter is to explore what further evidence for 'female clusters' might exist. If they are indeed real then two patterns might be expected. Firstly, that females within clusters preferentially associate with each other more than with other females, and secondly, a stronger social structure may exist in that pairs or groups of females from the same cluster tend to be present in the WCS study area simultaneously. In itself gregariousness will not highlight relationships but it does provide an opportunity to study selective association patterns. If selective association were then found, it would support the hypothesis that females within clusters may be more closely related, or at least more familiar with each other than with others, as would be expected if females do indeed settle in or near their natal range. An attempt is therefore made to determine if all individual orangutans show a tendency to gregariousness, in that they associate in parties more than would be expected from a null model (Waser's gas model; as shown by van Schaik 1999). I then explore the possibility that a relationship exists between the degree of range overlap between two females, and (a) the amount of time they spend together, and (b) the proportion of months they are both present within the study area simultaneously. Such relationships would support the idea that 'biosocial' mutual attraction between females exists within clusters, and that movements of females within clusters are to some degree coordinated, even if not in close association, and hence that there is some social organisation. The ages of infants are also examined in more detail to determine if there is evidence that reproduction is synchronised.

Naturally, it is necessarily difficult, if not impossible, to distinguish between biosocial mutual attraction and simple convergence on common resources, even though the latter would not necessarily lead to preferential association. Nonetheless, in light of the current lack of any evidence of social units among orangutans (other than lone individuals or mother offspring dyads) it is considered that any evidence for them warrants thorough investigation.

## 6.2. METHODS

During all focal animal follows, all events in which an individual approached to within 50 m of the focal animal were recorded as 'parties'. For each party event, the identity of the individuals involved (where known), the time of approach, and the time of departure to beyond 50 m were noted, giving details of the frequency and duration of parties between individuals. These data could then be compared to expected values of rates of encounter, duration of associations, and proportion of an individual's time spent in associations. Expected values were estimated using null models based on the behaviour of gas molecules moving randomly in a two dimensional plane (Waser 1982, 1984).

### 6.2.1. *Expected encounter rates*

Following Waser (1982, 1984, 1987), and as previously used for orangutans by Mitani *et al.* (1991), a group of species i with radius $r_i$ and average velocity $v_i$, moving randomly in two dimensional space will encounter groups of species j with radius $r_j$ and average velocity $v_j$ at a rate:

$$Z_{\text{exp}} = 2rp_j(v_i^2 + v_j^2)^{1/2}$$

where; $r = r_i + r_j + d$

$p_j$ = the density of groups of species j

$d$ = a distance criterion applied to define associations (in this case 50 m).

Since adult orangutans travel independently (with or without offspring), i and j are individuals as opposed to groups, and hence $r = d = 50$ m, and $p_j$ is the density of individuals in the study population. The density estimate used was 7.5 $km^{-2}$, since this lies between the inferred densities for swamp habitats of 5.5 $km^{-2}$ and 10 $km^{-2}$ (Chapter 3). Using this estimate gives expected encounter and association rates that are higher than using the lower estimate of 5.5 $km^{-2}$, and hence reduces the likelihood of regarding observed values as higher than expected. It should also be noted that these density estimates include infants and juveniles who almost always travel with their mothers, and who were not therefore recorded as entering parties when calculating observed association rates. Thus again the densities used in the calculations will result in overestimates of expected association rates, which can therefore be considered conservative, as they err on the high side.

Travel velocities were determined using plots of focal individual's routes (in GIS) during focal animal follows, and measuring the length of the route traversed by the orangutan that day. This was then divided by the follow duration to give velocity in metres per hour.

### 6.2.2. *Expected mean duration of associations*

The mean duration of associations expected by chance is given by Waser (1982, 1987) as:

$$T_{exp} = 2.467r(v_i^2 + v_j^2)^{-1/2}$$

where $r$, $v_i$ and $v_j$ are as above.

### 6.2.3. *Expected proportion of time spent in associations*

An estimate of the expected total proportion of an individuals time spent in associations with other individuals, if they range in a random manner, is then given by Waser (1987) as:

$$P_{exp} = Z_{exp} \text{ x } T_{exp} = 4.934r^2p_j$$

For the reasons given above, the density estimate of 7.5 $km^{-2}$ for swamp habitats was used.

### 6.2.4. *Expected association rates based on range overlap*

Due to the methods used in the collection and analysis of the ranging data (see Chapter 4), all adult females have a polygonal range, of which a portion of measurable area lies within the WCS study area. Further examination of these areas reveals that each also shares some of this portion of their polygonal range with that of each of the other females. Thus it is possible to calculate the size of the overlapping area as a crude estimate of the percentage of a female's true range that overlaps with that of each other female. This then permits an investigation to determine if a relationship exists between the degree of range overlap between two females, and the amount of time they spend together. For example, individual 'A' may have a polygonal range that totals 500 ha, of which 300 ha lies within the boundaries of the WCS study area. Likewise, individual 'B' may have a polygonal range of 600 ha of which 400 ha lies within the WCS study area. In such a scenario, a part of the 300 ha portion of A's range may lie within the 400 ha portion of B's range. If that part was 200 ha, then it could be inferred that individual A shares two thirds or 66.6% of her range with individual B. Naturally, when calculating percentages in this manner the values are not symmetrical between individuals, i.e. the percentage of individual A's range that lies within individual B's is not the same as the percentage of B's lying in A's. Hence two values are calculated for each combination.

From the above, an estimate of the amount of time an individual might be expected to associate with another is given by:

$$A_{oi} = \frac{Q_i}{\sum_i^j Q_i} \times \sum_i^j L_i$$

where;

$L_i$ = the proportion of an individuals total follow time spent with female i.

$Q_i$ = the proportion of the target individuals range that is overlapped by individual i. NB: $\Sigma Qi$ may be greater than 100% as several individuals included.

As an example, if female B's range covers 30% of A's, C's covers 30%, and D's covers 60%, and A spends 180% of her time with one other, of B, C, and D, then the amount of time A would be expected to associate with B, if they associate according to range overlap only, would be:

$$A_{oi} = \frac{30}{30+30+60} \times 180 = 45\,\%$$

### 6.2.5. *Expected simultaneous presence*

According to Rijksen and Meijaard (1999), careful fieldwork reveals that the same individuals are often seen in one particular area, whilst at other times most of them seem to be absent. If all parts of the regular range of a female are used with equal intensity, a crude estimate of the number of months a given female might be expected to be present within the WCS study area could be calculated, based on the proportion of her regular range that lies within it. This then would be given by the following simple formula:

$$PR_{exp} = N \times \frac{a}{b}$$

where;
N = number of months in the study (= 48),
a = the area of her regular range that lies within the WCS study area,
b = the estimated total area of regular female ranges.

Thus the number of months that two individuals (i and j) would be expected to be present within the study area simultaneously is given by:

$$S_{exp} = N \times \left( \frac{a_i}{b_i} \times \frac{a_j}{b_j} \right)$$

As an example, if two females (A and B) possess regular ranges of 500 ha each (the estimate for adult female core area size from Chapter 4), and 100 ha of A's range lies within the WCS study area, whilst 200 ha of B's lies within it, then the expected number of months out of 48, they should be found there simultaneously would be:

$$S_{\text{exp}} = 48 \times \left( \frac{1}{5} \times \frac{2}{5} \right) = 3.84 \text{ months}$$

It should be noted here, however, that this takes no account of the influence of ecological variables and therefore effectively assumes ranges are homogenous. This is of course extremely unlikely but the method was explored nevertheless, in case any clear relationships could still be inferred. The formula also assumes both that regular range sizes are known with some accuracy, and as stated, that they are used equally throughout. The first assumption can to some extent be overcome by calculating $S_{\text{exp}}$ several times for each pair of individuals using varying estimates of regular range size. However, using larger range sizes reduces the expected number of months that two females should be present simultaneously ($S_{\text{exp}}$), and therefore increases the list of 'partners' with whom observed simultaneous presence is higher than expected. But, the rank order of these partners for an individual remains the same. Thus using the minimum regular range estimate of 500 ha provides a conservative list of partners that are present simultaneously with a given female. The second assumption is less important, as by assuming that ranges are used near their periphery as intensively as near their centre will overestimate $S_{\text{exp}}$. Hence if the observed number of months the pair were present together still exceeds the expected number ($S_{\text{exp}}$) then the evidence for coordination of movements is even stronger.

## 6.3. RESULTS

To examine the party data, only follows of greater than 3 hours duration, and then only data pertaining to females with at least 10 such follows, were used. This resulted in a total of 1645 follows (amounting to 14,429 hours of follow data) of 32 individuals. During these follows, 3758 parties (amounting to 10,115 hours) were recorded, giving a mean of 2.284 parties per follow. Full day, or nest to nest follows constituted 620 or 37.69% of follows. The overall mean follow duration was 8 hours 46 minutes (SD = 2 hours 55 minutes, n = 1645), and mean party duration was 2 hours 41 minutes (SD = 3 hours 7 minutes, n = 3758). A total of 539 follows (32.76%) had no parties.

The results of travel velocity calculations are presented in Table 6.1. A one way ANOVA was performed to test for significant differences in travel velocities between age and sex classes but none were found ($F = 1.717_{(5,42)}$, $p = 0.152$). Therefore the overall mean travel velocity of 86.063 metres per hour was subsequently used.

**Table 6.1**: Mean travel velocities by age class (metres / hour). n = number of individuals.

| | n | Mean | SD | SE | 95%LCL | 95%UCL | min | max |
|---|---|---|---|---|---|---|---|---|
| Adult females | 17 | 78.946 | 22.433 | 5.441 | 67.412 | 90.480 | 41.04 | 109.08 |
| Adult males | 11 | 71.715 | 28.209 | 8.505 | 52.764 | 90.666 | 18.43 | 111.08 |
| Subadult females | 4 | 109.806 | 64.464 | 32.232 | 7.229 | 212.383 | 61.15 | 198.96 |
| Subadult males | 10 | 98.110 | 26.699 | 8.443 | 79.010 | 117.209 | 51.44 | 145.46 |
| Adolescent females | 3 | 97.390 | 19.355 | 11.175 | 49.310 | 145.470 | 76.01 | 113.72 |
| Adolescent males | 3 | 95.856 | 23.238 | 13.417 | 38.129 | 153.583 | 71.44 | 117.71 |
| Total | 48 | 86.063 | 30.675 | 4.428 | 77.155 | 94.970 | 18.43 | 198.96 |

### 6.3.1. *Expected values of* $Z_{exp}$, $T_{exp}$ *and* $P_{exp}$

The expected rate of encounters by chance ($Z_{exp}$), was calculated as 0.091 per hour and the expected mean duration of parties ($T_{exp}$), was 1.013 hours, or 1 hour and 1 minute. The proportion of an individual's time that would be expected to be spent in associations ($P_{exp}$), was 0.093 (or 9.3%).

### 6.3.2. *Observed values of* $Z_{obs}$, $T_{obs}$ *and* $P_{obs}$

The observed values of the encounter rate ($Z_{obs}$), length of associations ($T_{obs}$), and proportion of time spent in associations ($P_{obs}$), for each individual are presented in Table 6.2. All orangutans except the adult female Diana, had encounter rates ($Z_{obs}$) greater than the expected rate ($Z_{exp}$) of 0.091 encounters per hour.

All except the two adult males, Mack and Luwi, had observed mean party length ($T_{obs}$) greater than the expected figure ($T_{exp}$) of 1 hour and 1 minute. The average mean party duration for individuals was 2 hours and 22 minutes (SE = 1 hour; n = 32; minimum = 39 minutes; maximum = 4 hours and 44 minutes).

All except the adult male Mack, had an observed proportion of time in parties ($P_{obs}$) greater than the expected value ($P_{exp}$) of 0.093 (mean = 0.646; SD = 0.400; minimum = 0.067; maximum = 1.622).

**Table 6.2**: Calculation of association indices. AF = adult female, AM= adult male, SAF = subadult female, SAM = subadult male, ADOLF = adolescent female, ADOLM = adolescent male.

| Class | Name | No. of follows | Sum of follow duration (h:m:s) | Total no. of parties | Observed encounter rate (individuals per hour) ($Z_{obs}$) | Sum of party duration (h:m:s) | Mean party duration (h:m:s) ($T_{obs}$) | SD (h:m:s) | Party duration divided by follow duration ($P_{obs}$) |
|---|---|---|---|---|---|---|---|---|---|
| AF | Abby | 128 | 1239:26:00 | 289 | 0.233 | 420:34:00 | 1:27:19 | 1:36:27 | 0.339 |
| AF | Ani | 234 | 2208:19:00 | 673 | 0.305 | 2143:10:00 | 3:11:04 | 3:27:46 | 0.970 |
| AF | Butet | 28 | 263:02:00 | 90 | 0.342 | 426:31:00 | 4:44:21 | 3:40:27 | 1.622 |
| AF | Diana | 118 | 1140:07:00 | 103 | 0.090 | 132:00:00 | 1:16:54 | 1:32:07 | 0.116 |
| AF | Hanes | 32 | 299:14:00 | 106 | 0.354 | 432:23:00 | 4:04:45 | 3:47:56 | 1.445 |
| AF | Karen | 12 | 101:52:00 | 11 | 0.108 | 35:23:00 | 3:13:00 | 1:57:04 | 0.347 |
| AF | Mega | 81 | 766:30:00 | 300 | 0.391 | 945:35:00 | 3:09:07 | 3:22:17 | 1.234 |
| AF | Pelet | 46 | 429:09:00 | 46 | 0.107 | 66:16:00 | 1:26:26 | 1:24:58 | 0.154 |
| AF | Sela | 27 | 203:53:00 | 64 | 0.314 | 125:55:00 | 1:58:03 | 2:13:40 | 0.618 |
| AF | Tevi | 41 | 327:56:00 | 73 | 0.223 | 139:04:00 | 1:54:18 | 2:07:24 | 0.424 |
| AF | Una | 56 | 446:56:00 | 97 | 0.217 | 249:32:00 | 2:34:21 | 3:12:16 | 0.558 |
| AM | Agus | 22 | 137:01:00 | 23 | 0.168 | 44:01:00 | 1:54:50 | 2:31:48 | 0.321 |
| AM | Arno | 189 | 1670:58:00 | 374 | 0.224 | 960:59:00 | 2:34:10 | 3:12:59 | 0.575 |
| AM | Budi | 18 | 140:23:00 | 19 | 0.135 | 20:21:00 | 1:04:16 | 1:09:13 | 0.145 |
| AM | Luwi | 11 | 82:24:00 | 15 | 0.182 | 12:51:00 | 0:51:24 | 0:47:24 | 0.156 |
| AM | Mack | 23 | 175:25:00 | 18 | 0.103 | 11:42:00 | 0:39:00 | 1:10:52 | 0.067 |
| AM | Mukson | 13 | 109:10:00 | 15 | 0.137 | 23:01:00 | 1:32:04 | 1:33:15 | 0.211 |
| AM | Ngon | 12 | 98:22:00 | 16 | 0.163 | 49:02:00 | 3:03:52 | 3:59:04 | 0.498 |
| AM | Olly | 11 | 109:08:00 | 27 | 0.247 | 70:42:00 | 2:37:07 | 3:20:22 | 0.648 |
| SAF | Becky | 49 | 376:02:00 | 127 | 0.338 | 326:42:00 | 2:34:21 | 2:41:02 | 0.869 |
| SAF | Lena | 12 | 99:23:00 | 13 | 0.131 | 27:17:00 | 2:05:55 | 2:12:23 | 0.275 |
| SAM | Dio | 41 | 355:26:00 | 119 | 0.335 | 349:07:00 | 2:56:02 | 3:42:50 | 0.982 |
| SAM | Koen | 16 | 127:10:00 | 98 | 0.771 | 125:10:00 | 1:16:38 | 1:45:10 | 0.984 |
| SAM | Lito | 38 | 294:59:00 | 93 | 0.315 | 193:01:00 | 2:04:32 | 2:06:18 | 0.654 |
| SAM | Musa | 19 | 138:34:00 | 35 | 0.253 | 67:18:00 | 1:55:22 | 1:24:28 | 0.486 |
| SAM | Navi | 13 | 108:46:00 | 56 | 0.515 | 67:39:00 | 1:12:29 | 1:10:22 | 0.622 |
| SAM | Oloan | 16 | 130:52:00 | 41 | 0.313 | 127:35:00 | 3:06:42 | 3:02:56 | 0.975 |
| SAM | Robert | 16 | 148:03:00 | 33 | 0.223 | 86:37:00 | 2:37:29 | 3:23:25 | 0.585 |
| SAM | Syawal | 16 | 161:10:00 | 45 | 0.279 | 119:47:00 | 2:39:43 | 3:39:14 | 0.743 |
| SAM | Tomi | 47 | 427:39:00 | 109 | 0.255 | 488:27:00 | 4:28:52 | 3:59:53 | 1.142 |
| ADOLF | Andai | 54 | 486:52:00 | 168 | 0.345 | 472:44:00 | 2:48:50 | 2:42:21 | 0.971 |
| ADOLM | Meggi | 35 | 309:48:00 | 96 | 0.310 | 294:24:00 | 3:04:00 | 3:20:41 | 0.950 |

Of particular interest here is the fact that the southern females Butet, Hanes and Mega all had very high $P_{obs}$ (at greater than 1), as did the subadult male Tomi (who matured to full adult status during the period in question), showing that these individuals all associate with others to a very high degree, at least when in the WCS study area where most follows took place.

These results therefore show that all individuals in the Suaq Balimbing study area have more parties (except the adult female Diana), have longer parties (except the two adult males Mack and Luwi), and spend a greater proportion of their time in parties (except the adult male Mack) than the expected values. This confirms the previous findings of van Schaik (1999), in the same area. Thus it can be concluded that with the possible exception of the three individuals mentioned, orangutans at Suaq Balimbing are more gregarious than would be expected from the null model. As far as the adult female Diana is concerned, she appears to avoid encountering other individuals, but once met, she too tends to stay in parties for longer than expected. Regarding the two males, it appears that both encounter others more than expected, but do not engage in long parties.

### 6.3.3. *Evidence of reproductive synchrony*

As stated in Chapter 4, some adult females appeared to have very similar range boundaries (e.g. Abby and Karen in the north-east and Pelet, Diana and Becky in the north-west; Figures 4.6 and 4.7). Some also seemed to be located in the same general area (e.g. Ani, Tevi, Mega, Una, Novi whose ranges all appeared to cover most of the central zone of the WCS study area; Figure 4.2), and some were normally found entering or exiting from the same side or corner (e.g. several females only found in the south-eastern portion, and Butet, Hanes and a few others who normally enter and exit via the south-western boundary, despite also using much of the central zone on occasions). If the estimated ages of the youngest infants of these females are then tabulated (Table 6.3), it is possible to assess whether or not females with similar ranges also possess infants of approximately the same age.

Naturally, the age of the majority of infants can only be estimated, using prior knowledge of the size and behaviour of infants of known ages, and the location of an individuals core area only inferred from the combination of ranging and presence data. Even so, there does appear to be a degree of reproductive synchrony among females residing in similar areas. For example, four of the seven females regularly encountered in the central zone gave birth in 1996, another in 1995, and two more who were not seen in recent years had infants when they were last seen, of an age that would suggest they too should conceive again around 1996 (in fact Sela was confirmed to be pregnant when last seen in 1996, using a pregancy test kit on urine; C. P. van Schaik pers. comm.). Similarly, all the females regarded as being south-easterners had infants estimated to have been born around 1991.

**Table 6.3**: Inferred location of core area of adult females with estimated year of birth of youngest infant. If known for certain infant's birth year is given in bold.

| Location | Name | Infant's name | Infant's sex | Estimated year of birth |
|---|---|---|---|---|
| ? | Darlene | Dolly | M | 1990 |
| ? | Imar | Un-named | Unknown | 1992 |
| ? | Lily | Un-named | Unknown | 1995 |
| C | Ani | Aneka | F | **1996** |
| C | Mega | Martin | M | **1996** |
| C | Novi | Nahot | M | **1996** |
| C | Sara | Sylvia | F | 1988 |
| C | Sela | Sultan | M | 1988 |
| C | Tevi | Tedi | M | **1995** |
| C | Una | Uli | F | **1996** |
| E | Afrika | No infant | - | - |
| NE | Abby | Atti | F | 1990 |
| NE | Karen | Karim | M | 1992 |
| NW | Becky | Barry | M | **1997** |
| NW | Diana | Dedi | M | 1992 |
| NW | Pelet | Peter | M | 1992 |
| S | AF49 | Un-named | F | 1994 |
| S | AF75 | Un-named | M | 1991 |
| SE | Duck face | Un-named | M | 1991 |
| SE | Molly | Millie | F | 1991 |
| SE | Rini | Rico | M | 1991 |
| SE | Yinta | Yeni | F | 1991 |
| SW | Butet | Bobby (deceased) | F | **1996** |
| SW | Elsie | Edna | F | 1991 |
| SW | Hanes | Henke (deceased) | M | **1996** |
| SW | Ita | Irma | F | 1991 |
| SW | Ling-ling | Lang-lang | F | 1996 |
| SW | Nicola | Nico | M | 1993 |

Within groupings some exceptions will inevitably exist. For example Becky who only recently matured into adulthood gave birth in 1997, slightly early perhaps for her group, but as this was her first infant it might be expected that she may not yet be synchronized with the other north-western females. Loss of infants will also result in subsequent births being asynchronous to others in an area. Indeed among the south-western females, three of the six gave birth in 1996, but two of the infants (those of Butet and Hanes) subsequently disappeared, presumed dead. In this case, however, greater synchrony may result as the ages of the other female's infants suggests they would give birth again around 1998/1999, and in fact, during mid-1998 the dominant adult male was observed consorting with a number of females outside but to the south-west of the WCS study area. These consorts included both of the females who had lost their infants, and some other unidentified females, not known from within the WCS study area. A further point worth noting is that Butet and Hanes were also the two 'south-westerners' most frequently encountered within the WCS study area. Thus it is possible that they are in fact more a part of the central group, which also produced several infants in 1996, as mentioned.

### 6.3.4. *Expected association rates based on range overlap*

In order to search for evidence of female clusters, the party data pertaining only to adult females were examined in more detail. For this purpose Becky was also included despite the fact that she was regarded as a subadult female for much of the study, only maturing to adulthood in late 1997. The mean encounter rate ($Z_{obs}$), for these females was 0.252 per hour (SD = 0.105, min = 0.090, max = 0.391). The average mean length of parties ($T_{obs}$), was 2 hours and 38 minutes (SE = 1 hour and 5 minutes; minimum = 1 hour and 17 minutes; maximum = 4 hours and 44 minutes). The observed mean proportion of time spent in parties ($P_{obs}$), was 0.725, or 72.5% (SE = 0.503; minimum = 0.116; maximum = 1.622; n = 12).

The observed proportion of each female's time spent with each of the others ($L_i$), is given in Appendix 6. The proportion of each female's polygon range within the study area that overlaps with each other female ($Q_i$), is given in Appendix 7. The proportion of time females would be expected to associate with each other based on the degree to which their polygon ranges within the study area overlap ($A_{oi}$), is given in Appendix 8. The observed proportion of time each female spent with each other ($L_i$) was then divided by the expected value based on range overlap ($A_{oi}$), producing a table of values for each combination of females (Appendix 9). If these values are then compared, it is possible to determine for which combinations of females the tendency to associate with each other more than expected is reciprocated (i.e. the ratio of observed association rate ($L_i$) divided by the expected association rate ($A_{oi}$) is greater than one for both individuals of the pairing; see Appendix 10). It is then possible to refine these results to show the top three associates of a particular female (Table 6.4).

**Table 6.4**: Top three associates in descending order (L-R) of the ratio of observed proportion of time together ($L_i$) divided by the expected proportion ($A_{oi}$) among adult females for each of the focal individuals listed (column 1). Empty cells mean that there are no more associates for a focal individual that are reciprocated i.e. for which the ratio of $L_i$ / $A_{oi}$ is greater than 1 for both individuals in the pairing.

| Focal | No.1 | Ratio | No.2 | Ratio | No.3 | Ratio |
|---|---|---|---|---|---|---|
| Abby | Diana | 3.347 | Becky | 2.219 | Karen | 1.515 |
| Ani | Abby | 3.022 | Becky | 2.296 | Mega | 2.063 |
| Becky | Diana | 3.739 | Abby | 3.695 | Ani | 2.460 |
| Butet | Mega | 4.104 | Diana | 2.746 | Hanes | 1.386 |
| Diana | Becky | 4.183 | Butet | 2.110 | Tevi | 1.012 |
| Hanes | Mega | 3.976 | Butet | 2.507 | - | |
| Karen | Abby | 12.326 | - | | - | |
| Mega | Butet | 2.413 | Ani | 2.015 | Hanes | 1.024 |
| Pelet | Ani | 3.204 | Una | 2.133 | Becky | 1.998 |
| Sela | Abby | 4.382 | Becky | 3.956 | Ani | 1.441 |
| Tevi | Ani | 4.488 | Hanes | 1.895 | Butet | 1.093 |
| Una | Abby | 12.010 | Becky | 1.797 | Diana | 1.125 |

Comparing these findings with those in Table 6.3, it can be seen that females within from the same areas do tend to associate with each other more than would be expected by the measure of range overlap used. For example, Abby and Karen from the north-east spend a lot of time together, as do Butet and Hanes from the south-west, and Becky and Diana from the north-west. Remembering that Mega also appears to have a northern range boundary near the northern edge of the study area suggests that she too is to some degree a southerner, which explains why she also regularly associates with both Butet and Hanes. Thus there is evidence that females from the same areas are to some degree synchronised reproductively, and also tend to associate with each other more than would be expected from null models of random movements, or from the degree to which their ranges overlap, as measured within the WCS study area.

### 6.3.5. *Expected simultaneous presence*

Appendix 11 gives the observed number of months females were present in the WCS study area simultaneously and Appendix 12 gives the expected number ($S_{exp}$), if regular female ranges were 500 ha. Dividing the observed value by the expected value ($S_{exp}$), then gives the ratio of observed over expected simultaneous presence (Appendix 13). Table 6.5 summarises the results of this procedure and therefore shows which pairings of females tend to be present together more than expected from simple range overlap alone. For each female down the left, all those across the top of the table are present simultaneously with that female, for more months than would be expected (i.e. the ratio is greater than 1). Partners are also ranked (L-R) according to the ratio of observed divided by expected simultaneous presence.

Some anticipated results are apparent from the table. For example, Becky, Diana, and Pelet from the north-west are often present together. However, when they are, Abby and Karen from the north-east also tend to be there, as do the central females Ani, Mega, Sela, Tevi, Una. Interestingly, Butet and Hanes who are both without doubt southerners, do not tend to be present when the others are, nor are they present together as much as might be expected. Since by default the central females are relatively frequently found within the WCS study area it is to be expected that they would show high simultaneous presence with all others, but whilst this is certainly the case with the northern females, it is not therefore, with the two southern females.

## 6.4. DISCUSSION

### 6.4.1. *Evidence of female clusters*

In full agreement with the findings of van Schaik (1999), individual orangutans at Suaq Balimbing do exhibit a tendency towards gregariousness, as shown by the fact that the vast majority possess encounter and association rates that are higher than those expected from the null models. Gregariousness in itself does not provide evidence of social organisation, however, as it could simply result from convergence on common resources (e.g. a single

**Table 6.5**: Females for who are more often present simultaneously than expected i.e. the ratio of observed number of months both females are present simultaneously divided by the expected number ($S_{exp}$) is greater than 1, if regular ranges are 500 ha. Females are ranked according to this ratio.

| Name | No. 1 | Ratio | No. 2 | Ratio | No. 3 | Ratio | No. 4 | Ratio | No. 5 | Ratio | No. 6 | Ratio | No. 7 | Ratio | No. 8 | Ratio | No. 9 | Ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby | Diana | 4.716 | Becky | 4.325 | Pelet | 2.959 | Una | 2.58 | Karen | 2.523 | Ani | 2.326 | Tevi | 1.345 | Mega | 1.342 | Sela | 1.261 |
| Ani | Abby | 2.326 | Diana | 2.294 | Becky | 1.994 | Pelet | 1.612 | Karen | 1.241 | Una | 1.125 | | | | | | |
| Becky | Abby | 4.325 | Diana | 4.312 | Pelet | 2.951 | Karen | 2.662 | Una | 2.144 | Ani | 1.994 | Mega | 1.588 | Sela | 1.468 | Tevi | 1.317 |
| Butet | | | | | | | | | | | | | | | | | | |
| Diana | Abby | 4.716 | Becky | 4.312 | Karen | 2.843 | Una | 2.643 | Ani | 2.294 | Pelet | 1.819 | Mega | 1.69 | | | | |
| Hanes | | | | | | | | | | | | | | | | | | |
| Karen | Diana | 2.843 | Becky | 2.662 | Abby | 2.523 | Una | 1.251 | Ani | 1.241 | Sela | 1.223 | | | | | | |
| Mega | Diana | 1.69 | Becky | 1.588 | Pelet | 1.517 | Abby | 1.342 | | | | | | | | | | |
| Pelet | Abby | 2.959 | Becky | 2.951 | Diana | 1.819 | Ani | 1.612 | Mega | 1.517 | Una | 1.387 | Tevi | 1.136 | | | | |
| Sela | Diana | 1.551 | Becky | 1.468 | Abby | 1.261 | Karen | 1.223 | | | | | | | | | | |
| Tevi | Abby | 1.345 | Becky | 1.317 | Diana | 1.191 | Pelet | 1.136 | | | | | | | | | | |
| Una | Diana | 2.643 | Abby | 2.58 | Becky | 2.144 | Pelet | 1.387 | Karen | 1.251 | Ani | 1.125 | | | | | | |

large fruit tree). Nevertheless, it does offer an opportunity to look at preferential association between individuals, and in fact, association patterns do suggest some mutual attraction between individuals within clusters. This is shown by the fact that females thought to share range boundaries, or to be from similar areas, also tend to associate more with each other than would be expected on the basis of range overlap alone. These same individuals also exhibit a tendency to be reproductively synchronised, as females from the various areas have infants of very similar ages. This is further evident if it is noted that at least six of 28 females (21.43%) were known to give birth in 1996, and this increases to 25% with the inclusion of Ling-ling and her infant. This would therefore suggest a birth interval of 4 or 5 years if births were random events. However, the generally accepted birth interval of wild orangutans is around 8 years (Leighton *et al.* (1995), and estimates of the ages of infants at the onset of fieldwork at Suaq Balimbing, in conjunction with the known year of birth of subsequent infants, support this figure. This therefore constitutes further evidence of reproductive synchrony.

Simultaneous presence within the study area was less conclusive in differentiating between individuals from different clusters, as females from several clusters appear to be present at similar times. It appears that when the northern females are in the area, females from other areas also tend to be there, excepting Butet and Hanes. Indeed all of the top three 'simultaneously present' individuals, for each female (except Butet and Hanes from the south), are northerners. These results therefore show that presence in the WCS study area is not simply a function of who else is there. Instead it appears that when food attracts an individual to an area, it also attracts many others that can access that area (as it lies within their range). Thus simultaneous presence almost certainly results from convergence on common resources. This therefore supports the findings of Chapter 5, providing further evidence that female movements are more related to ecological variables (e.g. fruiting phenology).

Only the two southerners did not appear to be present simultaneously with the majority of the others. A possible explanation for this might be fruiting passing through the area in waves, as suggested as a possibility in Chapter 5. For example, if an area of peak fruit abundance existed slightly south of the WCS study area, Butet and Hanes would be expected to be there. The northern females, however, would probably be unable to reach the area, and instead would be more likely to be found within the study area, waiting and exploiting the northern edge of the wave. Thus, as the wave passed northwards through the study area and out, the majority of females would be expected to move with it and exit northwards. Butet and Hanes, would therefore appear to enter just as the rest were leaving and would show little simultaneous presence with at least the northern females. This does not explain, however, why Butet and Hanes are not more often present with each other, as the explanation above might suggest they should be. An alternative explanation could be that the method of recording presence overestimates true presence for these two females. Table 4.2, estimates their presence indices as approximately 33%, but as pointed out, an individual need only enter the WCS study area for one day of any given month to be scored as present for that month. Whilst it is true that Butet and Hanes are able to access virtually the entire WCS study area, it is suspected that they may make frequent short visits rather than remaining there for long periods. This might be expected, if the WCS study area is only a part of their respective excursion zones, as opposed to their core areas (see Chapter 4). Hence presence indices of 33% may be overestimates for these two. This would mean that their expected presence together with others, and indeed with each other would be biased high, and explain the lack of any ratios of observed divided by expected simultaneous presence that are greater than 1 (Appendix 13).

It is also important to note here that the probability of finding northerners will be higher than for southerners, simply as a result of fieldworkers entering the study area from the basecamp in the north-west when searching for orangutans. This will bias detection rates in favour of northerners, as once found orangutans were usually followed. To some extent this may have been countered by the fact that this study searched predominantly along the southern edge of the study area, but some bias is likely to remain.

It should also be noted that individual females differ in their tendency to engage in associations. This is evident from the standard error of the mean length of parties (1 hour and 5 minutes) and was also noted by van Schaik (1999). Van Schaik distinguished between 'active' females who more frequently engage in associations and 'slow' females who spend more time alone. An example of a 'slow' female would be Pelet ($Z_{obs} = 0.107$, $T_{obs} = 1$ hour 26 mins, $P_{obs} = 0.154$), whilst 'active' females would include Butet, Hanes Mega, Sela and Ani, (all with $Z_{obs} > 0.3$). This dichotomy would further serve to hide any relationships between individuals, and that some relationships were still apparent regarding the expected rate of association based on range overlap is perhaps, therefore, even more notable. Again Butet and Hanes are interesting as they spend a very high proportion of their time in parties ($P_{obs}>1$), at least when in the WCS study area. This therefore suggests that despite not being present simultaneously with others very much, or even together, they nevertheless associate with others almost constantly when they are there. Thus they may benefit from renewing old acquaintances, using individuals more familiar with the area to find food, or to navigate, or perhaps through a feeling of safety if at the edge of their range. This might especially be the case if they were indeed related, or at least familiar with females from neighbouring areas.

Some of the methods employed here are necessarily crude, particularly due to the inherent difficulties in determining range sizes, range boundaries and hence range overlap, but also to the potential error in estimating presence. It is also considered somewhat over simplistic to assume that ranges are homogenous with respect to ecological variables, especially fruit availability. Moreover, the results of Chapter 3 clearly indicate that individual movements are to a large extent determined by local fruit availability. However, whilst not conclusive, the results are still compatible with the hypothesis that clusters or 'social units' of orangutan females do exist.

### 6.4.2. *Possible benefits of clustering*

Female clusters may arise as a result of the common tendency of daughters to stay close to their natal range (Galdikas 1988, 1995a; Rodman 1973b), with the higher densities at Suaq Balimbing possibly leading to larger clusters, or at least more visible clusters, than exist elsewhere. Synchronising reproduction among females that are related, or at least familiar with each other, and preferentially associate with each other, is likely to offer distinct long-term benefits to offspring through familiarity with their peers. Orangutans at Suaq Balimbing are distinctly more gregarious when compared to other study sites (van Schaik 1999), and an observed high incidence of mother-mother associations, particularly involving mothers with younger infants (van Schaik 1999), would increase the importance of this as a factor. These benefits are nevertheless, likely to be no more than beneficial by-products of synchrony, in that they are unlikely to outweigh the costs that would be incurred, in lost time, were a female to actively delay conception for many months or even years. It should also be remembered that the swamp forests of northern Sumatra are the only habitats were orangutans have been recorded regularly making and using tools (van Schaik *et al.* 1996; Fox *et al.* 1999). This therefore could also be related to their gregariousness, as it offers enhanced opportunities for social learning.

Synchronisation of reproduction within clusters of females must also be extremely attractive to dominant adult males, as it would allow them to mate with several females over a period of weeks or months without the expense of covering large distances. It would also benefit females by attracting the dominant male to the area and maintaining his presence there long enough to avoid mating with less desirable, non-dominant and subadult males, during the period of peak receptivity. For example, if the dominant adult male had to regularly traverse large distances between females, females would more often be left unguarded, and copulations forced by subadult males would presumably result in many more conceptions than would otherwise be the case. That the dominant male does move into an area for some time when the females there are receptive is supported by the behaviour of Arno. In 1995, when many of the central females were receptive, Arno was most often in the study area. Similarly, during June and July 1998, he was observed to be in the area south-west of the WCS study area, with both Butet and Hanes soon after they had lost infants, and on another occasion with a number of unknown females, and adolescents (presumably their offspring) of an age that suggested their mothers should be beginning to cycle again.

MacKinnon (1989) had already noted that females within relatively localised areas somehow appear to synchronise reproduction, so that in one locality there are years when several females give birth, interspersed by several years when very few give birth. Mitani (1985a,b) also found that during his study at Mentoko, several females where receptive at once and that at the same time he had a very high number of males, and high levels of long-calling and sexual behaviour in his study area. MacKinnon suggested that this was adaptive, in giving both sexes the widest possible opportunity for selective mating. It might seem more likely, however, that the potential benefits outlined above may in reality be only by-products of clusters. Instead, reproductive synchrony may simply result from the fact that females within clusters share the same forest patches, and hence experience similar fluctations in diet quality. It has already been noted by Knott (1997) that ovarian hormone levels were correlated with changing energetic and nutritional status as a result of fluctuating food availability at Gunung Palung in Borneo. Thus it is perhaps to be expected that females with similar ranges would also experience similar hormone levels. Whether this alone would be sufficient to result in reproductive synchrony in a species with an 8 year inter-birth interval, however, might still be debated. In any case the previous observations by MacKinnon (1989) and Mitani (1985a,b) are supported by the results presented here though it must be realised that the conclusions drawn are necessarily tentative. Nevertheless these observations may represent the first indication of some form of social organisation within orangutan populations, other than the basic units of solitary individuals or mother-offspring dyads.

## 6.5. CONCLUSIONS

1. The vast majority of orangutans of both sexes at Suaq Balimbing are more gregarious than would be expected by null models of individuals moving randomly around the area.
2. Female ranges and association patterns indicate several clusters of females. The ages of infants provides compelling evidence of reproductive synchrony amongst females that normally inhabit similar areas and share similar range boundaries. These females also show physical similarities and may well be relatives (not yet confirmed by genetic analyses).
3. There is some evidence to suggest that females tend to associate more with females from similar areas or that share similar range boundaries than with others.
4. There was no evidence that females that share similar ranges appear simultaneously in the study area more often with each other than with females that do not share similar ranges. This supports the hypothesis that female movements are more related to ecological variables than to the presence or absence of other individuals.

# CHAPTER 7

# CONCLUSIONS AND IMPLICATIONS

## 7.1. DENSITY ESTIMATION

The density estimates produced using line transects of nests were considered to be underestimates for a variety of reasons. The main problem with using the all nest method to estimate densities was considered to stem from the use of a decay rate that was estimated with the inclusion of nests until total disappearance, whilst not detecting very old nests during one-off censuses. For the new nest method the main difficulties were considered to arise from a combination of small samples, missing some nests on or above the trail, and possibly also some errors in estimating perpendicular distances from the trail.

Despite these problems, however, absolute densities were inferred to lie between 5.5 $km^{-2}$ and 10.0 $km^{-2}$ in the swamps, and 1 $km^{-2}$ to 1.5 $km^{-2}$ in the hills. The number of new nests along a transect was also considered a reasonable indicator of relative densities, both between areas and over time. Densities at Suaq Balimbing are certainly among the highest (if not the highest) yet recorded, particularly in the area around IB, and the density of *Tetramerista glabra* trees (the principal diet species) is implicated as a major determinant of the spatial distribution of orangutans in these swamp forests.

It could be argued that the high densities at Suaq Balimbing might be a result of compression due to habitat destruction, but as pointed out by van Schaik (1999), monitoring of nests since 1992 has not shown any evidence of increases in densities, despite logging in the vicinity since 1993. Also, at Ketambe, the population has been relatively stable since the early 1970s, despite the near obliteration of all neighbouring floodplain habitat.

## 7.2. RANGING BEHAVIOUR OF INDIVIDUALS

The home ranges of adult females at Suaq Balimbing are larger than any yet reported from elsewhere. This is also the case for males when compared to those studies that have actually produced estimates. Female ranges at least have therefore either been underestimated in previous studies, or are genuinely larger than elsewhere. Both options are plausible. It could easily be argued that different habitat types (i.e. coarse-grained as opposed to fine-grained), would result in different range sizes. This is especially likely for females, for whom food is considered the most important factor influencing ranging behaviour. It is also easy to see how ranges could be underestimated. A researcher who regularly encounters a particular individual in a well defined and restricted area could easily be drawn to the conclusion that this area approximately represents their home range. The examples of the adult females Ani and Mega (Chapter 4), however, show clearly they are capable of travelling extensively outside the WCS study area, despite spending a large proportion of their time within it. Instead it can be seen that female home ranges appear to consist of a core area of around 500-600 ha, which is surrounded by a less intensively used ‘excursion’ zone, giving a total home range that is potentially as large as 1500 ha. Indeed the very existence of this excursion zone may itself lead to underestimates of range sizes, since it might be used only relatively infrequently and its existence could only be determined when it was actually used, i.e. during long forays away from core areas as when both Ani and Mega ventured far into the hills during the mast event.

It is also interesting to note that at Suaq Balimbing, ranges of circa 3 km across (which would equate to a circular area of 700 ha), or slightly less, would be sufficiently large to encompass forest areas that are one or two months out of phase with respect to fruiting, and in particular to fruit ripening. This therefore suggests that core areas of circa 500-600 ha may permit females to extend the period for which a particular fruit crop is available to them by gradually traversing their core area as fruiting passes through. This would therefore offer a sound ecological reason why ranges at Suaq Balimbing might be this size. Naturally an even larger excursion zone would extend the period of particular fruit crop availability even further.

No evidence was found that adult female ranges at Suaq Balimbing are anything other than stable over time. This concurs with the observations of Galdikas (1979) for Tanjung Puting. Some authors agree that at least a proportion of females remain in the same location (residents), but in contrast some also suggest that at least a proportion of females are transient (e.g. MacKinnon 1974; te Boekhorst *et al.* 1990; Rijksen and Meijaard 1999). This is not supported here. Instead I propose that these conclusions could be the result of misinterpreting data. The most obvious explanation is that researchers have simply observed females that were normally resident in adjacent areas, at or near the limits of their ranges. This would explain the sporadic nature of encounters with such females within study areas, especially given the existence of 'excursion' zones. Some authors have been more conservative, and simply classified such individuals as non-residents (e.g. Utami *et al.* 2000b). This would seem more appropriate than assuming that they are transient as well, since they would probably be regarded as resident in the adjacent area.

In accordance with all other studies, the home ranges of both fully adult and subadult males at Suaq Balimbing are much larger than those of females. The results suggest that ranges of both classes of sexually mature males are almost certainly in excess of 3000 ha but are quite possibly much larger still, perhaps even reaching 10000 ha or more. However, the fact that virtually all fully adult males do occasionally return to the study area does not support the idea of true transience or nomadism amongst this class. Instead, it implies that fully adult male ranges are simply very large, but nevertheless limited in extent.

There is evidence that the dominant adult male, Arno, may behave differently with respect to ranging, to other fully adult but non-dominant males. His presence in the WCS study area suggests that when he is absent he does not travel far. Adopting a smaller range would only seem to be to his advantage if he could increase his reproductive success by defending receptive females within his range from other males during the critical periods of peak receptivity. It would also seem likely that if he ventured further from this limited range there would be a higher risk of losing his dominant status, missing oestruses amongst the females there, and of conflict and potential injury from other adult males he may encounter. Thus I propose that the benefits to dominant adult males of remaining in a limited range may outweigh those of wandering over a larger area, resulting in smaller home ranges for these males, at least during their period of dominance.

In contrast to the dominant adult male, non-dominant adult males would seem to have much to gain from occupying very large ranges. If dominant adult males are able to effectively guard a large proportion of receptive females in a given area, then wandering over larger areas in the hope of encountering occasional, unguarded receptive females may represent their only realistic option for reproduction. Even then non-dominant adult males may actually achieve very few successful copulations. As noted by Rijksen and Meijaard (1999), when a subadult male attains typical adult physiognamy (i.e. secondary sexual characteristics), rapes become rare if not impossible, due to the discrepancy in agility between fully adult males and females. Thus they must presumably rely on female mate choice, and this would tend to select against them if females preferentially mate with dominant adult males.

It was not possible to determine the true extent of subadult male ranges, though again these are clearly very large. Transience remains a possibility for this class despite the fact that some individuals do occasionally return to the WCS study area (which suggests large but limited ranges, rather than random or directed movements, as would occur during long distance dispersal). The number that were unknown, or seen only briefly and then never again, strongly suggests that at least a portion of subadult males may be genuine wanderers, perhaps in the process of dispersal. There also appears to be further evidence that subadult males constitute a dispersal phase. From the modelling of different estimates of range size, with the observed degree of range overlap within each age and sex class (Chapter 4), it seems that a net loss of males occurs as the population matures, at least at Suaq Balimbing. This is due to a discrepancy between the estimated sex ratios of mature and of immature individuals. In addition, analysis of wild orangutan DNA from Ketambe did conclude that none of the subadult males there were related to any of the adult males (Utami 2000a), and therefore further supports subadult male dispersal, if it can be shown that infants sired by these adult males should by now be subadults.

The discrepancy in sex ratios also suggests that dispersal of males from Suaq Balimbing may not be reciprocated by an equal influx of males from elsewhere. These conclusions remain tentative, however, as the true number of subadult males that passed through the WCS study area cannot be known with absolute certainty. This is due partly to some identification difficulties among this class, but also because an unknown number will have gone undetected. It is therefore possible that a much larger number of subadult males may possess overlapping ranges, than the 20 or 30 used in the range modelling process (Table 4.7). If this is indeed the case then the discrepancy in sex ratios would be expected to be less marked, either reducing the evidence for subadult male dispersal, or suggesting that at least some compensatory influx does occur.

Still, it remains possible that there is indeed a net loss of males from the study area as the population matures. Such a phenomenon could occur due to male biased mortality, as a result of male conflict, but whilst this will almost certainly account for some losses, to date relatively few deaths of wild orangutans have ever been reported. Thus it is considered that deaths due to fights may account for relatively few losses. An alternative explanation would exist if there are genuine reasons why other areas might be more attractive to subadult males. The exceptionally high densities of orangutans, and particularly of females at Suaq Balimbing, may result in greater success for dominant adult males attempting to guard receptive females than is possible elsewhere. Under these circumstances, non-dominant adult males and subadult males would presumably have relatively little reproductive success with a strategy that relies on finding unguarded receptive females. Therefore, it may be to the advantage of these individuals to emigrate to areas where female densities are lower, and dominant males are less able to guard them due to their greater dispersal.

A further very important point to note is that despite the fact that ranges are larger than reported elsewhere, so are densities. Thus for conservation purposes assuming that an area contains a high density of orangutans does not mean that their ranges are smaller, and hence that protected areas could be smaller, as might be presumed.

### 7.3. EVIDENCE FOR SEASONAL MOVEMENTS

The results of Chapter 5 do not support the occurrence of large-scale seasonal movements of orangutans. If they did occur, greater correlation would be expected between plots with respect to monthly orangutan densities (or numbers of new nests). Instead, there was little correlation between plots. Neither does the ranging data support seasonal movements. No evidence was found that any adult females are transient, nor at least the majority of adult males. It has been suggested, however, that males are attracted to an area by the number of receptive females (e.g. Galdikas 1979; Mitani, 1985a,b; Rodman and Mitani 1986; Utami *et al.* 2000b), but again it does not appear that this necessarily results in large increases in absolute densities. Instead it seems that there is a shift in the structure of male populations with respect to the number of receptive females in an area, rather than in overall numbers. For example, the presence results suggest that when several females are receptive, the dominant male can be expected to be in the area, along with a number of subadult males. When the females are no longer receptive, however, these males are more often absent, but are replaced by non-dominant adult males, and the overall number of males in an area does not appear to fluctuate dramatically as a result. That some subadult males may be transient, however, remains a possibility. Therefore if any age or sex class was to undertake large-scale movements, it is most likely to involve the latter as there is evidence that they constitute a dispersal phase and may not in fact have range boundaries, at least temporarily. Subadult males may therefore contribute more than adult females and adult males to any large fluctuations in densities that might occur in an area. Nevertheless, it would seem unlikely that such movements of this class would be driven primarily by food, and could thus be considered to be seasonal.

Rather than being large-scale, movements in and around the WCS study area were instead found to be mostly relatively small-scale compensatory movements between locations, individuals only being able to move within large, but nonetheless limited home ranges. Fruit was implicated as a major determinant to movements, and evidence was found that female home ranges may be just large enough to include areas that are 1 or 2 months out of synchrony with respect to fruiting. Absence of fruit was also found to influence movements, as individuals appear to utilise some forest patches when fruit is generally scarce throughout the area. Thus it seems that orangutans may require a variety of habitats within their ranges to sustain them through periods of fruit scarcity, and hence, that they will use these different areas according to variations in fruit availability. Furthermore, the fact that orangutans appeared to move into the backswamp areas when fruit was scarce, in conjunction with the simultaneous arrival of many individuals in the hills during the mast event there, clearly shows that relatively large numbers will on occasions converge on a particular area. This would therefore seem to represent the most likely explanation for the apparent seasonal movements of orangutans reported in other study areas, as from within a relatively small area, such convergence would appear as a dramatic simultaneous arrival (and subsequent departure) of individuals. However, this explanation does not require any age or sex class to be transient, as has been inferred by some authors. Instead it simply requires individuals to posses home ranges that are larger than the area in question, and to use different parts of their ranges according to local variations in resource availability.

## 7.4. FEMALE CLUSTERS

It has been stated many times in the literature that the basic units of orangutan populations are individuals, or individuals with dependent offspring (Rodman 1973a; Galdikas 1979; MacKinnon 1974; Horr 1977; Suzuki 1992; Schürmman and van Hooff 1986). Rijksen and Meijaard (1999), however, speculated as to the existence of 'groups' and stated that group formation is most obvious among adolescents and subadults who may commonly move in close proximity to one another. Sugardjito *et al.* (1987) also concluded that orangutan sociality increases (larger groupings) with increasing fruit availability. Thus it appears that where and when resources permit, orangutans do possess a tendency to gregariousness, which concurs with observations in captivity (e.g. Maple 1980; Edwards 1982; Sodaro 1997). Van Schaik (1999), however, points out that sociality, as measured by associations, also results from males gathering around oestrus females, and hence may bear only a very indirect relationship to food abundance, even if relationships seem apparent.

A few field studies have also reported that in a given area several females appear to be synchronised reproductively (e.g. Mitani 1985a,b; MacKinnon 1989), and that on maturation, females settle in home ranges that overlap or are adjacent to those of their mothers (e.g. Galdikas 1988, 1995a; Rodman 1973b). Naturally the latter is difficult to prove without genetic analysis or very long-term field studies, but the results presented here are consistent with these observations. Furthermore, they also suggest that females may exist in 'clusters' at Suaq Balimbing, within which females do indeed appear to be reproductively synchronised to a degree, and also to associate more with each other than with other females. An attempt was made to determine if members of these clusters also tended to appear in the same areas at the same time, but the findings were inconclusive. Instead, the pattern was confused by the simultaneous arrival in areas of many individuals from different clusters. However, when an area such as the WCS study area is producing a lot of fruit, it would be expected that females from clusters to the north, south, east, and west might arrive there at the same time, unless their ranges allowed them access to even better resources elsewhere. Therefore, despite the fact that the attempt to determine if cluster members arrived in the study area simultaneously could not show this conclusively, the results were not incompatible with the idea.

The findings and observations noted above all constitute mounting evidence that small groups or 'clusters' exist, consisting of females that are probably related, synchronise reproduction to the best of their ability, and preferentially associate with each other more than with females that are not part of their cluster. That similar 'clusters' have not so far been noted elsewhere does not mean they do not exist. It could simply be a function of densities, since presumably lower densities would make any relationships even less apparent, either due to greater spatial dispersal of cluster members, or perhaps if clusters contain fewer females.

It also remains possible that their movements may be coordinated to some degree as this could not be ruled out. Perhaps these findings constitute the first evidence of the existence of female groupings, and hence social groups of orangutans. MacKinnon (1989) suggested that it would be adaptive for females to be reproductively in phase with other local females, as this results in their being in oestrus simultaneously, when the widest possible choice of males is available. He also suggests that it would leave the problems of infant rearing to conditions of social calm and reduced food competition due to reduced numbers of males in the area. However, as was noted earlier, there may not be reduced overall numbers of males in the area. Instead, there may simply be a shift in the structure of the male contingent toward fewer subadult males and more non-dominant but fully adult males. This may still confer advantages of relative calm as non-dominant adult males do not harass females to the extent that subadults do. An alternative explanation of reproductive synchrony is suggested by the findings of Knott (1997), who provides evidence that it could simply be a result of nutritional factors, as ovarian hormone levels were correlated with changing energetic and nutritional status, as a result of fluctuating food availability. She hypothesised that these changes in hormone levels would affect the probability of conception. Consequently reproductive synchrony may not be adaptive, but simply an artefact of females in a given area sharing similar resources. Whatever the fundamental reasons for synchrony, however, it would seem likely to confer some benefits to females, through attracting and maintaining the presence of high quality males during receptive periods. It might also offer advantages to infants as they mature amongst similar aged peers, and as a result, may enhance opportunities for social learning.

## 7.5. MATING SYSTEM AND SOCIAL ORGANISATION

For male orangutans, there seem to be two main options for achieving reproductive success: (1) travel widely and try to encounter cycling females; or (2) try to monopolise several females in a particular area (Utami and Mitrasetia 1995). MacKinnon (1978, 1979), suggests that it is virtually impossible for a dominant male to achieve exclusive breeding rights in a large area of forest which takes him several days to cross, and of which he can see only a fraction at any one time. However, higher densities of females would presumably make this option easier and indeed the behaviour of Arno at Suaq Balimbing, strongly suggests that he adopts such a strategy.

Many authors have tried to classify the orangutan's mating system. Clutton-Brock (1989) suggested that at least some orangutan populations appear to adopt 'roving male' strategies. With such strategies, females range widely, but are solitary, or live in small groups that are unpredictably distributed at low population densities, whilst males range widely in search of oestrus females, consorting with them and defending them against other males. MacKinnon (1974, 1979) on the other hand, suggested that some form of spatially dispersed, age-graded male group characterises their social organisation, with adult males acting as range guardians for their reproductively active subadult male relatives. Rodman and Mitani (1987) proposed a dispersed social unit with a promiscuous mating system and strong inter-male competition. A variant of this was suggested by Schurman and van Hooff (1986), and van Hooff (1995), who emphasised the pivotal role of female choice. Their system relies on the fact that females select dominant adult males over all others, with the result that subadult males are tolerated by adult males because they do not compete effectively with dominant adult males, and as adult males are not capable of expelling them. However, the findings at Suaq Balimbing suggest that subadult males do out-compete some fully adult males. Subadult males regularly force copulations, and presumably sire occasional infants as a result, whilst non-dominant adult males were seen to mate with females only once over several years.

Van Schaik and van Hooff (1996) concluded that only two plausible models for orangutans exist, both of which are partly consistent with the published evidence. The first of these is a roving male promiscuity system in which males cannot defend access to female ranges and females do not congregate at predictable areas. Thus all males have large and widely overlapping ranges within which they search for receptive females. The second is a spatially dispersed but socially distinct community organised around one or more large adult males. They also admit, however, that extensive additional observational work would be required to assess whether or not either of these two models correctly describe the situation for orangutans. Both models require that paternity is highly concentrated in the adult males, but this not supported by recent results from Ketambe. Utami *et al.* (2000a) found, through genetic analysis, that about half of infants born at Ketambe were in fact sired by subadult males, and furthermore, that subadult males are unrelated to adult males in the population. They also note, however, that many of these infants were conceived during a period when the male dominance hierarchy was unstable, and hence in the absence of a single clearly dominant adult male.

A further model for the social system of orangutans is a 'lek'-type system (Rijksen and Meijaard 1999). In mammals and birds, extreme sexual dimorphism (as exists in orangutans) is usually a characteristic of either a one-male group, or a lek-type mating system, as it is considered to result from female choice for male physical characteristics or assertiveness, rather than additional care of offspring (Rijksen and Meijaard 1999). Clutton-Brock (1989) proposes five reasons why receptive females may mate on classical leks. Two of these may apply to orangutans: (1) females benefit from increased opportunities to choose mates; and (2) leks in the form of clustered male territories offer some protection from the attentions of other (subadult) males during periods of receptivity. Of particular interest, however, is that according to Clutton-Brock (1989), in mammals leks are replaced by dispersed male territories, or roving strategies, in low-density populations. Rijksen and Meijaard (1999) point out that the lekking system they suggest for orangutans differs from others, in that orangutans seem to establish and entertain long lasting relationships between adult males and females and therefore adopt the term 'social arena' in preference to lek.

The results of the present study are compatible with a social system in which groups or 'clusters' of females exist, several of which can be included within the range of a single dominant adult male. If, as appears to be the case at Ketambe (Utami *et al.* 2000a), subadult males at Suaq Balimbing also sire infants then this is not a monopolisation of females by the dominant adult male and sperm competition might be expected. Small testes size relative to body weight in orangutans, however, does not support this (Dixson 1998). Instead it appears that within female clusters, reproduction is more or less synchronised. Thus the dominant adult male is still likely to sire more than any other single male by monopolising the cluster at the time of peak receptivity, before moving on to the next 'receptive' cluster within his range. In this manner subadult males may still sire occasional infants through forced copulations with asynchronous females.

A particularly interesting observation from the Suaq Balimbing data is the lack of observed copulations involving fully adult but non-dominant adult males. Since the station was established in 1994 only once has an adult male other than Arno been observed to mate with a female (pers. obs.; van Schaik unpubl.). This therefore supports the contention that the dominant male can to some extent prevent them from breeding. It also implies that it would be to a male's advantage to remain as a subadult until the potential benefits of secondary sexual characteristics (i.e. a chance to compete for dominant status and thus increase reproductive opportunities) outweigh the risks of becoming a non-dominant adult male with very few reproductive opportunities.

For this reason I suggest that subadult males may develop in a cyclical fashion. In the presence of a particularly successful dominant adult male, any subadult male that develops SSCs would either have to compete with this male if he wishes to sire infants, or leave the area. However, if the dominant adult male were to show signs of weakening or die, it would seem reasonable to expect a number of subadult males to rapidly mature and compete for the new vacancy. Males that are already fully adult but non-dominant, may also compete, but it could be argued that many would be past their prime, and unlikely to succeed as a result. Such a scenario would mean that development of SSCs would be a huge gamble to subadult males, as the majority would fail to accede to the dominant position in the immediate area. Instead they would be forced to wander in search of unguarded receptive females, or areas where the resident dominant position may be contestable, such as they appear to do at Suaq Balimbing. The discrepancy between sex ratios observed in Chapter 4, also supports the hypothesis that the acquisition of SSCs is not age related. Instead it implies that only a small proportion of subadult males mature into full adults at any one time, the remainder perhaps being suppressed by the presence (or quality) of the dominant adult male, which again is compatible with cyclical maturation to full adult status.

This proposition, that development of SSCs proceeds in cycles or waves, can of course only be speculation due to a lack of any real evidence to date, but would be entirely compatible with the results of this study. It would also be compatible with previous speculation that the presence of fully adult males does suppress the development of SSCs in subadult males, as suggested by Kingsley (1982) and van Schaik and van Hooff (1996). Further research on wild populations as part of long term field studies, or re-examination of existing data from other sites might help in this respect but it seems that relatively few 'maturations' have been reliably witnessed. Almost certainly some will have been missed, or not recognised for what they were, as facial characteristics change so dramatically from subadulthood to fully flanged adulthood.

## 7.6. IMPLICATIONS FOR HABITAT PROTECTION, TRANSLOCATION AND REHABILITATION

As home ranges at Suaq Balimbing are considerably larger than any yet reported from elsewhere, attempts to delineate forest areas for the protection of viable orangutan populations should be extremely cautious. Clearly, many thousands of hectares are required to sustain even a small population based around a single dominant adult male and for a population to be viable in the long term it must contain several breeding males. In fact, using the data in Table 4.7, it is possible to estimate how many orangutans would be supported in 100 km$^2$ of forest of similar quality to Suaq Balimbing (assuming that ranging patterns are also similar). If the range sizes and degree of overlap for each age/sex class yield a density of 7.25 km$^{-2}$, then 100 km$^2$ would support a total of 725 orangutans. Of these, however, 229 would be adult females and 100 would be subadult males, but only 33 would be fully adult males. Furthermore, of these 33 only 6.67 fully adult males would be expected to be dominant at any one time, and thus contribute significantly to the gene pool. It must also be remembered that these densities are much higher than elsewhere, such that much larger areas of other forest types would be required to sustain similar numbers. In addition, given the fact that only a percentage of adult males are likely to accede to dominancy, there would be no guarantee that any introduced males would achieve this status. Hence even translocating males may not achieve the desired goal of introducing new genes to a population. Thus where protected areas are small and fragmented, emphasis must be on creating corridors, to allow the free movement of individuals between forest patches, rather than relying on supplanting new genes into populations via translocation projects. An additional consideration must also be the extremely long life-span of orangutans. This means that the commonly used criteria for conservation protocols, i.e. of maintaining 95% heterozygosity over 100 years, is perhaps meaningless for this species, since 100 years is only a few generations, and therefore requires only a small number of individuals.

Given that females at least, and probably also many fully adult and subadult males appear to be sedentary and remain in fixed home ranges, even large-scale rehabilitation projects must exercise great caution in determining the forest areas where orangutans should be released, and how many can be accomodated. If orangutans are introduced into areas that already contain populations at or near carrying capacity, it is to be expected that some individuals will die as a result of density dependent effects. Certainly there is no evidence from the data presented here that adult females are able to relocate. It could be argued that the high densities at Suaq Balimbing could be a result of compression due to habitat destruction, but as pointed out by van Schaik (1999), monitoring of nests since 1992 has not shown any evidence of increases in densities, despite logging in the vicinity since 1993. At Ketambe, the population has been relatively stable since the early 1970s, despite the near obliteration of all neighbouring floodplain habitat. These observations therefore support the contention that orangutans do not disperse very readily, in that when forests are destroyed they do not seem to appear in any numbers in neighbouring areas.

If this is indeed the case, then either females that are introduced will have to search widely before they find areas suitable for establishing a range, or wild residents will be forced to move. If they do not they will have to compete in an area that is then above its carrying capacity. There would appear little doubt that a likely outcome of all three options would be prolonged existence on a sub-optimal diet, eventually resulting in malnutrition and death. Males might also succumb to these problems.

The results of this study also have ramifications for rehabilitation projects into areas with no existing wild populations. As noted above, even swamp forests such as at Suaq Balimbing an area of 100 km$^2$, could only hold up to a maximum of around 725 orangutans. But moreover, only around 388 mature individuals could be accommodated in the long term if they adopted similar range sizes to those observed here (model B in Table 4.7). Therefore, as ex-captive individuals would tend to be approximately the same age (i.e. between infancy and 8 or 9 years of age) and would hence also mature at around the same age, this must represent the maximum number that could be introduced in to similar habitats of this size. This figure concurs with Rijksen and Meijaard's (1999) recommendation that no more than half the carrying capacity of an area should be introduced if the reintroduced population is to have an opportunity to grow and adapt. In other forest types, that are able to support only very low densities, the numbers that could be accommodated would naturally also be very much reduced, though perhaps by less of a degree if orangutans adopt smaller ranges in such areas.

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**APPENDIX 1**: Densities (km$^{-2}$) and strip widths (metres) estimated by DISTANCE using minimum AIC, r = 57.79, and new nests, with the three swamp based transects HJPLX, X and SM pooled for each month. From May to September 1997. Confidence limits are 95%.

| Month | No. nests | ESW | %CV | LCL | UCL | Density | %CV | LCL | UCL | df |
|---|---|---|---|---|---|---|---|---|---|---|
| May-97 | 45 | 27.287 | 17.51 | 19.218 | 38.744 | 3.276 | 23.00 | 2.072 | 5.178 | 43 |
| Jun-97 | 36 | 21.039 | 15.64 | 15.341 | 28.853 | 3.399 | 22.85 | 2.149 | 5.376 | 34 |
| Jul-97 | 40 | 32.844 | 11.69 | 25.943 | 41.580 | 2.419 | 19.66 | 1.631 | 3.588 | 38 |
| Aug-97 | 48 | 33.959 | 9.51 | 28.055 | 41.104 | 2.808 | 17.28 | 1.988 | 3.966 | 46 |
| Sep-97 | 47 | 22.248 | 15.71 | 16.244 | 30.471 | 4.196 | 21.44 | 2.738 | 6.431 | 45 |
| Oct-97 | 59 | 27.832 | 4.31 | 25.532 | 30.339 | 4.211 | 13.71 | 3.204 | 5.534 | 58 |
| Nov-97 | 40 | 29.389 | 10.24 | 23.903 | 36.134 | 2.703 | 18.84 | 1.853 | 3.944 | 39 |
| Dec-97 | 39 | 26.297 | 8.48 | 22.154 | 31.214 | 2.946 | 18.12 | 2.047 | 4.239 | 38 |
| Jan-98 | 46 | 26.298 | 4.94 | 23.808 | 29.048 | 3.474 | 15.55 | 2.545 | 4.743 | 45 |
| Feb-98 | 35 | 25.000 | 7.80 | 21.341 | 29.286 | 2.781 | 18.61 | 1.911 | 4.046 | 34 |
| Mar-98 | 34 | 31.848 | 6.53 | 27.888 | 36.370 | 2.120 | 18.35 | 1.464 | 3.071 | 33 |
| Apr-98 | 32 | 28.619 | 9.42 | 23.627 | 34.667 | 2.221 | 20.03 | 1.482 | 3.328 | 31 |
| May-98 | 20 | 33.334 | 25.00 | 19.911 | 55.806 | 1.192 | 33.54 | 0.602 | 2.360 | 19 |
| Jun-98 | 33 | 23.131 | 12.83 | 17.832 | 30.004 | 2.834 | 21.62 | 1.833 | 4.380 | 32 |
| Jul-98 | 66 | 24.993 | 7.65 | 21.455 | 29.116 | 5.245 | 14.49 | 3.932 | 6.996 | 64 |
| Aug-98 | 29 | 20.260 | 14.16 | 15.182 | 27.038 | 2.843 | 23.35 | 1.773 | 4.558 | 28 |
| Sep-98 | 41 | 29.097 | 6.99 | 25.270 | 33.505 | 2.799 | 17.11 | 1.986 | 3.945 | 40 |
| Mean ESW | | 27.263 | | Mean Density | | 3.027 | | | | |
| SD ESW | | 4.228 | | SD | | 0.923 | | | | |

**APPENDIX 2**. Mean ratio of nest to nest distance divided by total day journey length for focal individuals. Only nest to nest follows included in calculations. * Denotes individuals that changed classes during the study and figures for these are based on data only from the period in which they fell into the relevant class.

| Class | Name | Number of nest to nest follows | Mean ratio (Distance / Djl) | SD | Minimum ratio | Maximum ratio |
|---|---|---|---|---|---|---|
| Adolescent females | Andai | 20 | 0.351 | 0.183 | 0.042 | 0.752 |
| | Beti | 1 | 0.210 | . | 0.210 | 0.210 |
| Adolescent males | Herdi | 1 | 0.368 | . | 0.368 | 0.368 |
| | Meggi | 14 | 0.362 | 0.178 | 0.137 | 0.640 |
| | Uno | 3 | 0.284 | 0.155 | 0.156 | 0.456 |
| Adult females | Abby | 83 | 0.447 | 0.179 | 0.109 | 0.843 |
| | Ani | 117 | 0.375 | 0.168 | 0.000 | 0.735 |
| | Becky* | 3 | 0.544 | 0.255 | 0.263 | 0.760 |
| | Butet | 13 | 0.409 | 0.246 | 0.028 | 0.788 |
| | Diana | 52 | 0.384 | 0.190 | 0.048 | 0.860 |
| | Hanes | 15 | 0.485 | 0.181 | 0.252 | 0.796 |
| | Karen | 4 | 0.407 | 0.082 | 0.301 | 0.493 |
| | Lily | 1 | 0.431 | . | 0.431 | 0.431 |
| | Mega | 38 | 0.418 | 0.187 | 0.107 | 0.723 |
| | Molly | 3 | 0.394 | 0.134 | 0.298 | 0.546 |
| | Novi | 3 | 0.533 | 0.249 | 0.245 | 0.685 |
| | Pelet | 25 | 0.454 | 0.204 | 0.086 | 0.785 |
| | Sara | 2 | 0.267 | 0.152 | 0.160 | 0.374 |
| | Sela | 8 | 0.544 | 0.211 | 0.190 | 0.804 |
| | Suci | 2 | 0.279 | 0.299 | 0.068 | 0.491 |
| | Tevi | 12 | 0.585 | 0.129 | 0.361 | 0.868 |
| | Una | 17 | 0.378 | 0.185 | 0.105 | 0.791 |
| | Yinta | 5 | 0.304 | 0.044 | 0.245 | 0.359 |
| Adult males | Agus | 2 | 0.690 | 0.073 | 0.638 | 0.741 |
| | Arno | 86 | 0.479 | 0.205 | 0.023 | 0.872 |
| | Budi | 6 | 0.469 | 0.180 | 0.163 | 0.646 |
| | Caca | 2 | 0.802 | 0.013 | 0.792 | 0.811 |
| | David | 2 | 0.632 | 0.102 | 0.560 | 0.704 |
| | Hotma | 5 | 0.614 | 0.121 | 0.490 | 0.812 |
| | Luwi | 3 | 0.397 | 0.197 | 0.207 | 0.600 |
| | Mack | 5 | 0.337 | 0.207 | 0.198 | 0.701 |
| | Mukson | 5 | 0.484 | 0.116 | 0.324 | 0.650 |
| | Ngon | 3 | 0.453 | 0.149 | 0.331 | 0.619 |
| | Olly | 6 | 0.436 | 0.263 | 0.194 | 0.859 |
| | Tomi* | 1 | 0.049 | . | 0.049 | 0.049 |

Appendix 2 continued.

| Class | Name | Number of nest to nest follows | Mean ratio (Distance / Djl) | SD | Minimum ratio | Maximum ratio |
|---|---|---|---|---|---|---|
| Subadult females | Becky* | 8 | 0.504 | 0.195 | 0.149 | 0.780 |
| | Eva | 1 | 0.525 | . | 0.525 | 0.525 |
| | Gama | 3 | 0.508 | 0.274 | 0.200 | 0.722 |
| | Lena | 5 | 0.515 | 0.223 | 0.218 | 0.760 |
| | Tina | 1 | 0.356 | . | 0.356 | 0.356 |
| Subadult males | Dio | 19 | 0.371 | 0.139 | 0.076 | 0.599 |
| | Fin | 1 | 0.582 | . | 0.582 | 0.582 |
| | Koen | 3 | 0.193 | 0.062 | 0.125 | 0.245 |
| | Lito | 4 | 0.537 | 0.205 | 0.308 | 0.771 |
| | Musa | 5 | 0.535 | 0.093 | 0.447 | 0.683 |
| | Oloan | 4 | 0.422 | 0.198 | 0.268 | 0.689 |
| | Robert | 5 | 0.298 | 0.253 | 0.041 | 0.627 |
| | Stan | 1 | 0.426 | . | 0.426 | 0.426 |
| | Syawal | 9 | 0.288 | 0.136 | 0.094 | 0.503 |
| | Tomi* | 20 | 0.424 | 0.126 | 0.111 | 0.633 |
| All orangutans | All | 657 | 0.424 | 0.190 | 0.000 | 0.872 |

**APPENDIX 3**: Percentage of monthly orangutan diet comprised of the main food types. Unidentified food items and water excluded from all calculations. Other includes several miscellaneous items, i.e. roots, fungi and animal matter.

| Month | No. of follows | Sum of duration (h:m:s) | No. of feeding records | Fruit | Non-fruit | Young leaves | Flowers | Insects | Stems | Bark | Other |
|---|---|---|---|---|---|---|---|---|---|---|---|
| M | 12 | 139:48:00 | 2498 | 81.665 | 18.335 | 4.524 | 0.160 | 8.006 | 4.163 | 1.441 | 0.040 |
| J | 4 | 45:20:00 | 748 | 64.572 | 35.428 | 3.209 | 0.000 | 27.273 | 4.144 | 0.134 | 0.668 |
| J | 15 | 179:06:00 | 2842 | 83.392 | 16.608 | 1.513 | 0.000 | 9.887 | 5.032 | 0.070 | 0.106 |
| A | 13 | 151:46:00 | 1914 | 72.518 | 27.482 | 3.710 | 0.052 | 19.958 | 2.926 | 0.052 | 0.784 |
| S | 12 | 127:40:00 | 2390 | 66.485 | 33.515 | 15.021 | 0.000 | 11.255 | 7.238 | 0.000 | 0.000 |
| O | 3 | 32:24:00 | 649 | 61.633 | 38.367 | 6.780 | 0.000 | 10.478 | 7.704 | 0.000 | 13.405 |
| N | 14 | 143:36:00 | 2606 | 52.302 | 47.698 | 11.857 | 0.000 | 22.064 | 7.214 | 6.562 | 0.000 |
| D | 9 | 99:32:00 | 1876 | 72.708 | 27.292 | 9.435 | 0.000 | 11.194 | 6.290 | 0.373 | 0.000 |
| J | 10 | 106:56:00 | 1657 | 44.840 | 55.100 | 27.278 | 0.000 | 9.777 | 5.673 | 12.432 | 0.000 |
| F | 10 | 113:20:00 | 1955 | 81.330 | 18.670 | 9.258 | 0.102 | 3.325 | 4.194 | 1.790 | 0.000 |
| M | 22 | 247:36:00 | 3869 | 79.633 | 20.315 | 8.142 | 0.000 | 2.378 | 3.670 | 6.100 | 0.078 |
| A | 5 | 56:02:00 | 926 | 67.063 | 32.937 | 11.231 | 0.000 | 15.551 | 6.156 | 0.000 | 0.000 |
| M | 9 | 98:36:00 | 1621 | 63.479 | 36.151 | 13.263 | 0.247 | 6.909 | 9.315 | 5.737 | 1.049 |
| J | 16 | 174:54:00 | 3024 | 24.669 | 75.165 | 31.746 | 12.335 | 14.021 | 5.556 | 11.045 | 0.628 |
| J | 11 | 124:18:00 | 2331 | 50.794 | 49.206 | 17.975 | 1.544 | 20.635 | 8.623 | 0.429 | 0.000 |
| A | 4 | 44:50:00 | 866 | 56.697 | 42.725 | 14.896 | 0.000 | 16.282 | 6.813 | 5.312 | 0.000 |
| S | 1 | 10:52:00 | 221 | 60.181 | 39.819 | 4.977 | 0.000 | 28.507 | 6.335 | 0.000 | 0.000 |
| MEAN |  | 111:33:53 | 1881.941 | 63.763 | 36.165 | 11.460 | 0.849 | 13.971 | 5.944 | 3.028 | 3.028 |
| SE |  | 61:02:11 | 973.837 | 15.197 | 15.153 | 8.258 | 2.983 | 7.651 | 1.782 | 4.090 | 4.090 |
| MIN |  | 10:52:00 | 221 | 24.669 | 16.608 | 1.513 | 0.000 | 2.378 | 2.926 | 0.000 | 0.000 |
| MAX |  | 247:36:00 | 3869 | 83.392 | 75.165 | 31.746 | 12.335 | 28.507 | 9.315 | 12.432 | 13.405 |

**APPENDIX 4**: Percentage representation of tree and liana species constituting at least 5% of the fruit part of orangutan diets (in WCS study area), in at least one month (unidentified species and species not represented in any plots excluded).

| Month | No. of follows | Total fruit time | Malaka | Puwin | Sepang | Kuli batu | Resak | Kayu kapur | Durian | Cempedak | Tampu licin | Cemengang | Pala hutan kecil |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M | 12 | 2040 | 13.088 | 0.000 | 2.108 | 0.000 | 0.000 | 58.039 | 8.039 | 0.539 | 0.000 | 0.000 | 0.000 |
| J | 4 | 483 | 65.217 | 0.000 | 2.899 | 0.000 | 0.000 | 14.079 | 6.625 | 10.973 | 0.000 | 0.000 | 0.000 |
| J | 15 | 2370 | 14.895 | 6.962 | 0.000 | 0.000 | 0.000 | 7.679 | 1.561 | 4.768 | 37.046 | 0.169 | 0.084 |
| A | 13 | 1388 | 27.233 | 41.210 | 2.233 | 2.305 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 2.522 |
| S | 12 | 1589 | 23.348 | 1.196 | 4.909 | 0.378 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 34.928 |
| O | 3 | 400 | 34.500 | 0.000 | 26.250 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| N | 14 | 1363 | 49.376 | 19.222 | 1.761 | 0.000 | 0.147 | 0.000 | 0.000 | 5.869 | 0.000 | 7.777 | 0.000 |
| D | 9 | 1364 | 39.443 | 50.953 | 9.384 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| J | 10 | 743 | 39.300 | 5.922 | 3.634 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 12.786 | 0.000 |
| F | 10 | 1590 | 7.296 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 73.836 | 0.000 |
| M | 22 | 3073 | 11.455 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 73.350 | 0.000 |
| A | 5 | 621 | 41.546 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 40.902 | 0.000 |
| M | 9 | 1029 | 22.643 | 0.000 | 0.292 | 36.929 | 0.000 | 0.000 | 0.000 | 0.000 | 0.194 | 14.869 | 0.000 |
| J | 16 | 746 | 61.662 | 0.000 | 0.000 | 0.536 | 0.000 | 0.000 | 0.000 | 1.340 | 0.000 | 0.000 | 0.000 |
| J | 11 | 1184 | 94.341 | 0.338 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 3.125 | 0.000 | 0.000 | 0.000 |
| A | 4 | 491 | 84.521 | 0.000 | 0.000 | 0.000 | 15.479 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| S | 1 | 133 | 48.872 | 0.000 | 4.511 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

Appendix 4 continued.

| Month | Peradah | Bunga Piring | Ubar | Kayu Kacang | Ketapang | Jambu air | Mangga hutan | Tapis batu | Resak payo | medang kersik | Resak ubar |
|---|---|---|---|---|---|---|---|---|---|---|---|
| M | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 8.480 |
| J | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| J | 0.084 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| A | 0.000 | 10.879 | 1.297 | 4.827 | 0.000 | 0.000 | 0.000 | 0.000 | 1.441 | 0.000 | 0.000 |
| S | 5.916 | 0.000 | 1.070 | 10.950 | 0.000 | 0.000 | 0.000 | 0.189 | 15.733 | 0.000 | 0.000 |
| O | 6.000 | 0.000 | 18.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 11.500 | 0.000 |
| N | 1.174 | 5.503 | 5.282 | 0.514 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.541 | 0.000 |
| D | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| J | 2.826 | 0.000 | 0.000 | 0.000 | 0.135 | 0.135 | 3.365 | 0.000 | 0.000 | 0.000 | 0.000 |
| F | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 13.459 | 5.157 | 0.000 | 0.000 | 0.000 |
| M | 0.000 | 0.000 | 0.000 | 0.000 | 0.390 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| A | 0.000 | 0.000 | 0.000 | 0.000 | 6.119 | 7.890 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| M | 0.000 | 0.000 | 0.000 | 0.000 | 8.260 | 5.831 | 0.000 | 0.680 | 0.000 | 0.000 | 0.000 |
| J | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.134 | 0.000 | 0.000 |
| J | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| A | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| S | 0.000 | 0.000 | 0.000 | 46.617 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

**APPENDIX 5**: Raw values of phenology indices for each site (as percentages), before conversion to proportions and arcsine transformation.

| GB | >5% of diet spp. | >5% of diet spp. | Dominant species | Dominant species | All species | All species | All species | All species |
|---|---|---|---|---|---|---|---|---|
| Month | All fruit | Ripening fruit | All fruit | Ripening fruit | All fruit | Flowers | Ripening fruit | Young leaves |
| M | | | | | | | | |
| A | | | | | | | | |
| M | 7.647 | 0.000 | 16.393 | 0.000 | 10.484 | 8.602 | 0.269 | 3.919 |
| J | 8.824 | 0.588 | 21.311 | 1.639 | 10.753 | 6.989 | 0.538 | 2.849 |
| J | 7.647 | 4.118 | 19.672 | 11.475 | 9.140 | 11.828 | 6.183 | 2.223 |
| A | 10.588 | 5.882 | 21.311 | 16.393 | 12.366 | 5.914 | 8.871 | 2.121 |
| S | 10.588 | 9.412 | 18.033 | 16.393 | 12.097 | 5.645 | 10.753 | 2.056 |
| O | 8.235 | 5.882 | 18.033 | 11.475 | 11.321 | 7.817 | 8.625 | 4.930 |
| N | 7.101 | 2.959 | 19.672 | 8.197 | 11.622 | 10.811 | 6.486 | 9.308 |
| D | 9.467 | 4.734 | 24.590 | 11.475 | 12.703 | 5.946 | 7.027 | 8.927 |
| J | 5.325 | 5.325 | 14.754 | 14.754 | 10.541 | 4.865 | 8.378 | 6.078 |
| F | 5.325 | 0.000 | 14.754 | 0.000 | 6.757 | 3.243 | 3.514 | 2.719 |
| M | 5.325 | 4.734 | 14.754 | 13.115 | 7.297 | 9.730 | 5.676 | 4.500 |
| A | 5.325 | 0.000 | 14.754 | 0.000 | 7.609 | 13.315 | 3.533 | 3.916 |
| M | 13.018 | 5.325 | 16.393 | 0.000 | 11.685 | 8.424 | 6.522 | 2.264 |
| J | 6.509 | 4.142 | 16.393 | 9.836 | 9.783 | 8.967 | 7.609 | 2.655 |
| J | 7.738 | 2.381 | 15.000 | 6.667 | 9.836 | 7.377 | 4.645 | 2.943 |
| A | 7.831 | 4.819 | 16.667 | 10.000 | 10.165 | 7.692 | 7.143 | 4.165 |
| S | 11.446 | 6.024 | 23.333 | 11.667 | 12.088 | 9.615 | 7.692 | 4.841 |

| HJP -LX | >5% of diet spp. | >5% of diet spp. | Dominant species | Dominant species | All species | All species | All species | All species |
|---|---|---|---|---|---|---|---|---|
| Month | All fruit | Ripening fruit | All fruit | Ripening fruit | All fruit | Flowers | Ripening fruit | Young leaves |
| M | | | | | 11.300 | 8.700 | 3.190 | 5.560 |
| A | | | | | 9.280 | 2.030 | 1.740 | 4.170 |
| M | 9.467 | 0.000 | 14.085 | 0.000 | 9.860 | 10.430 | 1.450 | 2.400 |
| J | 17.857 | 7.143 | 32.394 | 16.901 | 15.120 | 7.560 | 7.850 | 2.430 |
| J | 17.262 | 10.119 | 32.394 | 23.944 | 16.570 | 8.140 | 10.470 | 2.480 |
| A | 13.690 | 7.143 | 22.535 | 12.676 | 14.830 | 3.200 | 8.430 | 1.780 |
| S | 9.581 | 6.587 | 12.676 | 5.634 | 11.730 | 4.400 | 10.260 | 4.770 |
| O | 7.186 | 2.994 | 9.859 | 1.408 | 10.230 | 3.510 | 6.730 | 8.790 |
| N | 7.831 | 1.205 | 12.676 | 0.000 | 8.800 | 5.280 | 4.110 | 8.400 |
| D | 9.036 | 1.205 | 16.901 | 1.408 | 9.380 | 4.110 | 3.230 | 4.440 |
| J | 6.627 | 1.205 | 9.859 | 2.817 | 7.920 | 5.280 | 2.930 | 4.140 |
| F | 5.422 | 2.410 | 9.859 | 4.225 | 8.800 | 3.520 | 4.110 | 5.410 |
| M | 4.217 | 1.807 | 7.042 | 2.817 | 7.920 | 4.400 | 3.230 | 4.460 |
| A | 7.879 | 1.212 | 8.451 | 2.817 | 9.120 | 4.120 | 3.820 | 1.980 |
| M | 7.879 | 3.030 | 8.451 | 1.408 | 7.650 | 5.880 | 3.820 | 2.240 |
| J | 7.879 | 0.606 | 12.676 | 1.408 | 7.940 | 5.590 | 2.940 | 3.900 |
| J | 9.697 | 3.636 | 11.268 | 7.042 | 7.940 | 5.290 | 3.240 | 4.040 |
| A | 11.515 | 4.848 | 14.085 | 7.042 | 11.470 | 10.000 | 3.820 | 4.410 |
| S | 13.253 | 4.217 | 18.310 | 4.225 | 12.610 | 8.500 | 4.400 | 4.070 |

Appendix 5 continued.

| HILL Month | >5% of diet spp. All fruit | >5% of diet spp. Ripening fruit | Dominant species All fruit | Dominant species Ripening fruit | All species All fruit | All species Flowers | All species Ripening fruit | All species Young leaves |
|---|---|---|---|---|---|---|---|---|
| M | | | | | 9.200 | 3.980 | 0.000 | 3.260 |
| A | | | | | 10.500 | 3.560 | 0.000 | 4.690 |
| M | 25.806 | 12.903 | 29.630 | 14.815 | 10.100 | 2.730 | 1.260 | 1.790 |
| J | 9.677 | 9.677 | 11.111 | 11.111 | 10.500 | 0.630 | 8.160 | 1.240 |
| J | 6.452 | 6.452 | 7.407 | 7.407 | 10.100 | 1.890 | 8.810 | 1.530 |
| A | 3.226 | 3.226 | 3.704 | 3.704 | 8.200 | 1.260 | 6.280 | 1.890 |
| S | 0.000 | 0.000 | 0.000 | 0.000 | 3.300 | 2.300 | 1.670 | 1.980 |
| O | 0.000 | 0.000 | 0.000 | 0.000 | 2.700 | 1.890 | 1.050 | 5.580 |
| N | 0.000 | 0.000 | 0.000 | 0.000 | 2.700 | 2.310 | 1.680 | 4.460 |
| D | 0.000 | 0.000 | 0.000 | 0.000 | 2.500 | 2.300 | 1.260 | 2.920 |
| J | 0.000 | 0.000 | 0.000 | 0.000 | 2.300 | 1.260 | 1.680 | 2.150 |
| F | 0.000 | 0.000 | 0.000 | 0.000 | 2.500 | 1.260 | 1.470 | 3.610 |
| M | 0.000 | 0.000 | 0.000 | 0.000 | 1.940 | 1.500 | 0.640 | 5.120 |
| A | 0.000 | 0.000 | 0.000 | 0.000 | 1.940 | 1.080 | 1.300 | 3.770 |
| M | 6.452 | 0.000 | 7.407 | 0.000 | 2.380 | 1.950 | 0.650 | 2.460 |
| J | 3.226 | 0.000 | 3.704 | 0.000 | 3.030 | 2.380 | 1.300 | 2.890 |
| J | 3.333 | 3.333 | 3.846 | 3.846 | 5.490 | 2.420 | 1.760 | 3.580 |
| A | 0.000 | 0.000 | 0.000 | 0.000 | 4.840 | 1.100 | 2.860 | 4.670 |
| S | 6.667 | 0.000 | 7.692 | 0.000 | 2.190 | 1.530 | 0.880 | 3.100 |

| IB Month | >5% of diet spp. All fruit | >5% of diet spp. Ripening fruit | Dominant species All fruit | Dominant species Ripening fruit | All species All fruit | All species Flowers | All species Ripening fruit | All species Young leaves |
|---|---|---|---|---|---|---|---|---|
| M | | | | | 10.000 | 14.063 | 0.625 | 4.191 |
| A | | | | | 10.972 | 19.749 | 0.000 | 6.567 |
| M | 20.000 | 1.143 | 14.545 | 3.636 | 22.884 | 10.972 | 1.254 | 4.063 |
| J | 18.857 | 2.286 | 12.727 | 5.455 | 17.868 | 7.210 | 1.254 | 2.796 |
| J | 14.368 | 3.448 | 12.727 | 5.455 | 14.465 | 11.006 | 6.289 | 1.994 |
| A | 17.241 | 11.494 | 9.091 | 5.455 | 15.723 | 8.805 | 10.692 | 1.821 |
| S | 12.644 | 6.322 | 9.091 | 1.818 | 12.303 | 11.041 | 7.256 | 3.801 |
| O | | | | | | | | |
| N | | | | | | | | |
| D | | | | | | | | |
| J | | | | | | | | |
| F | | | | | | | | |
| M | | | | | | | | |
| A | | | | | | | | |
| M | | | | | | | | |
| J | | | | | | | | |
| J | | | | | | | | |
| A | | | | | | | | |
| S | | | | | | | | |

Appendix 5 continued.

| SM | >5% of diet spp. | >5% of diet spp. | Dominant species | Dominant species | All species | All species | All species | All species |
|---|---|---|---|---|---|---|---|---|
| Month | All fruit | Ripening fruit | All fruit | Ripening fruit | All fruit | Flowers | Ripening fruit | Young leaves |
| M | | | | | 6.863 | 9.559 | 2.941 | 3.696 |
| A | | | | | 6.388 | 10.319 | 0.246 | 6.791 |
| M | 9.000 | 0.000 | 18.333 | 0.000 | 9.606 | 9.113 | 0.246 | 3.325 |
| J | 11.500 | 0.000 | 20.000 | 0.000 | 10.864 | 6.667 | 0.247 | 2.067 |
| J | 11.500 | 1.500 | 20.000 | 3.333 | 10.370 | 6.667 | 4.444 | 2.543 |
| A | 13.500 | 7.500 | 25.000 | 21.667 | 10.617 | 2.716 | 7.160 | 1.640 |
| S | 10.000 | 7.500 | 16.667 | 13.333 | 8.889 | 3.457 | 6.667 | 1.516 |
| O | 12.429 | 9.040 | 23.684 | 15.789 | 9.406 | 7.178 | 7.426 | 3.859 |
| N | 7.345 | 2.260 | 23.684 | 0.000 | 8.168 | 4.950 | 4.208 | 10.473 |
| D | 5.114 | 1.136 | 23.684 | 5.263 | 7.711 | 2.488 | 4.229 | 7.699 |
| J | 3.977 | 1.705 | 18.421 | 7.895 | 5.970 | 2.488 | 4.229 | 3.863 |
| F | 2.857 | 0.571 | 5.263 | 0.000 | 4.478 | 3.234 | 3.483 | 4.117 |
| M | 2.857 | 2.857 | 5.263 | 5.263 | 4.489 | 12.219 | 3.990 | 4.641 |
| A | 14.368 | 1.149 | 2.632 | 0.000 | 10.750 | 13.500 | 4.000 | 3.298 |
| M | 24.138 | 16.667 | 10.526 | 0.000 | 13.854 | 9.068 | 9.824 | 2.378 |
| J | 6.358 | 0.000 | 10.811 | 0.000 | 6.566 | 12.879 | 2.273 | 3.043 |
| J | 12.791 | 1.163 | 16.216 | 5.405 | 9.645 | 6.853 | 3.299 | 2.312 |
| A | 13.953 | 3.488 | 18.919 | 5.405 | 9.137 | 6.853 | 3.553 | 2.107 |
| S | 18.605 | 6.395 | 24.324 | 10.811 | 11.929 | 8.122 | 5.330 | 3.033 |

| X | >5% of diet spp. | >5% of diet spp. | Dominant species | Dominant species | All species | All species | All species | All species |
|---|---|---|---|---|---|---|---|---|
| Month | All fruit | Ripening fruit | All fruit | Ripening fruit | All fruit | Flowers | Ripening fruit | Young leaves |
| M | | | | | 12.000 | 5.870 | 4.110 | 4.870 |
| A | | | | | 9.700 | 10.290 | 2.940 | 6.010 |
| M | 11.386 | 2.475 | 25.373 | 7.463 | 11.800 | 9.700 | 2.060 | 2.790 |
| J | 12.376 | 6.436 | 26.866 | 14.925 | 12.980 | 8.260 | 9.140 | 2.490 |
| J | 14.356 | 8.416 | 28.358 | 20.896 | 14.200 | 10.950 | 10.060 | 1.660 |
| A | 17.822 | 11.881 | 32.836 | 26.866 | 15.700 | 6.510 | 11.540 | 1.690 |
| S | 9.406 | 3.465 | 17.910 | 7.463 | 10.700 | 6.210 | 5.920 | 4.330 |
| O | 9.406 | 3.960 | 14.925 | 2.985 | 10.700 | 6.210 | 5.620 | 7.910 |
| N | 8.911 | 2.970 | 19.403 | 1.493 | 10.400 | 6.800 | 5.330 | 9.900 |
| D | 11.386 | 4.455 | 25.373 | 10.448 | 11.800 | 5.620 | 6.510 | 5.150 |
| J | 6.436 | 0.990 | 13.433 | 1.493 | 8.000 | 3.850 | 4.140 | 4.710 |
| F | 5.941 | 2.970 | 11.940 | 5.970 | 7.700 | 6.210 | 5.920 | 6.720 |
| M | 8.911 | 1.980 | 14.925 | 2.985 | 10.100 | 9.470 | 5.330 | 3.930 |
| A | 14.356 | 0.000 | 14.925 | 0.000 | 13.300 | 8.260 | 4.130 | 2.450 |
| M | 12.376 | 6.436 | 14.925 | 1.493 | 10.950 | 5.030 | 7.100 | 2.000 |
| J | 7.921 | 2.970 | 13.433 | 5.970 | 7.400 | 6.210 | 4.440 | 3.720 |
| J | 9.453 | 3.483 | 13.433 | 8.955 | 9.800 | 8.060 | 4.740 | 3.880 |
| A | 12.935 | 3.980 | 22.388 | 8.955 | 11.570 | 6.530 | 5.040 | 2.740 |
| S | 15.075 | 2.513 | 24.242 | 7.576 | 11.940 | 12.540 | 2.990 | 4.020 |

**APPENDIX 6**: Observed proportion of female's total follow time (follows > 3 hours) spent with each of the other females ($L_i$). Focal individual down the left. $L_{ij}$ = sum for all females i to j.

| Focal | No. of follows | Total follow duration (h:m:s) | Abby | Ani | Becky | Butet | Diana | Hanes |
|---|---|---|---|---|---|---|---|---|
| Abby | 128 | 1239:26:00 | 0.000 | 0.019 | 0.026 | 0.000 | 0.029 | 0.000 |
| Ani | 234 | 2208:19:00 | 0.019 | 0.000 | 0.016 | 0.005 | 0.006 | 0.004 |
| Becky | 49 | 376:02:00 | 0.050 | 0.043 | 0.000 | 0.000 | 0.053 | 0.000 |
| Butet | 28 | 263:02:00 | 0.002 | 0.022 | 0.000 | 0.000 | 0.086 | 0.115 |
| Diana | 118 | 1140:07:00 | 0.005 | 0.006 | 0.031 | 0.015 | 0.000 | 0.000 |
| Hanes | 32 | 299:14:00 | 0.000 | 0.036 | 0.000 | 0.182 | 0.002 | 0.000 |
| Karen | 12 | 101:52:00 | 0.199 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Mega | 81 | 766:30:00 | 0.013 | 0.088 | 0.000 | 0.101 | 0.000 | 0.042 |
| Pelet | 46 | 429:09:00 | 0.004 | 0.024 | 0.011 | 0.011 | 0.000 | 0.000 |
| Sela | 27 | 203:53:00 | 0.021 | 0.013 | 0.021 | 0.000 | 0.000 | 0.011 |
| Tevi | 41 | 327:56:00 | 0.001 | 0.089 | 0.001 | 0.021 | 0.001 | 0.037 |
| Una | 56 | 446:56:00 | 0.039 | 0.007 | 0.007 | 0.000 | 0.004 | 0.000 |

| Focal | Karen | Mega | Pelet | Sela | Tevi | Una | All parties with females ($L_{ij}$) | All parties with all orangutans |
|---|---|---|---|---|---|---|---|---|
| Abby | 0.014 | 0.012 | 0.000 | 0.007 | 0.001 | 0.014 | 0.123 | 0.339 |
| Ani | 0.002 | 0.028 | 0.002 | 0.003 | 0.014 | 0.006 | 0.105 | 0.970 |
| Becky | 0.000 | 0.000 | 0.000 | 0.010 | 0.000 | 0.003 | 0.158 | 0.869 |
| Butet | 0.000 | 0.310 | 0.000 | 0.030 | 0.022 | 0.000 | 0.588 | 1.622 |
| Diana | 0.000 | 0.000 | 0.000 | 0.000 | 0.007 | 0.002 | 0.067 | 0.116 |
| Hanes | 0.000 | 0.259 | 0.000 | 0.000 | 0.029 | 0.000 | 0.509 | 1.445 |
| Karen | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.199 | 0.347 |
| Mega | 0.000 | 0.000 | 0.000 | 0.027 | 0.002 | 0.011 | 0.284 | 1.234 |
| Pelet | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.013 | 0.064 | 0.154 |
| Sela | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.008 | 0.074 | 0.618 |
| Tevi | 0.000 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | 0.152 | 0.424 |
| Una | 0.000 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | 0.057 | 0.558 |

**APPENDIX 7**: Observed proportion of focal females polygon range within the WCS study area range (size of which is given by 'Area'), shared with that of other females ($Q_i$). Sum over all females = $Q_{ij}$.

| Focal | Area (ha) | Abby | Ani | Becky | Butet | Diana | Hanes |
|---|---|---|---|---|---|---|---|
| Abby | 169.1907 | 0.000 | 0.998 | 0.819 | 0.963 | 0.596 | 0.880 |
| Ani | 423.4463 | 0.399 | 0.000 | 0.428 | 0.941 | 0.344 | 0.920 |
| Becky | 185.053 | 0.748 | 0.980 | 0.000 | 0.953 | 0.784 | 0.954 |
| Butet | 405.1915 | 0.402 | 0.984 | 0.435 | 0.000 | 0.358 | 0.948 |
| Diana | 150.1349 | 0.672 | 0.972 | 0.967 | 0.967 | 0.000 | 0.916 |
| Hanes | 395.075 | 0.377 | 0.986 | 0.447 | 0.973 | 0.348 | 0.000 |
| Karen | 158.6066 | 0.702 | 0.994 | 0.760 | 1.000 | 0.445 | 0.989 |
| Mega | 389.9797 | 0.371 | 0.929 | 0.344 | 0.894 | 0.239 | 0.883 |
| Pelet | 114.4459 | 0.466 | 0.978 | 0.724 | 0.950 | 0.846 | 0.949 |
| Sela | 268.4402 | 0.514 | 1.000 | 0.559 | 0.997 | 0.451 | 0.993 |
| Tevi | 320.5177 | 0.462 | 0.995 | 0.563 | 0.949 | 0.447 | 0.969 |
| Una | 262.4946 | 0.460 | 0.997 | 0.561 | 0.999 | 0.453 | 1.000 |

| Focal | Karen | Mega | Pelet | Sela | Tevi | Una | Sum (Qij) |
|---|---|---|---|---|---|---|---|
| Abby | 0.658 | 0.856 | 0.316 | 0.816 | 0.875 | 0.714 | 8.489 |
| Ani | 0.372 | 0.856 | 0.264 | 0.634 | 0.753 | 0.618 | 6.531 |
| Becky | 0.652 | 0.724 | 0.448 | 0.810 | 0.975 | 0.795 | 8.825 |
| Butet | 0.392 | 0.861 | 0.268 | 0.660 | 0.751 | 0.647 | 6.707 |
| Diana | 0.471 | 0.620 | 0.645 | 0.806 | 0.954 | 0.791 | 8.780 |
| Hanes | 0.397 | 0.871 | 0.275 | 0.674 | 0.786 | 0.667 | 6.800 |
| Karen | 0.000 | 0.937 | 0.197 | 0.778 | 0.981 | 0.864 | 8.647 |
| Mega | 0.381 | 0.000 | 0.168 | 0.605 | 0.678 | 0.581 | 6.074 |
| Pelet | 0.273 | 0.572 | 0.000 | 0.771 | 0.976 | 0.818 | 8.324 |
| Sela | 0.460 | 0.879 | 0.329 | 0.000 | 0.885 | 0.866 | 7.932 |
| Tevi | 0.485 | 0.825 | 0.349 | 0.741 | 0.000 | 0.787 | 7.573 |
| Una | 0.522 | 0.864 | 0.357 | 0.886 | 0.961 | 0.000 | 8.059 |

**APPENDIX 8**: Expected proportion of time focal females should associate with other females ($A_{oi}$) based on the proportion of polygon range overlap within the WCS study area.

|  | Associate: |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Focal | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
| Abby |  | 0.015 | 0.012 | 0.014 | 0.009 | 0.013 | 0.010 | 0.012 | 0.005 | 0.012 | 0.013 | 0.010 |
| Ani | 0.006 |  | 0.007 | 0.015 | 0.006 | 0.015 | 0.006 | 0.014 | 0.004 | 0.010 | 0.012 | 0.010 |
| Becky | 0.013 | 0.018 |  | 0.017 | 0.014 | 0.017 | 0.012 | 0.013 | 0.008 | 0.015 | 0.017 | 0.014 |
| Butet | 0.035 | 0.086 | 0.038 |  | 0.031 | 0.083 | 0.034 | 0.076 | 0.024 | 0.058 | 0.066 | 0.057 |
| Diana | 0.005 | 0.007 | 0.007 | 0.007 |  | 0.007 | 0.004 | 0.005 | 0.005 | 0.006 | 0.007 | 0.006 |
| Hanes | 0.028 | 0.074 | 0.033 | 0.073 | 0.026 |  | 0.030 | 0.065 | 0.021 | 0.050 | 0.059 | 0.050 |
| Karen | 0.016 | 0.023 | 0.017 | 0.023 | 0.010 | 0.023 |  | 0.022 | 0.005 | 0.018 | 0.023 | 0.020 |
| Mega | 0.017 | 0.043 | 0.016 | 0.042 | 0.011 | 0.041 | 0.018 |  | 0.008 | 0.028 | 0.032 | 0.027 |
| Pelet | 0.004 | 0.007 | 0.006 | 0.007 | 0.006 | 0.007 | 0.002 | 0.004 |  | 0.006 | 0.007 | 0.006 |
| Sela | 0.005 | 0.009 | 0.005 | 0.009 | 0.004 | 0.009 | 0.004 | 0.008 | 0.003 |  | 0.008 | 0.008 |
| Tevi | 0.009 | 0.020 | 0.011 | 0.019 | 0.009 | 0.019 | 0.010 | 0.017 | 0.007 | 0.015 |  | 0.016 |
| Una | 0.003 | 0.007 | 0.004 | 0.007 | 0.003 | 0.007 | 0.004 | 0.006 | 0.003 | 0.006 | 0.007 |  |

**APPENDIX 9**: Observed proportion of time each focal individual spent with each other ($L_i$, from Appendix 6) divided by the expected proportion ($A_{oi}$ from Appendix 8).

| Focal | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby |  | 1.336 | 2.219 | 0.016 | 3.347 | 0 | 1.515 | 0.998 | 0 | 0.553 | 0.061 | 1.362 |
| Ani | 3.022 |  | 2.296 | 0.327 | 1.029 | 0.3 | 0.252 | 2.063 | 0.405 | 0.306 | 1.195 | 0.556 |
| Becky | 3.695 | 2.46 |  | 0 | 3.739 | 0 | 0 | 0 | 0 | 0.68 | 0 | 0.205 |
| Butet | 0.07 | 0.261 | 0 |  | 2.746 | 1.386 | 0 | 4.104 | 0 | 0.51 | 0.341 | 0 |
| Diana | 0.922 | 0.838 | 4.183 | 2.11 |  | 0 | 0 | 0 | 0 | 0 | 1.012 | 0.375 |
| Hanes | 0 | 0.489 | 0 | 2.507 | 0.073 |  | 0 | 3.976 | 0 | 0 | 0.497 | 0 |
| Karen | 12.33 | 0 | 0 | 0 | 0 | 0 |  | 0 | 0 | 0 | 0 | 0 |
| Mega | 0.742 | 2.015 | 0 | 2.413 | 0 | 1.024 | 0 |  | 0 | 0.936 | 0.078 | 0.42 |
| Pelet | 1.088 | 3.204 | 1.998 | 1.571 | 0 | 0 | 0 | 0 |  | 0 | 0 | 2.133 |
| Sela | 4.382 | 1.441 | 3.956 | 0 | 0 | 1.215 | 0 | 0 | 0 |  | 0 | 0.948 |
| Tevi | 0.143 | 4.488 | 0.099 | 1.093 | 0.131 | 1.895 | 0 | 0.065 | 0 | 0 |  | 0 |
| Una | 12.01 | 0.926 | 1.797 | 0 | 1.124 | 0 | 0 | 0 | 0 | 0.107 | 0 |  |

**APPENDIX 10**: Pairings of females for which association rates are higher than expected for both individuals i.e. reciprocated, in that values from Appendix 9 are greater than 1 for both pairings.

| Focal | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby |  | y | y |  |  |  | y |  |  |  |  | y |
| Ani |  |  | y |  |  |  |  | y |  |  | y |  |
| Becky |  |  |  |  | y |  |  |  |  |  |  |  |
| Butet |  |  |  |  | y | y |  | y |  |  |  |  |
| Diana |  |  |  |  |  |  |  |  |  |  |  |  |
| Hanes |  |  |  |  |  |  |  | y |  |  |  |  |
| Karen |  |  |  |  |  |  |  |  |  |  |  |  |
| Mega |  |  |  |  |  |  |  |  |  |  |  |  |
| Pelet |  |  |  |  |  |  |  |  |  |  |  |  |
| Sela |  |  |  |  |  |  |  |  |  |  |  |  |
| Tevi |  |  |  |  |  |  |  |  |  |  |  |  |
| Una |  |  |  |  |  |  |  |  |  |  |  |  |

**APPENDIX 11**: Observed number of months females were recorded as present in the study area during the same month, out of 48 months.

| Name | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby | 34 | 32 | 26 | 10 | 23 | 10 | 13 | 17 | 11 | 11 | 14 | 22 |
| Ani |  | 43 | 30 | 15 | 28 | 15 | 16 | 25 | 15 | 15 | 16 | 24 |
| Becky |  |  | 34 | 12 | 23 | 9 | 15 | 22 | 12 | 14 | 15 | 20 |
| Butet |  |  |  | 16 | 9 | 7 | 7 | 12 | 4 | 6 | 6 | 6 |
| Diana |  |  |  |  | 31 | 9 | 13 | 19 | 6 | 12 | 11 | 20 |
| Hanes |  |  |  |  |  | 16 | 5 | 13 | 7 | 4 | 8 | 11 |
| Karen |  |  |  |  |  |  | 17 | 10 | 2 | 10 | 5 | 10 |
| Mega |  |  |  |  |  |  |  | 30 | 13 | 10 | 14 | 14 |
| Pelet |  |  |  |  |  |  |  |  | 16 | 1 | 8 | 8 |
| Sela |  |  |  |  |  |  |  |  |  | 16 | 4 | 11 |
| Tevi |  |  |  |  |  |  |  |  |  |  | 20 | 10 |
| Una |  |  |  |  |  |  |  |  |  |  |  | 26 |

**APPENDIX 12**: Expected number of months females should be present simultaneously ($S_{exp}$), out of 48 months if regular ranges are 500 ha.

| Name | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby | | 13.755 | 6.011 | 13.162 | 4.877 | 12.834 | 5.152 | 12.668 | 3.718 | 8.720 | 10.412 | 8.527 |
| Ani | | | 15.045 | 32.943 | 12.206 | 32.120 | 12.895 | 31.706 | 9.305 | 21.825 | 26.059 | 21.341 |
| Becky | | | | 14.397 | 5.334 | 14.037 | 5.635 | 13.856 | 4.066 | 9.538 | 11.388 | 9.326 |
| Butet | | | | | 11.680 | 30.736 | 12.339 | 30.339 | 8.904 | 20.884 | 24.935 | 20.421 |
| Diana | | | | | | 11.388 | 4.572 | 11.242 | 3.299 | 7.738 | 9.239 | 7.567 |
| Hanes | | | | | | | 12.031 | 29.582 | 8.681 | 20.362 | 24.313 | 19.911 |
| Karen | | | | | | | | 11.876 | 3.485 | 8.175 | 9.761 | 7.994 |
| Mega | | | | | | | | | 8.569 | 20.100 | 23.999 | 19.655 |
| Pelet | | | | | | | | | | 5.899 | 7.043 | 5.768 |
| Sela | | | | | | | | | | | 16.520 | 13.529 |
| Tevi | | | | | | | | | | | | 16.154 |
| Una | | | | | | | | | | | | |

**APPENDIX 13**: Ratio of observed number of months present simultaneously divided by expected number ($S_{exp}$), out of 48 months, if regular ranges are 500 ha. Ratio shown only if greater than 1.

| Name | Abby | Ani | Becky | Butet | Diana | Hanes | Karen | Mega | Pelet | Sela | Tevi | Una |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abby | | 2.326 | 4.325 | | 4.716 | | 2.523 | 1.342 | 2.959 | 1.261 | 1.345 | 2.580 |
| Ani | | | 1.994 | | 2.294 | | 1.241 | | 1.612 | | | 1.125 |
| Becky | | | | | 4.312 | | 2.662 | 1.588 | 2.951 | 1.468 | 1.317 | 2.144 |
| Butet | | | | | | | | | | | | |
| Diana | | | | | | | 2.843 | 1.690 | 1.819 | 1.551 | 1.191 | 2.643 |
| Hanes | | | | | | | | | | | | |
| Karen | | | | | | | | | | 1.223 | | 1.251 |
| Mega | | | | | | | | | 1.517 | | | |
| Pelet | | | | | | | | | | | 1.136 | 1.387 |
| Sela | | | | | | | | | | | | |
| Tevi | | | | | | | | | | | | |
| Una | | | | | | | | | | | | |