ECOLOGY AND BEHAVIOUR OF *Tarsius syrichta* IN BOHOL, PHILIPPINES: IMPLICATIONS FOR CONSERVATION

By

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DEDICATION

To Niccolo and Marco
and the rest of the younger generations…
may you always hold in wonder, awe and respect the treasures of this beautiful planet
and embrace the opportunity to work for its preservation in your own time

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the Department of Applied and Molecular Ecology thesis collection following examination and correction, being available for loan and photocopying. Any reference of this thesis or the information contained therein must be fully acknowledged in any publication.

Irene Neri-Arboleda

ABSTRACT

The Philippine tarsier *Tarsius syrichta* is a small, nocturnal, insectivorous prosimian that is distributed in the islands of Leyte, Bohol, Samar, Maripipi, Dinagat, Siargao and Mindanao. It was first described in the late 17th century by J. G. Camel and the description was later published by Petiver in 1705 (Hill, 1955). The Philippine tarsier was described as a 'small monkey with big, round eyes that never or rarely closed; hairless ears; mouse-like fur and a tail and hindfeet as long as the rest of its body'. Its primary mode of locomotion is through vertical cling and leap, and the species is arboreal and cryptic in habits. There is limited knowledge of the species in captivity and very insufficient data on its ecology and behaviour in the wild.

The IUCN/SSC Primate Specialist Group has given *T. syrichta* a Conservation Priority rating 4, which defines the species as highly vulnerable (Eudey, 1987). The IUCN Red Data Book (2000) has further classified it under the Data deficient category. It was only in 1997 that *T. syrichta* was protected by law in the Philippines (PTFI, 1997). In order to implement an effective conservation plan for *T. syrichta*, a species whose landscape is becoming increasingly fragmented, it is important to understand its spatial and habitat requirements. In order to achieve this objective, a radio-tracking study was conducted in Corella, Bohol. The principal objectives of this study were: 1) to determine home range sizes and configurations and from which social group characteristics can be inferred from patterns of home range use; 2) to describe movements and activity patterns of the animal; 3) to examine habitat associations using vegetative cover and land use patterns; and 4) to evaluate conservation prospects of the species.

Home ranges, spatial movements and habitat utilisation patterns were determined for four male and six female Philippine tarsier *T. syrichta* in Corella, Bohol from early March-October 1999. The field site was a 174 ha area that has been proposed as a sanctuary for the Philippine tarsier and being developed for ecotourism activities. The forest itself forms a mosaic of different successional stages and adjacent to it are flat lands cultivated for agriculture. This was the first radiotracking study of the Philippine tarsier that included both breeding adult males and females. Home ranges were calculated using the Geographic Information Systems (GIS)/ Arcview 3.2 program extension Animal Movement Analyst

software package (Hooge and Eichenlaub, 1997). Home ranges averaged 6.45 ha for males and 2.45 ha for females (average for MCP and Kernel 95%), allowing for a density of 16-41 tarsiers per 100 hectares. The home range of one male overlapped extensively with that of one female and to a lesser extent that of a second female. Male home ranges (Kernel 95%) showed little overlap (2.71%) and the same had been observed among the females (3.35%). Nightly travel distance averaged 1,636 m for males and 1,119 m for females. Individuals were observed to forage and sleep solitarily. *T. syrichta* form groups of one adult male and one or two adult females and their offspring.

The study suggests that the social organisation of *T. syrichta* is polygynous, supported by the following factors: The overlapping home ranges between males and females, and the fact that paired males and females foraged apart and did not share the same sleeping site indicated opportunities for extra pair matings. No paternal care was observed during the study and males not investing in parental care duties can expend increased time and energy on intrasexual competition for resources and mates. Morphometric data indicated dimorphism in body size between males and females; there was a significant difference between male and female body weights, with males being larger than females (two-sample *t*-test, $P = 0.019$). Larger males increase their reproductive success by defending a larger territory that overlaps with that of multiple females, thereby maximizing the frequency of matings. The fragmented forest and the propensity of the tarsiers to forest edges suggested uneven spatial distribution of resources (arthropods) that encourages polygamy, as some individuals gain control over a larger quantity or better quality of resources.

The habitats utilised are primarily located in secondary lowland rainforest in early to mid succession stage, but individual tarsiers readily traversed narrow grassland areas to move in between forest patches. They also utilised shrubs, palm and bamboo. However, the tarsiers avoided, residential areas, adjacent clearings and agricultural plantations. The preference of *T. syrichta* for regrowth forest in early to mid succession stage indicates the importance of maintaining the cycle of regrowth of tropical rainforest in areas where tarsiers are known to inhabit, to provide adequate habitat for the species. This habitat preference further suggests that tarsier conservation is not incompatible with regulated exploitation of the forests' resources.

Chapter 1:

General Introduction

CHAPTER 1: GENERAL INTRODUCTION

1.1 Philippine Biodiversity

The Philippines is among the 12 top-priority countries for biodiversity conservation (Myers, 1988, Myers *et al.*, 2000). Species richness and exceptionally high endemism characterize its flora and fauna. These are mainly attributed to the tropical climate and the large number of islands (7,100) in the archipelago (Alcala, 1983; Heaney, 1986; Heaney and Regalado, 1998; Heaney *et al.*, 1998). The flora include an estimated 8,000 indigenous species of flowering plants and at least 3,200 of these are endemic to the Philippines (Fernando, 1988; Madulid, 1993,1994). The number of known endemic flowering and non-flowering plant species is 5,832 (Mittermeier, 1998).

Some of the vertebrates found only in the Philippines are the Philippine eagle (*Pithecophaga jefferyi)*, tamaraw (*Bubalus mindorensis*), Visayan spotted deer (*Cervus alfredi*), golden-crowned flying fox (*Acerodon jubatus*), northern slender tailed cloud rats (*Phloemys pallidus*) and the Philippine tarsier (*Tarsius syrichta*). A major concern for the survival status of these species in the wild is widespread habitat loss and degradation (Braatz *et al.*, 1992, Heaney, 1993, Wildlife Conservation Society of the Philippines, 1997). Surveys reveal that forest loss between 1969 and 1988 was on average 2,100 sq. km. or 2.5% per year (Collins *et al.*, 1991; Kummer, 1992; Kummer and Turner, 1994, Whitmore, 1997), three times the average for all other tropical rain forests. Pressure on remnant forests is brought about by a higher than average annual population growth rate of 2.4% (DENR/UNEP, 1998), weak enforcement of the total and selective log ban, lack of management plans for protected areas (Leonen and La Vina, 1994), shifting agriculture (Myers, 1980; 1988), loss of fertility, erosion of previously cleared land and destruction of watersheds (David, 1986). Less than 5% of the original primary forest cover of the Philippines remains (DENR/UNEP, 1998).

A crucial factor for implementing protective measures on Philippine biological diversity is the lack of public awareness and interest. Environment education needs to be incorporated in school curricula across the country. It is only during the past decade that more field biologists have undertaken research to gather information on the country's biological resources (Bagarinao, 1998; Heaney and Regalado, 1998). At present, there are still inadequate ecological data on several species.

The focus of this study is the Philippine tarsier (*Tarsius syrichta)*, a small, nocturnal, insectivorous prosimian (**Figure 1.1**). The IUCN/SSC Primate Specialist Group has given *T. syrichta* a Conservation Priority rating 4 that defines the species as highly vulnerable (Eudey, 1987). It is currently listed by the International Union for the Conservation of Nature and Natural Resources (World Conservation Union) Red List of Threatened Animals (IUCN, 2000) under the Data deficient category. It is the only species of the genus *Tarsius* found in the Philippines. Data available on the species are derived mainly from earlier captive studies on respiration (Clarke, 1943); estrous cycle (Catchpole and Fulton, 1939, 1943); parasitic fauna (Hill *et al.*, 1952); general behaviour and morphological measurements (Cook, 1939; Lewis, 1939; Wharton, 1950; Hill *et al.*, 1952; Ulmer, 1960, 1963; Evans, 1967; Schreiber, 1968); support use (Reason, 1978); vocal calls (Wright and Simons, 1984); social behaviour (Haring *et al.*, 1985); body temperature and mass-specific rate of oxygen consumption (McNab and Wright, 1987); infant development (Haring and Wright, 1989); sexual dimorphism based on anatomical features (Acebes, 1999); urine characterictics (Timoteo, 1999) and limited observations in the field (Cook, 1939; Hoogstraal, 1947, 1951;

Photo courtesy of PTFI

Figure 1.1. The Philippine tarsier *Tarsius syrichta*

Wharton, 1948, 1950; Lagapa, 1993; Rickart *et al.*, 1993). Although these studies contributed greatly to a better understanding of the species, extended systematic studies in the field are essential to formulate effective conservation measures.

1.2 THESIS FORMAT

In this thesis, the results of an 8-month field study of Philippine tarsier ecology and behaviour on Corella, Bohol is presented. Chapter 1 provides a background on the current state of natural resources in the Philippines and the major problems that the country faces in terms of protecting remaining biological resources.

Chapter 2 presents a review on previous field studies of the 5 species of the genus *Tarsius*. This review chapter emphasises the gap of information on the ecology and behaviour between these species. This reiterates the need to conduct more field studies on the lesser-known members of the genus *Tarsius* including *T. syrichta*, in order to provide a sound basis for the planning and implementation of management and conservation programs. The review also serves as a comparison to the results that are presented in Chapters 4, 5 and 6. Comparative analysis will further show the interspecies variation on behaviour as related to differences in habitat structure and ecological variables.

Chapter 3 describes the study site and methods used to collect different behavioural data and ecological parameters.

Data on home range sizes and configurations, extent of range overlap, movements of the animals and habitat associations are presented in Chapter 4. Chapter 5 discusses the results generated from actual field observations on reproductive behaviour as well as mating and social systems inferred from patterns of home range use and morphological measurements. Chapter 6 deals with the patterns of foraging and travelling behaviour. Chapter 7 presents a population viability analysis of *T. syrichta* population using the simulation model Analysis for the Likelihood of Extinction (ALEX). Chapter 8 is the concluding chapter and I discuss past and present conservation efforts on the species and present implications for conservation based on gathered data as well as recommendations for further research.

1.3 PROJECT AIMS

This study aims to provide data on the ecology of the Philippine tarsier *Tarsius syrichta* on which the management of the species can be based. It will examine the following:

(1) Home range size and shape among adult male and female Philippine tarsier.

(2) Patterns of home range overlap between male-male, female-female and male-female and infer social structure based on these.

(3) Preferred habitat according to vegetation structure and land use pattern

(4) Reproductive behaviour based on occurrence of births, weaning period and form of parental care

(5) Nocturnal foraging behaviour and movements.

(6) Appropriate conservation strategies for the species.

Chapter 2:

Review of Tarsier Biology

CHAPTER 2: REVIEW OF TARSIER BIOLOGY

2.1 History and Distribution

2.1.1 History of Discovery

Among the currently recognised species of tarsiers, the first to be described was the Philippine tarsier. During the late 17th century, a Jesuit missionary, J. G. Camel gave a description based on an individual reportedly from the island of Luzon (**Figure 2.1**). This source location was found to be refutable (Hill, 1955) and at present, the Philippine tarsier is confined to the southern islands of the Philippines (**Figure 2.1**). In his description, Camel described the Philippine tarsier as a small monkey with big, round eyes that never or rarely closed; skinny, hairless ears; mouse-like fur and the length of the tail and hindfeet similar to the length of the rest of the body. In 1705, the descriptions were published by J. Petiver in the *Philosophical Transactions* of the Royal Society who named the animal *Cercopithecus luzonis minimus* (Hill, 1955). It was the first binomial name to be given to any tarsier (Hill, 1955; Niemitz, 1984). Linnaeus (1758) called the species *Simia syrichta,* based on Petiver's account of Camel's discovery. In 1765, Buffon also described a juvenile tarsier of undetermined origin that was eventually included under the name Indian jerboa based on the exceptional character of two pairs of incisors. It was in his 13th edition of *Systema naturae* that Linnaeus recognised Buffon's description and named the animal *Didelphis macrotarsus* believing that the tarsier was related to the opossums. Erxleben in 1777 first recognised the systematic affinities of the tarsier and its link with the prosimians, giving the name *Lemur tarsier* (Hill, 1955). Later, Cabrera, (1923) and Hill (1953, 1955) validated the name *Tarsius syrichtus* (*syrichta*) for the Philippine tarsier.

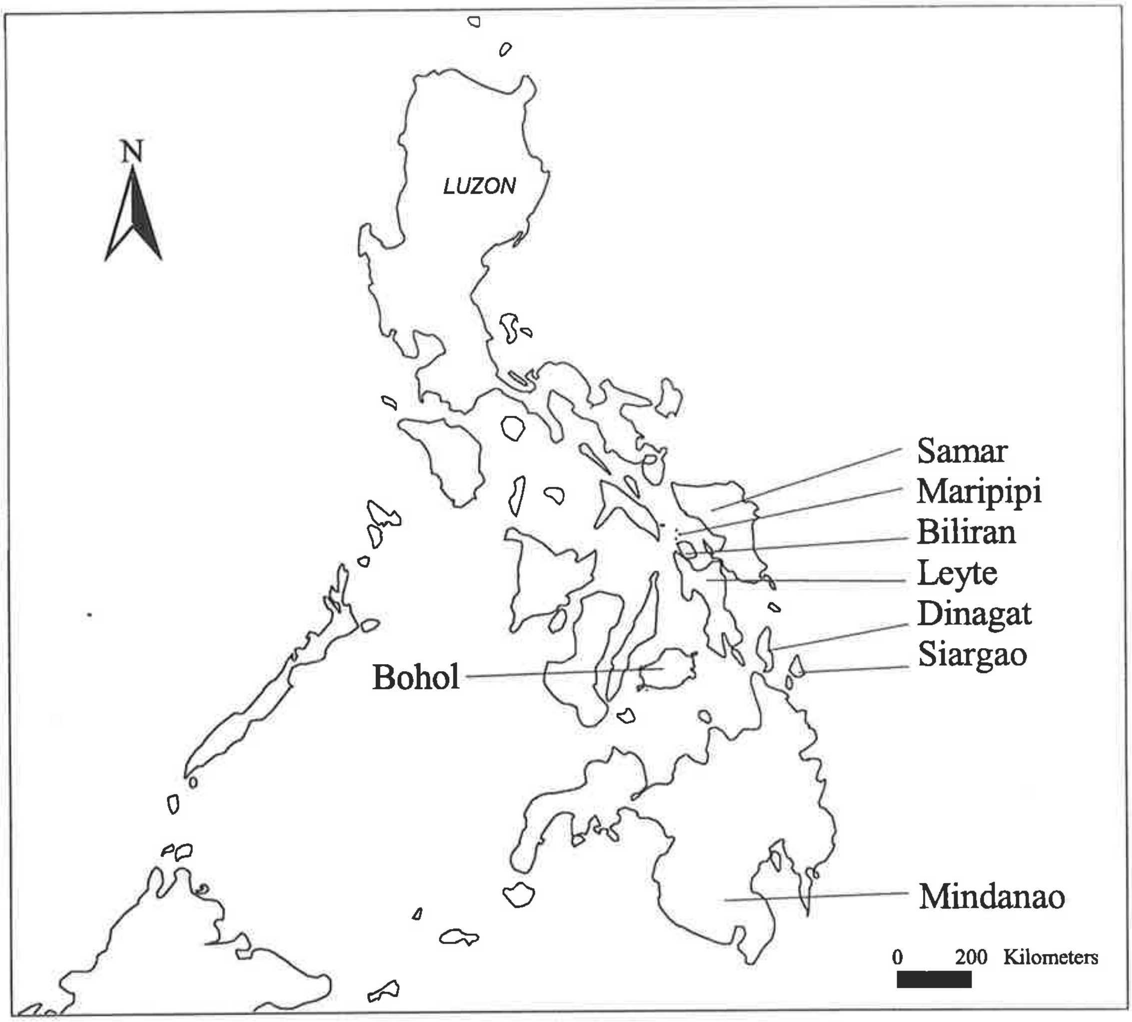


Figure 2.1. Map of the Philippines identifying the islands on which the Philippine Tarsier is found (in reference to Luzon).

2.1.2 Distribution

Five species of tarsier are recognised today: (1) *Tarsius syrichta* (Linnaeus, 1758) is distributed on the southern Philippine islands of Samar, Bohol, Leyte, Dinagat, Siargao, Maripipi, Biliran and Mindanao (**Figure 2.1**). (2) *Tarsius bancanus* (Horsfield, 1821) is distributed within mainland Borneo, Pulau Serasan in the South Natuna islands, Pulau Belitung and Pulau Bangka. (3) *Tarsius pumilus* (Miller and Hollister, 1921; Musser and Dagosto, 1987) is found in the montane mossy forest of central Sulawesi. (4) *Tarsius spectrum* (Pallas, 1778) is distributed throughout Sulawesi, Sangihe, Peleng and Selajar. (5) *Tarsius dianae* (Niemitz *et al.*, 1991) is from the lowland forest of Kamarora in central Sulawesi (**Figure 2.2** and **Figure 2.3**). The studies of Nietsch and Kopp (1998) and Nietsch (1999) on the acoustic structure of the calls of tarsiers of Sulawesi confirmed major biological differences between *T. dianae*, *T. spectrum* and tarsiers from Kebun Kopi and Togian islands (not officially recognised) based on behavioural responses to playback experiments. Although the duets of Kebun Kopi tarsiers were less distinct from those of *T. dianae*, the Togian tarsiers, on the other hand, had significantly distinct vocal structure from *T. spectrum* and *T. dianae*. These studies further support the recommendation to recognise the tarsiers from the Togian islands, Tomini Bay, Sulawesi as a distinct species (*T. togianensis*) (**Figure 2.2** and **Figure 2.3**).

2.1.3 Subspecies of T. syrichta

Three subspecies of *Tarsius syrichta* have been described: *T. syrichta syrichta*, from Leyte and Samar; *T. s. fraterculus* (Miller, 1911) from Bohol and *T. s. carbonarius* (Heude, 1898) from Mindanao. However, Hill (1955) and Niemitz (1984) question the significance of this classification due to the small sample sizes and very limited variation between individual

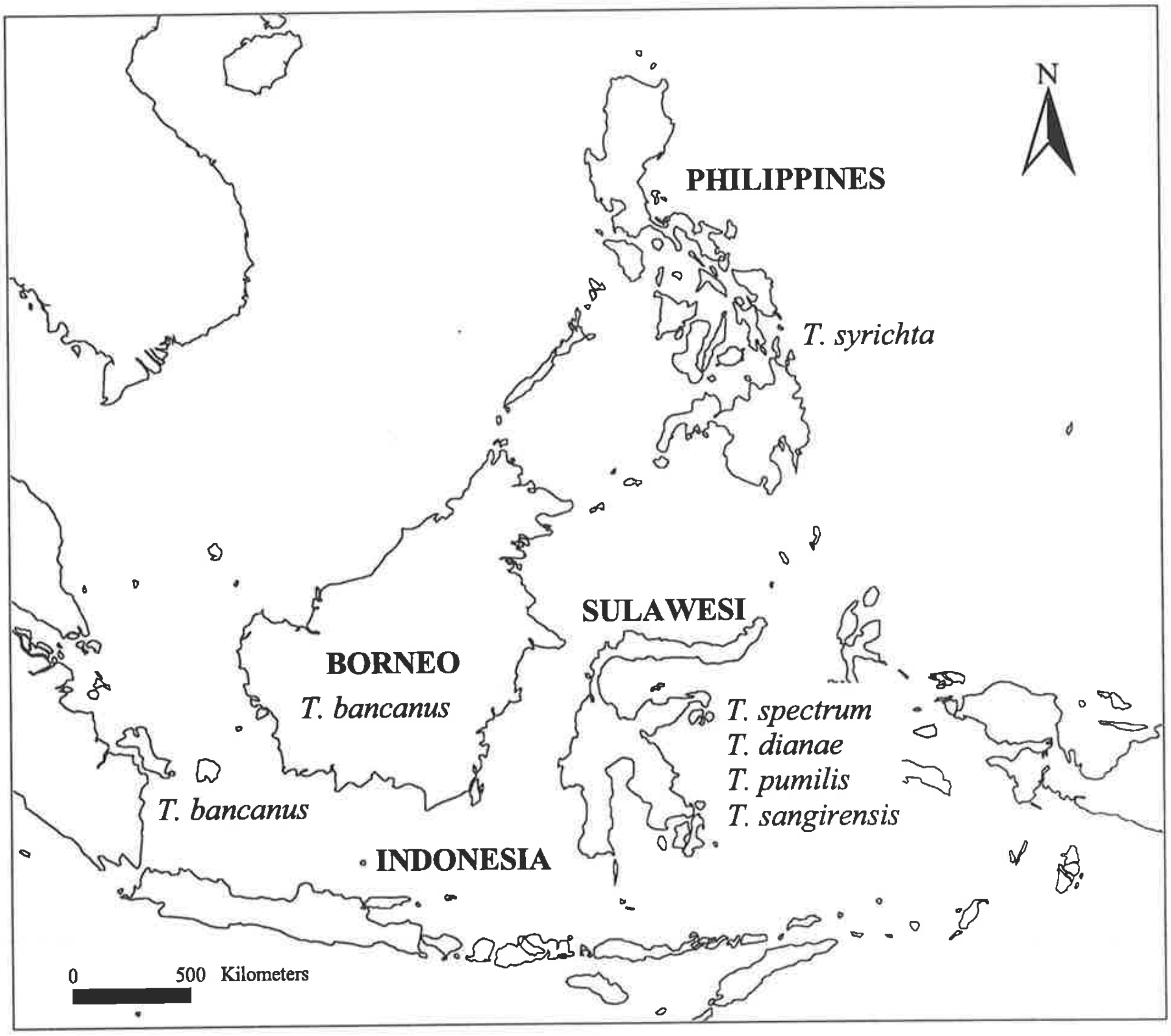


Figure 2.2. Map of South-East Asia showing the distribution of the six formally recognised tarsier species (all capital).

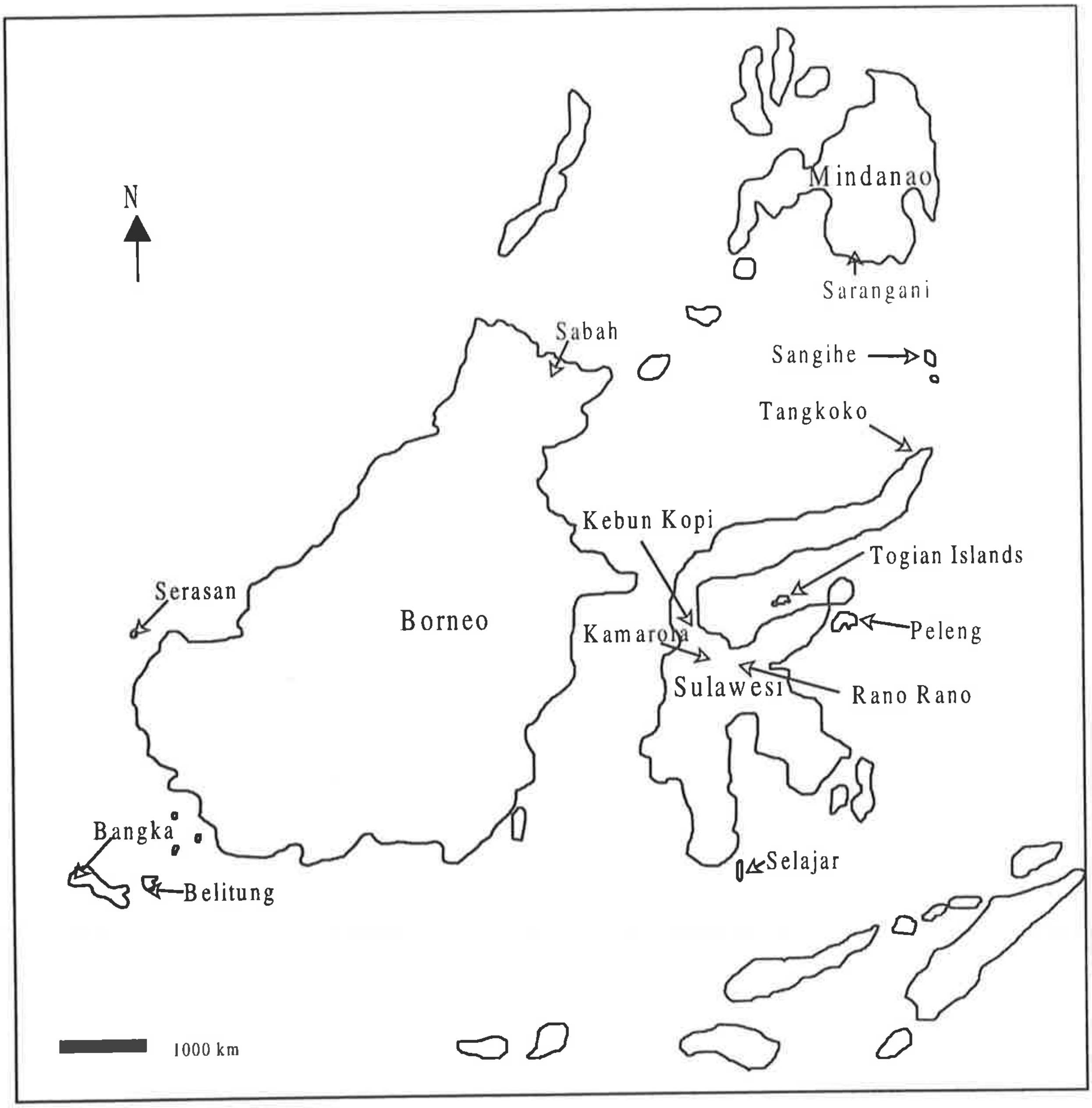


Figure 2.3. Selected localities of tarsier distribution and study sites as cited in the literature

morphological measurements. The sample size of Musser and Dagosto's (1987) morphometric data was also too limited to support the recognition of these subspecies.

2.2 BEHAVIOUR AND ECOLOGY

Previous behavioural and ecological studies of wild, free-ranging and semi-captive tarsiers have concentrated on the three species: *T. bancanus* (Fogden, 1974; Niemitz, 1972, 1974, 1979a, 1979b, 1984; Crompton and Andau, 1986, 1987); *T. spectrum* (MacKinnon and MacKinnon, 1980; Nietsch, 1993, 1999; Nietsch and Kopp, 1998; Gursky, 1993, 1994, 1995, 1997, 1998a, 1998b, 2000a, 2000b) and *T. dianae* (Tremble *et al.*, 1993). *T. pumilis* has never been the subject of long term ecological studies. The above-mentioned studies on *T. bancanus*, *T. spectrum* and *T. dianae* will comprise the main literature for this review which aims to compare the differences between the member species of the genus *Tarsius* with respect to their behaviour, and how these variations are related to the different structures of their habitat. A summary is given at the end of the review to emphasise the importance of conserving this species in the wild.

2.2.1 Home Ranges

The study of home range and spatial requirements of an animal is essential for conservation. The information on the individual's requirement for an area that provides adequate food and shelter can assist in making informed decisions regarding areas to be set aside as reserves. The early work of Fogden (1974) on *T. bancanus* suggested that the Bornean tarsier's home range is between 2.5 and 3.0 ha. This study was conducted over a two-year period on 26 individuals that had been trapped and retrapped using mist nets. Niemitz (1979b) conducted his own observations on *T. bancanus* under semi-wild conditions within a 90-m^2 cage enclosure. He utilised urine and epigastric gland marking sites to determine the home range size of the animal. Niemitz's study indicated the species' home range size to vary from 0.9-1.6 ha. The home range of the species was noted to be remarkably stable with an individual recaptured in exactly the same area after more than one year. The technique used in Niemitz's (1979b) study to determine home range is highly prone to error, as it is obviously difficult to pinpoint a certain individual's own marking sites and the frequency that the marking site has been visited.

The first field study on the tarsiers involving radiotelemetry was done by Crompton and Andau (1987) in Sabah, Borneo. They collected a total of 120 hours of observation over the unspecified duration of their study. The results of this work, involving four *T. bancanus* (2 males and 2 females), indicated a larger home range size of 8.75-11.25 ha for adult males and 4.5-9.5 ha for adult females, considerably larger than those from the previous works of Fogden (1974) and Niemitz (1979b, 1984). Individuals travelled a mean distance of 1,800 m during a normal activity period with males moving significantly farther (x = 2,081.6 m) than females (x = 1,448.1 m). Patterns of home-range utilisation showed males to utilise 50-75% of their total home range and females utilised between 66-100% of their total home range per night. Radiotelemetry will yield more accurate data on size of home range than those techniques utilised by Fogden (1974) and Niemitz (1979b, 1984). However, the number of individuals used in Crompton and Andau's (1987) study was too small to form a representative sample.

Gursky's (1997) dissertation on the behaviour and ecology of the *T. spectrum* utilised radiotelemetry on sixteen individuals over a fifteen-month period in Tangkoko, north Sulawesi. The home range of adult females in different reproductive stages was computed using both convex and concave polygons for comparative purposes. The mean convex home range was 2.32 ha and the mean concave home range was 4.05 ha. Convex polygons should overestimate home range size and therefore have a greater value than concave polygons with a constant population. Home range of individuals varied from 1.6 to 4.1 ha, with males having larger home ranges than females (mean of 3.07 ha and 2.32 ha respectively). This is notably larger than the 1 ha range size previously estimated by MacKinnon and MacKinnon (1980) based on sightings of the family male.

A field study on *T. dianae* by Tremble *et al.* (1993) indicated a home range size of 0.5-0.8 ha. Gursky (1997) mentioned that some confounding variables in Tremble *et al.*'s (1993) study contributed to the small home range size, such as the heavy weight of the transmitter package and the short duration of the study.

Dagosto and Gebo (1997) radiocollared four male Philippine tarsiers in Mt. Pangasugan, Leyte over a period of 5 weeks. Male home range size was estimated to be 0.6-2.0 ha. They have emphasised that their data were very preliminary. No data on female home range size nor the degree of overlap between sexes were collected.

It is apparent that tarsiers in general have relatively small home ranges and that these ranges can be stable over some period of time. However, the interspecies variation of home range sizes cannot really be compared with accuracy as data were collected using different techniques (trap-retrap vs. scent-marked trees vs. radiotracking); different sample sizes (two vs. four vs. sixteen) and varying duration of field studies.

2.2.2 *Social Structure*

Size and composition of primate groups are influenced by ecological as well as social factors (Emlen and Oring, 1977). Field observations on *T. bancanus* suggested that that this species may have a non-monogamous breeding system. Fogden (1974) observed ranges of males to be larger and extensively overlap with more than one female, although there was no evidence that females associated with more than one male. The ranges of individuals of the same sex were generally exclusive although a small degree of overlap occured between females. It was not determined whether these ranges were actually defended territories. Niemitz's (1984) study suggested that this species most likely form male-female pairs with either an infant or juvenile per home range. Crompton and Andau (1986) noted an overlap of home ranges between two adult males and a single female, as well as those of four adult males with the home range of another female. Gursky (1995) suggested occurrence of intra-specific variation in social organization in *T. bancanus*, taking into consideration that the above mentioned studies of *T. bancanus* were conducted at different field sites with different groups. It is possible that this species exhibits both pair bonds and the noyau social system.

Gursky (1995, 1997) surveyed 33 groups of *T. spectrum,* for a total of 101 individuals. Results suggested that spectral tarsiers have considerable variation in social structure, with some groups having monogamous pairs and others with at least two females. A male's range overlaps that of one or more females, and females' ranges overlap as well. Facultative polygamy may best describe the social structure of *T. spectrum* (Gursky, 1997). Although. A. Mueller (pers. comm.) suggested that perhaps it's not facultative polygamy but facultative monogamy.

The primary mode of social interaction among the tarsiers is vocalization. Crompton and Andau (1987) recorded the calls of *T. bancanus* and found that most vocal calls were single calls. The second classification was simultaneous calls or duets and the third was the calling concert, with 3-4 or more tarsiers calling simultaneously. *T. spectrum* were characterised by the loud vocal calls that they give when leaving from and returning to their sleep sites at dusk and at dawn respectively (MacKinnon and MacKinnon, 1980, Niemitz, 1984; Gursky, 1997). The vocalisations of *T. spectrum*, *T. dianae*, Togian tarsier and Kebun Kopi tarsier have been analysed by Nietsch and Kopp (1998) and Nietsch (1999). The vocal calls of the three species have been found to be distinct from each other, though the duets of the Kebun Kopi tarsiers are less different from those of *T. dianae* suggesting a closer relation between the two populations. The males and the females of the sample population differ in the acoustical structure of their calls.

Wright and Simons (1984) studied the calls of a pair of captive *T. syrichta*. Three different types of calls were recorded from the male under three different behavioural conditions. The recordings of the female calls were very limited and were not classified into any distinct type. Wild (pers. observ.) and captive *T. syrichta* do not give duet or dawn calls. Dagosto and Gebo (1997) noted wild Philippine tarsiers calling from the edges of home ranges. These interspecies variations in calling behaviour further indicate the differences in social organizations between tarsiers.

2.2.3 Reproductive Behaviour

Fogden (1974) reported that wild *T. bancanus* had a sharply defined breeding season with mating in October through December and births in January through March. It was observed to be a non-seasonal breeder in semi-wild conditions (Niemitz, 1984) and in captivity

(Roberts and Kohn, 1993; Wright *et al.*, 1988). Wild *T. spectrum* have also been reported to be a seasonal breeder with two distinct breeding seasons within a year (MacKinnon and MacKinnon, 1980; Gursky, 1997): April-May and November- December (Gursky, 1997). Captive *T. syrichta* has not been reported to be a seasonal breeder (Catchpole and Fulton, 1943; Haring and Wright, 1989). The gestation period for captive *T. bancanus* is 178 days (Izard *et al.*, 1985), which is comparable to the mean gestation period of 191 days estimated by Gursky (1997) on wild *T. spectrum.* Her study also revealed that none of the female spectral tarsiers reproduced twice in one year. This indicates the relatively low fecundity rate of the species.

Litter size for tarsiers has been reported to be strictly limited to one offspring. Wild female *T. spectrum* gave birth to single infants with no variation in litter size *i.e.* occasional twins (Gursky, 1997). The same has been observed on captive *T. bancanus* and *T. syrichta* (Roberts and Kohn, 1993). Gursky (1997) cited two anatomical factors that do not conform to the absolute single- births characteristic of the species:

(1) Tarsiers possess a bicornuate uterus enabling for the production of twins and

(2) Tarsier species have 2-3 mammary glands (Niemitz, 1984; Gursky, 1997; Acebes, 1999; pers. observ.) which can allow nursing for more than one infant. Yet they exhibit a life history strategy that minimizes the number of offspring per year.

2.2.4 Diet and Feeding Behaviour

Observations by Niemitz (1979b, 1984) on semi-wild *T. bancanus* indicated that the species is totally carnivorous. Diet included beetles, ants, locusts, cicadas, crickets, cockroaches, birds (nectarine, forest kingfisher and blue winged pitta), smaller fruit bats, spiders and poisonous snakes. It is important to note that early observations made on the food intake were purely descriptive. Fogden (1974) reported that the vertical distribution of *T. bancanus* in the forest may be influenced by the seasonal variation of fruit bearing trees. Tarsiers have been easily trapped close to the ground during the time of fruit and insect abundance, which has been difficult to do otherwise. “Tarsiers were not attracted to the fruit itself, but by the insects and other animals which were attracted to the fruit” (Fogden, 1974 p. 161). This observation illustrates the possible effect of forest phenology on the habitat use and space utilization of *T. bancanus*.

A quantitative study was done by Gursky (1997; 2000a) involving foraging return rates of *T. spectrum* females in varying reproductive stages. It was done by comparing the mean size of insects caught per unit time spent foraging. The findings indicated that there were few significant differences in the size of insects captured by females in different reproductive states. However, pregnant females had higher rates of unsuccessful pursuits for insects compared to lactating and non-reproductive females. This was mainly attributed to impaired mobility of pregnant females as a result of carrying a large load (gestating a large infant). *T. spectrum* has been observed by MacKinnon and MacKinnon (1980) to be 100% insectivorous . Prey items included moths, termites, crickets, sleeping dragonfly, cockroaches and beetles.

Tremble *et al.*’s (1993) observation on the dietary items of wild *T. dianae* included moths, crickets and a lizard. The study further suggested that although the most common activity was foraging (44%), *T. dianae* spent considerable time sitting (21%). Taking into consideration that its habitat is located at higher altitudes, occasional torpor can occur and further investigation on this aspect was recommended.

2.2.5 *Locomotion and Activity Patterns*

Previous field studies show 'vertical cling and leap' (VCL) to be the predominant locomotor modes for free- ranging tarsier species (Crompton and Andau, 1986, 1987; MacKinnon and MacKinnon, 1980; Tremble *et al.*, 1993; Dagosto and Gebo, 1997). Niemitz (1979a) developed a model showing the relationship between anatomy, behaviour and ecology in the genus *Tarsius*. Based on morphometric data of three species: *T. bancanus*, *T. syrichta* and *T. spectrum* and observations of captive *T. syrichta* and semi-wild *T. bancanus*; Niemitz (1979a) hypothesized *T. bancanus* to be most specialized for vertical clinging and leaping. This was attributed to *T. bancanus* having the relatively longest forelimbs and hindlimbs and largest digital pads. *T. spectrum* was predicted to be more generalized in its locomotion having the shortest limbs and smallest digital pads. *T. syrichta* was foreseen to be intermediate in both morphology and behaviour.

Niemitz (1979a) discussed that the strong correlation between anatomical traits and behaviour further extends to the ecology of the species with *T. bancanus* being exclusively arboreal and preferring almost exclusively vertical substrates relative to *T. syrichta* which can be both arboreal and ground dwelling and prefers predominantly oblique substrates. *T. spectrum* was predicted to be less arboreal and less adapted for bipedal jumping than *T. syrichta.* Niemitz (1979a) emphasized that his predictions needed to be tested further and should not be interpreted with absolute certainty. However, his propositions were confirmed in succeeding field studies: Crompton and Andau (1986, 1987); MacKinnon and MacKinnon (1980); Tremble *et al.*, (1993); Dagosto and Gebo (1997). The differences of locomotion and activity patterns in relation to support type frequencies and substrate used is further summarized in **Table 2.1.** The similarities and differences between my results and that of

Table 2.1. Mode of Locomotor, activity patterns, support type and substrate use frequencies of free ranging tarsiers. Data for *T. bancanus* is from Crompton and Andau (1986); for *T. spectrum* from MacKinnon and MacKinnon (1980); for *T. dianae* from Tremble *et al.*, (1993); for *T. syrichta* from Dagosto and Gebo (1997).

Species	***T. bancanus***	***T. spectrum***	***T. dianae***	***T. syrichta***
Study Site	Sepilok Forest Reserve, Sandakan Bay, Sabah, sea level Mixed 1° & 2° forest	Tangkoko-Batuangas, NE Sulawesi, 1000m above sea level, Mixed 1°& 2° forest,grassland	Lore Lindu National Park, Central Sulawesi, 1000 m above sea level, mixed 1°&2° forest	Mt. Pangasugan, Leyte, *c.* 100 m above sea level, secondary forest
Locomotor:				
Leap/VCL	66	63	58	58
Hop	2	8	6	-
Quad/Walk	3	3	11	11
Climb	28	11	22	26
Cantilevering	1	-	4	-
Unaccounted	-	15	-	5
Activity:				
Forage	60	No quantified data	44	No quantified data
Feed	2		4 ?	
Travel	27		27	
Rest	11		21	
Groom	0.6		7	
Scentmarking	incorporated in grooming		-	
Calling	-		-	
Support:				
Vertical 80-90°	72	*c.* 60	59	64
Angled 45-80°	19	*c.* 15 combined with sloping	20	20 combined with sloping
Sloping 10-40°	2.5		12	
Horizont0-10°	0.9 excluding ground	*c.* 23 including ground	10	10
Substrate:				
Sapling	81	No quantified data	31	No quantified data
Tree trunk	3.5		3	
Branch	-		19	
Climber/vine	4		14	
Ground	5.3		8	

Dagosto and Gebo (1997) and the model of Niemitz (1979a) will be discussed in Chapter 6 on Foraging and Travelling behaviour.

The highly crepuscular nature of tarsiers has also been documented with biphasic patterns of nocturnal activity (peak of activity at dusk and at dawn) described for *T. bancanus* (Niemitz, 1984; Crompton and Andau, 1986, 1987) and *T. spectrum* (MacKinnon and MacKinnon, 1980; Gursky, 1995, 1997), not only in terms of distance travelled but with respect to calling behaviour as well. The results of my observations of *T. syrichta* show that variations in activity patterns can occur among individuals and these will further be discussed in Chapters 4 and 5 on Home Ranges and Social Organization respectively.

2.2.6 Population Density

Based on home range patterns, the population density of *T. bancanus* has been estimated to be 14-20 animals per km^2 (Crompton and Andau, 1987). The figure from Niemitz's (1984) population estimate using capture and recapture techniques was 80 individual tarsiers per km^2. The discrepancies of population density estimates can be attributed to several factors: 1) the different techniques used to estimate home range sizes; 2) intraspecific and population differences; 3) seasonal variation in resource availability; 4) the studies were conducted in different habitat types, or a combination of two or more of the mentioned variables.

MacKinnon and MacKinnon (1980) estimated *T. spectrum* population density to be 3-10 individuals per hectare. This was based on spot observations in several different habitat types at varying altitudes in northern Sulawesi. Gursky (1997, 1998a) conducted a modified fixed point count and quadrat census methods on *T. spectrum* individuals within one-km^2 plot. The procedure was repeated for a total of 25 one-hectare plots where fourteen tarsier groups containing 39 individuals were locatcd by their loud vocal calls as they returned to their sleeping sites at dawn. The number of groups for the entire sampled area (100 ha) was calculated to be 56. The total population for the same sampled area was calculated to be 156 tarsier individuals per km^2. The higher density can be attributed to *T. spectrum* being more social, hence having a more intense degree of overlap among home ranges. The discrepancy between MacKinnon and MacKinnon (1980) and Gursky's (1997, 1998a) figures can again be attributed to dissimilar survey techniques and varying habitat types. It is important to note that with very small nocturnal cryptic animals, Gursky's (1997, 1998) modified census methods can only be utilised when they do give distinct vocalizations during a particular time of the day and these calls are sex-specific as in the case of the *T. spectrum.*

Lagapa (1993) used a line transect method to estimate the population density of tarsiers in Bohol. The estimated population was calculated to be 1-3 individuals per ha Dagosto and Gebo (1997) calculated a similar estimate of 0.5-2 individuals per ha based on the home ranges of four radiotracked animals in Leyte. They further supported the contention of Heaney and Utzurrum (1991) that tarsiers may in fact be common. However, it would be erroneous for the densities observed by Lagapa (1993) in Bohol and those observed by Dagosto and Gebo (1997) in Leyte to be extrapolated to determine the total population of tarsiers over the whole of the respective islands. This is because the projection would be based on the assumption that all forests in Bohol (Lagapa, 1993) or all the primary forests in Leyte (Dagosto and Gebo, 1997) are suitable habitat for the tarsiers.

2.2.7 Habitat Preferences

Crompton and Andau (1986) observed that *T. bancanus* spends three-quarters of their time below a height of 1 m, although they do move as high as 6-10 m above the ground if necessary. Their study further showed that major activities occurred at significantly different mean heights (using Duncan's multiple range test): *T. bancanus* preferred to stay at mean heights of 2.17 m when they groom; at 1.97 m when they rest; travel at 0.99 m; forage at 0.66 m and feed close to the ground at 0.53 m . These figures approximate that with Niemitz's (1979b) rather than with Fogden's (1974) observation that *T. bancanus* typically move at around 3m. Crompton and Andau (1986) raised the possibility that Fogden's results are a consequence of observing unhabituated animals. Crompton and Andau (1986) noted the average height of the sleeping sites of *T. bancanus* to be 4.0-5.5 m. and were usually branches or vines angled between 50°-90° and 2 cm in diameter. However, vine tangles and 'platforms' of creepers, in the lower and more open part of the forest canopy, were the most common preferred sleeping sites. The study site of Crompton and Andau (1987) in Sepilok Forest Reserve, Sabah (**Figure 2.3**) was characterized by lowland primary evergreen forest, secondary and near-climax secondary forest. The most common large trees within the study area were: *Shorea xantophylla, S. multiflora, S. smithiana, S. glaucens, S. gibbosa, Dipterocarpus grandiflorus, D. acutangulus, Parashorea tomentella, Hopea* spp., and *Eusideroxylon zwageri*. The most common fruit bearing trees were of the genera *Macarangus and Ficus.*

Gursky (1997) observed *T. spectrum* to prefer sleeping trees of the *Ficus spp.*, with *Ficus caulocarpa* being used more frequently than all other species. The mean height of the sleep trees was 20.17 m and the mean circumference was 287 cm. The observations of MacKinnon and MacKinnon (1980) on the spectral tarsiers revealed the species' affinity to a variety of sleeping sites which they classified into four main types: 1) Dense thickets of grass, *Saccharum spontaneum*, bamboo or *Pandanus*; 2) Dense tangles of vines or epiphytic ferns in a bush or a tree; 3) Cracks or holes in a tree with more than one exit; 4) Complex aerial roots of strangling figs. Gursky (1997) was not able to confirm MacKinnon and MacKinnon's (1980) observation in the field that *T. spectrum* utilised grass platforms for sleeping or nesting. Gursky's (1997, 1998a) data showed the preference of *T. spectrum* for a much higher sleeping site in the forest canopy than to those used by *T. bancanus.* These variations manifest the tarsiers' preferences for a considerable variety of forest strata. The six most important tree species in Gursky's study site at Tangkoko Dua Saudara Nature Reserve (**Figure 2.3**) are: *Leea indica, Morinda citrifolia, Piper aduncum, Palaquium obvatum, Barringtonia acutangula* and *Vitex quinata.*

Tremble *et al.* (1993) located sleeping sites of *T. dianae* in dense thicket of lianas and in a tree cavity. Wharton (1950) noted three *T. syrichta* individuals to have utilised tree hollows during his collection trip in Caburan, Sarangani Peninsula, Mindanao. Dian's tarsiers' sleeping sites are located in early successional habitat near secondary forest with primary vegetation consisting of bushes, ferns and small trees. *T. dianae* has been observed to generally stay within 1.6-3.0 m in the forest canopy and has also been found to stay at heights of 6.1 m. There was no attempt to systematically sample the vegetation in the Lore Lindu Park, Kamarora study area (**Figure 2.3**).

Dagosto and Gebo (1997) reported that, in the wild, each Philippine tarsier individual used 3-4 sleep sites. The sleep sites were generally low to the ground (less than 1 m) and these areas are characterized by trees of *Arctocarpus* sp., *Pterocarpus* sp. and *Ficus* sp. Lagapa (1993) observed individuals to stay not more than 2.6 m from the ground. A few sleep sites were also found in leafy tangles up to 4 m high (Dagosto and Gebo, 1997). Dagosto and Gebo (1997) noted individuals to forage and travel very low to the ground.

Musser and Dagosto (1987) described the habitat of *T. pumilus* as part of a larger study documenting the mammalian diversity in Sulawesi and the natural history of the species. The pygmy tarsier has only been collected between 1,800 and 2,200 m above sea level in the mossy upper montane rain forests of Central Sulawesi, Rano Rano. It is the type locality of *T. pumilus* (**Figure 2.3**) and has been described to be in the lower portion of upper montane forest and is similar in structure with that of Gunung Nokilalaki. The two belong to the same mountain region. The following description is that of the forest in Gunung Nokilalaki. The forest canopy was 10-20 m high and is predominated by the species: *Lithocarpus*, *Litsea*, *Cryptocarya*, *Podocarpus*, *Dacrydium*, *Aromadendron*, *Adinandra*, *Weinmannia* and *Engelhardtia*. The understory has greater diversity and is mainly comprised by the species: *Eugenia*, *Tristania*, *Planchonella* and occasional species of *Ficus*, *Ilex*, *Eurya*, *Carallia*, *Praravinia*, *Psychotria*, *Vaccinium*, *Drimys*, *Symplocos* and *Ternstroemia*. The forest is open and has a luxuriant growth of bryophytes and lichens. A field study on this virtually unknown tarsier species is clearly warranted. *T. pumilis* may also be at risk of extinction considering the exploitation of its known habitat which has just been described.

It is clear that different tarsier species prefer various forest types. It is therefore important to be able to identify the suitable types in a particular region where tarsiers are known to occur in order to set aside areas for reserves and be able to effectively manage these animals *in situ.*

2.3 SUMMARY OF REVIEW

Based on the preceding review, there are several factors which render the survival of studied tarsier species vulnerable: (1) Diet preferences show that the species is a specialist such that destruction of habitats can lead to loss of food sources causing population decline; (2) Long gestation length of 170-190 days limits the birth rate so that it will take the species a longer time to recover from possible population collapse caused by adverse conditions such as flood, drought and fire; (3) restricted geographical distribution places the species at high risk to potential impacts of extensive deforestation; for example, removal of substrate used and isolation of forest patches thereby reducing gene flow.

It is important to note that knowledge of the behaviour and ecology of wild *T. syrichta* is very limited as is also true with the case of *T. dianae, T. pumilus* and *T. sangirensis*. Studies of these species in the field can greatly contribute to understanding on how to conserve them and manage their natural habitats. It is therefore important that further studies be done on the Philippine tarsier and the other three lesser-known species, in order to effectively protect these species in the wild.

Chapter 3:

Field Site and General Methods

CHAPTER 3: FIELD SITE AND GENERAL METHODS

3.1 FIELD SITE

3.1.1 Geological History of the Philippines

The composition and distribution of mammalian fauna of the Philippines is largely influenced by its geological history. The Philippine archipelago comprises a complex of late Mesozoic and Cenozoic arc systems and continental fragments that were brought together as a result of oceanic plate movements (Heaney, 1985). This interpretation is supported by earlier tectonic and later palaeomagnetic and stratigraphical studies (Hamilton, 1979; Hashimoto, 1981; Fuller *et al.*, 1983; Mitchell *et al.*, 1986; Hall, 1996). The complexity and high mobility of the region would indicate that the current configuration of the archipelago has been recently attained (Hall, 1996) and geological processes will continue (Heaney, 1985). There is widespread evidence of volcanic activity throughout the Neogene (Hall, 1996). The presence of several active volcanoes, at least 8 on Mindanao alone (Hamilton, 1979), indicates that the islands are still geologically active. In Luzon, the most devastating eruptions in recent times were those of Mt. Pinatubo in 1991 and Mt. Mayon in 2000.

Uplifting during the middle-late Pleistocene, substantial volcanic activity and significant changes in sea levels resulted in the formation of four major islands: Greater Luzon, Greater Mindanao, Negros-Panay and Greater Palawan. These comprise the four major regions that harbor terrestrial mammalian fauna, and are significantly distinct based on degree of endemism, composition and richness (Heaney and Rabor, 1982; Heaney, 1986). It is important to note that among the four faunal regions, the Palawan fauna is most similar to Borneo compared with the other three. This similarity suggests the presence of land bridge connections between Palawan and Borneo and hence to the rest of Asia during the middle

Pleistocene (Walker, 1982; Hcancy, 1985,1986). Palawan exhibits a Sundaic mammalian fauna while the other three faunal regions have more affinity to Wallacea. The separation of Palawan faunal region from the rest of the Philippines by Wallace's Line further illustrates the high species richness and endemicity of the islands (Oliver, 1994) **Figure 3.1**. Geological evidence indicates land bridges did occur within parts of the Philippines during the late Pleistocene when sea level was *c.* 120 m lower than at present (Heaney, 1985). Bohol together with Leyte, Samar, Maripipi, Biliran, Dinagat, Siargao and Mindanao were then encompassed within the single large island of Greater Mindanao (Heaney, 1985, 1991). However, no evidence of land bridge connections between the Philippine archipelago (except Palawan) and mainland Asia exists during the middle-late Pleistocene (Heaney, 1985). Patterns of distribution of some non-endemic mammalian genera *i.e. Nycticebus*, *Tarsius*, *Rattus* and *Crunomys* imply the possibility of route dispersal via the Sulu archipelago (Groves, 1984).

3.1.2 Research Area: Corella, Bohol

Bohol is the tenth largest island in the Philippines. The island has an area of 4, 117 square kilometres and lies 9 degrees north of the equator. It lies between southern Leyte on the east and Cebu on the west. The island is further situated 450 km north of the northern-most point on Mindanao. Camotes Sea, the Bohol Sea to the south, the Canigao Channel on the east and the Cebu Strait on the west (**Figure 3.2**), bound it on the north. Most of the island is composed of fossiliferous Eocene limestone. The north-central portion of the island consists primarily of andesite, basalt and clastic strata (Hamilton, 1979). The coastline of Bohol is 161 km long and it is almost oval in shape and quite regular except for the slight protrusion of the Anda Peninsula. Approximately 72 islets or sandbars surround Bohol. The north, west and

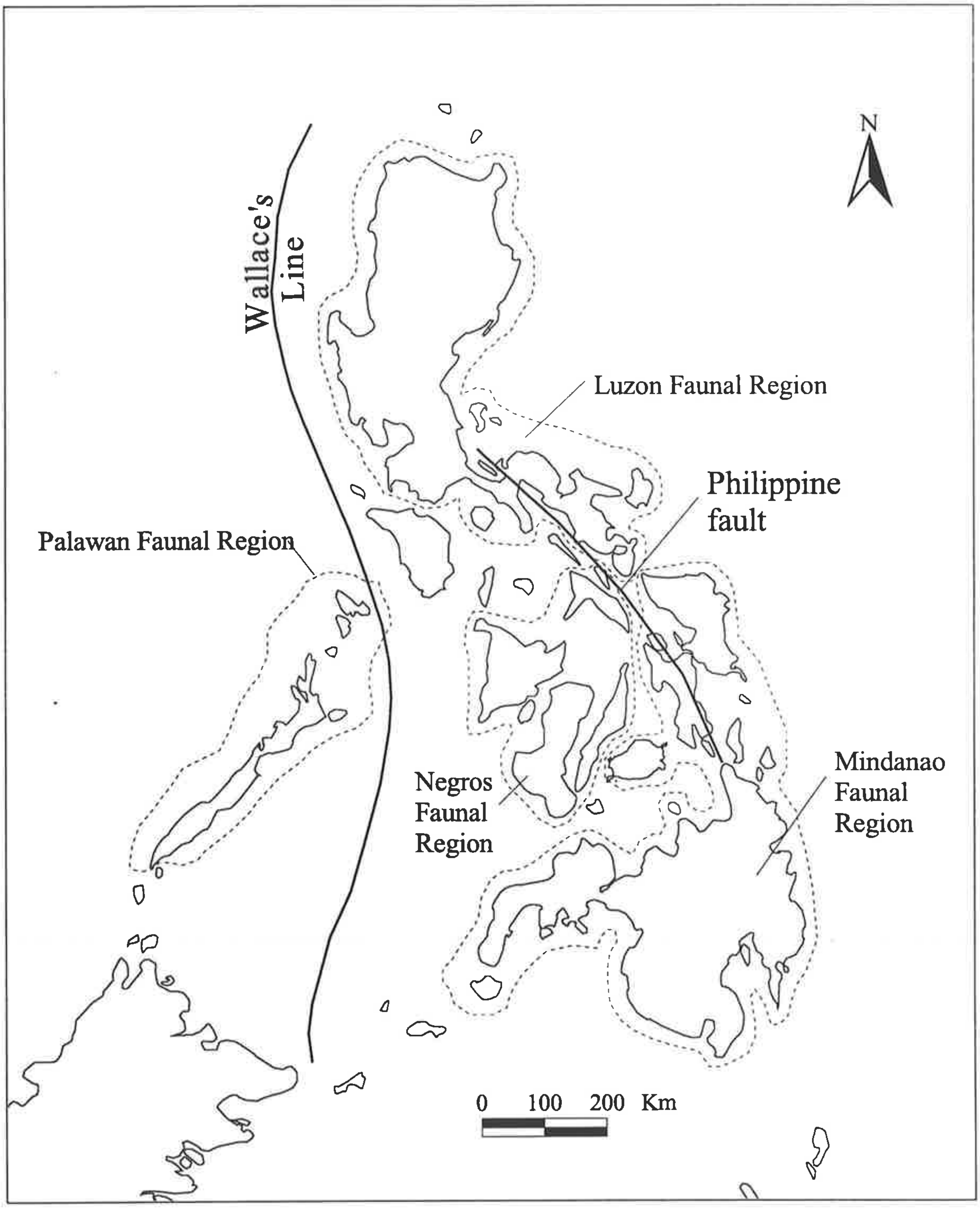


Figure 3.1. Principal faunal regions and tectonic features of the Philippines. Modified from Heaney (1986) and Oliver (1994).

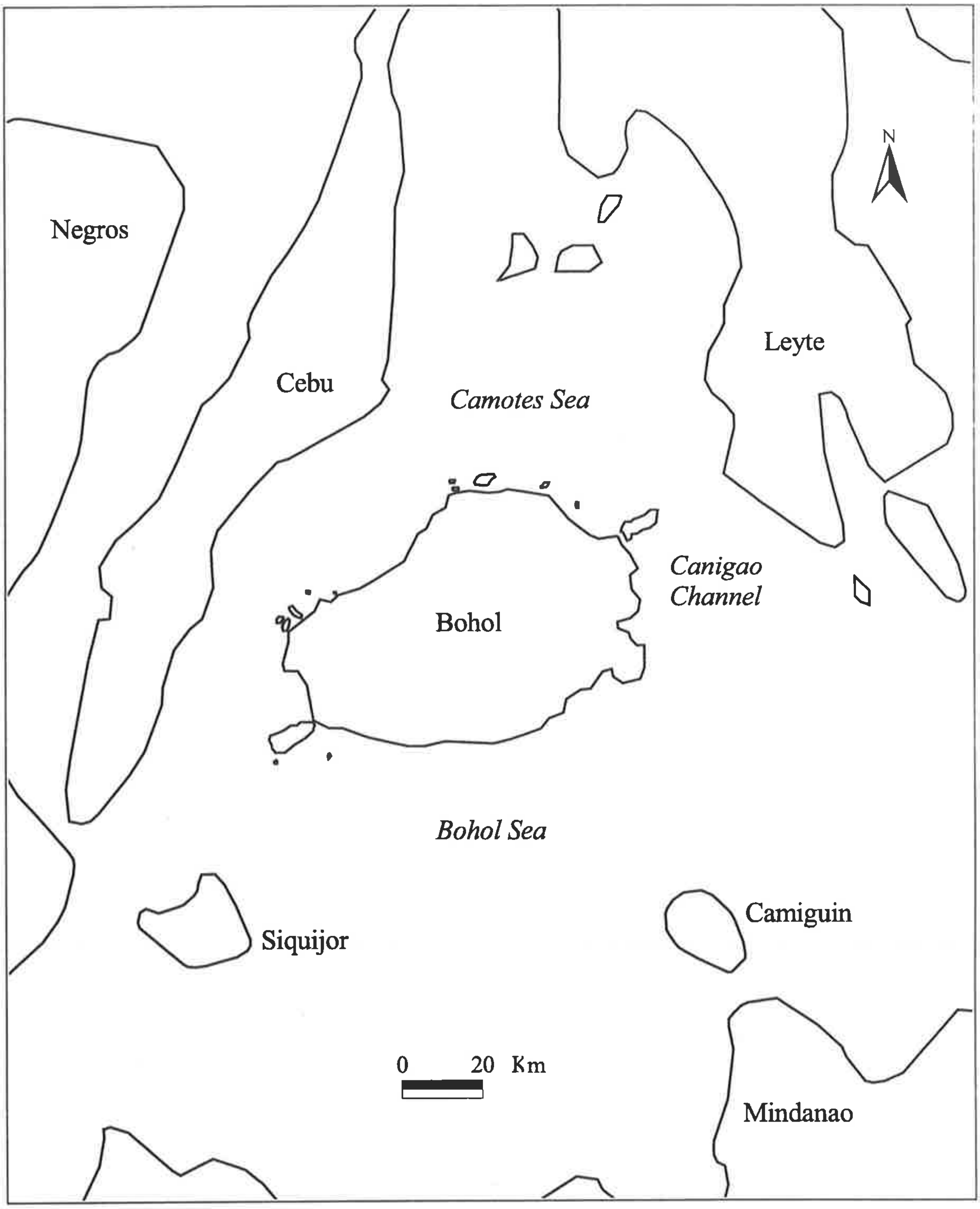


Figure 3.2. Map of Bohol and its boundaries.

northeast coast are surrounded by coral reefs. Mangrove forests are found adjacent to the shoreline predominated by *Rhizophora sp.* and transition to nipa (*Nypa fruticans*) forest stands can be observed in estuarine areas. This field study was conducted in the municipalities of Corella and Sikatuna which are located in the southwest portion of Bohol (09°41'36.7''N, 123°57'33.7''E) where a 174 ha proposed tarsier sanctuary is located. It is bounded by the municipalities of Sikatuna, Balilihan, Cortes and Baclayon and is 17 km northwest of the capital city Tagbilaran (**Figure 3.3** and **Figure 3.4**).

3.1.3 Physical Setting

The reserve area is representative of the general topography of Bohol, hence the description presented here will be of the island as a whole. Bohol is characterized by rolling hills forming ridges and steep slopes. Towards the interior, the lands are irregular and rise to a plateau that is dotted with numerous conical hills. Ridges of the eastern and western sides of the island rise from the center up to a maximum elevation of 870 m (Mt. Mayana), but along the coast the ridges slope down steeply towards the sea. The southern side of the island where Corella is situated is generally mountainous with a rough terrain broken by deep gullies and gorges with abrupt slopes (**Figure 3.4**).

3.1.4 Climate

There have been four established classifications of the climate in the Philippines based on patterns of rainfall distribution. Bohol falls under the fourth type wherein there is a fairly even distribution of rainfall throughout the year. It can be very heterogeneous throughout the island. Further analysis on climate trends reveal dry periods of relatively short duration which can occur within the year but do not exhibit any seasonal pattern (Morris and Rumbao, 1985).

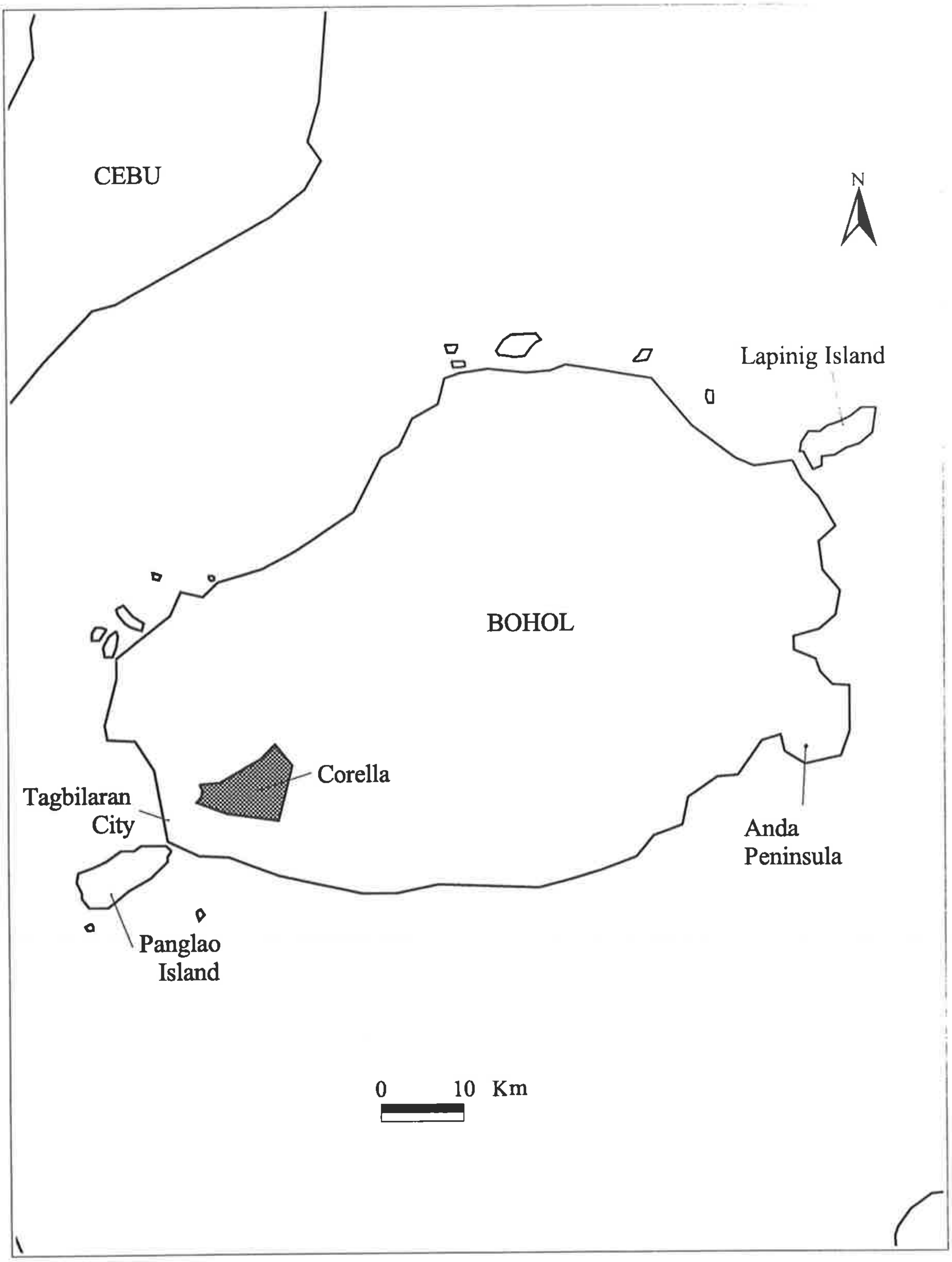


Figure 3.3. Map of Bohol showing the location of Corella.

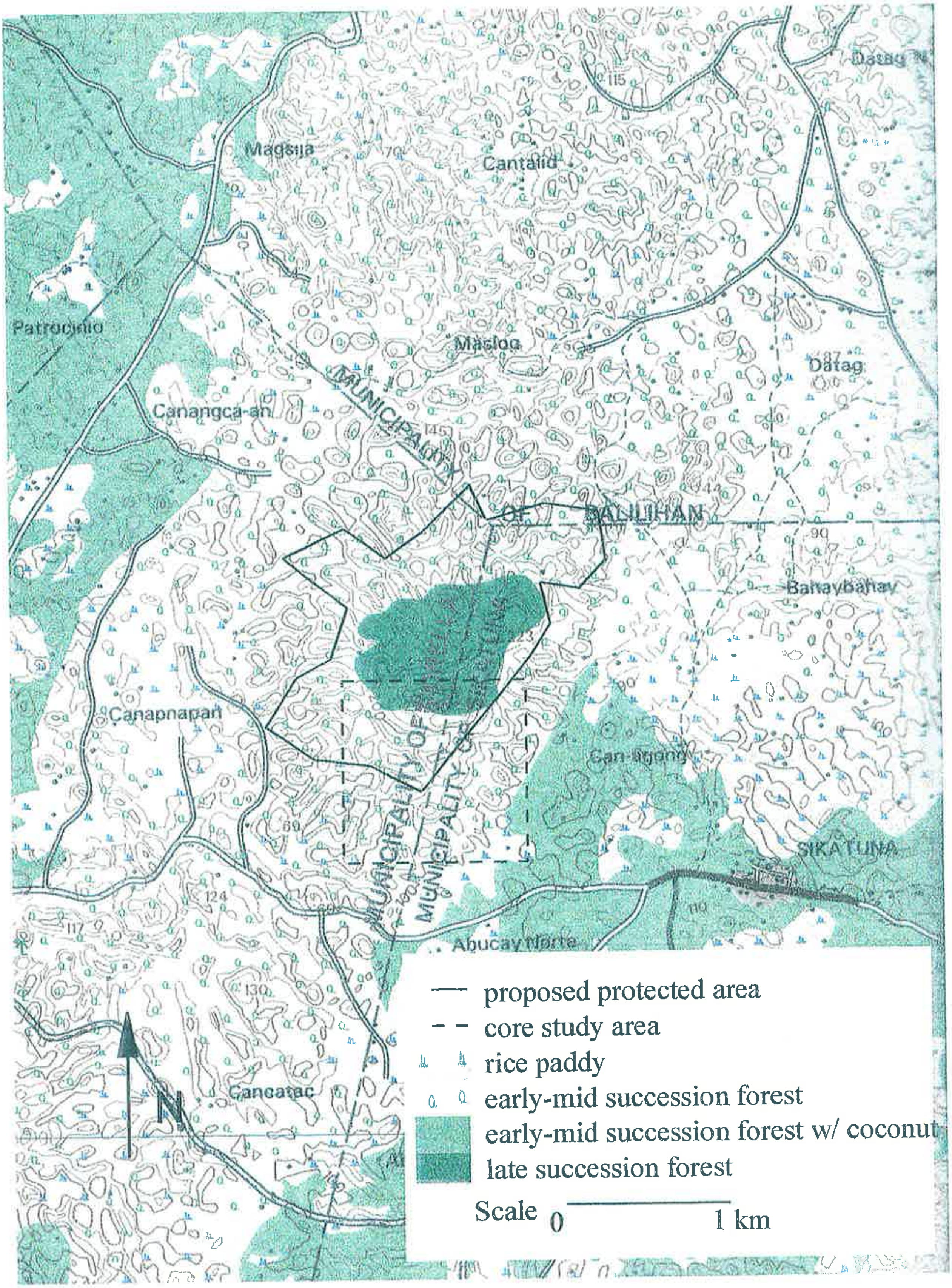


Figure 3.4. Topographic map of the study site

The mean temperature during the study was 26.9 °C (range: 24-29 °C). The total amount of rainfall received for 11 months (February-December 1999) was 2,094 mm which was higher than the annual average of 1,307 mm for the years 1961-1998 (**Figure 3.5 and Figure 3.6**). This can possibly be attributed to 1999 being a La Nina year, which was usually characterised by increased precipitation in the tropics (Ogallo, 2000). There are no patterns of extreme dry and wet. The island province is partially sheltered by its adjacent islands therefore typhoons are infrequent. Foraging and ranging behavioural patterns of animals can be influenced by climatic factors such as rainfall. Therefore it is important to consider this aspect when studying the ecology and behaviour of a particular species.

3.1.5 Flora

Molave (*Vitex parviflora*) forest was formerly predominant on the island of Bohol. However, due to excessive timber harvesting, only a few scattered remnants of this forest remains. Bohol has lost all its primary forest cover (DENR/UNEP, 1997). A brief survey around the island show the main vegetation types to be: (1) Beach formation forest along the coastline dominated by species adapted to sandy soil such as *Barringtonia* and *Casuarina* ; (2) Mangrove/Nipa forest predominated by *Rhizophora sp.* and occurs on the shoreline and in mouths of rivers where fresh and salt water mix. The nipa (*Nypa fruticans*) forest stand is common in estuaries; (3) Coconut and rice plantations; (3) Grassland (*Imperata* and *Saccharum spp.*); (4) Secondary growth forest with moderate-high level of disturbance; (5) Lowland evergreen forest which contain several number of species and stretches from sea level to approximately 500 m.

A total of 102 species of trees were identified in the study area. Trees with dbh greater than or equal to 5 cm were counted in the 4 x 4 100-metre vegetation sampling transects (for a

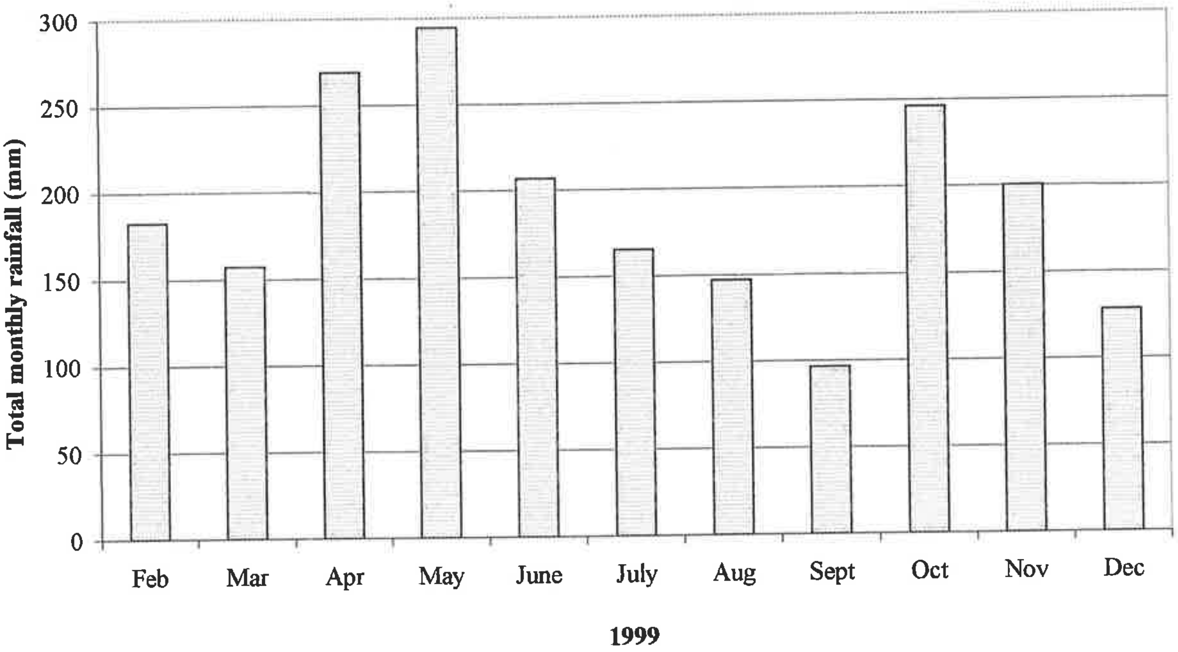


Figure 3.5. Monthly rainfall in Corella, Bohol.

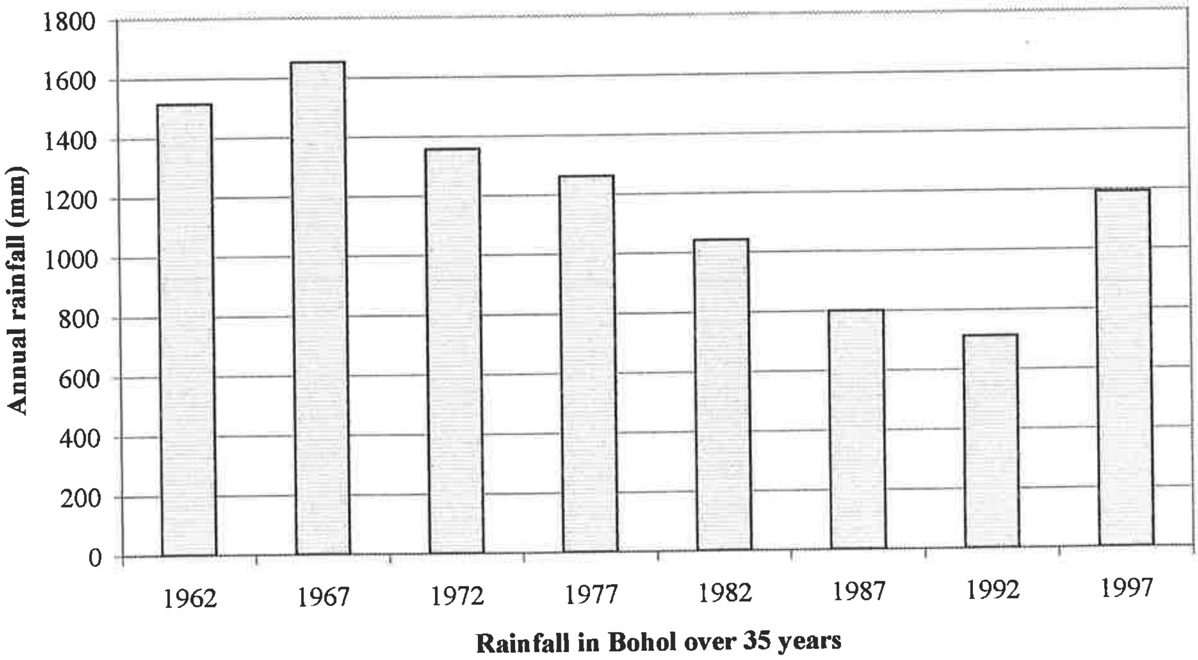


Figure 3.6. Annual rainfall in Bohol over 35 years.

total of 16 transects). **Appendix 1** givcs a list of all trees identified. There were 165, 182, 183 and 172 trees in each of the 4 x 4 100-m transects respectively. **Appendix 2** lists each tree species within the four vegetation survey sites in terms of their relative density, relative frequency, relative coverage and the importance value index. There was a total number of 33, 28, 31 and 26 species in each of the 4 x 4 100-m transects respectively. The six most important species in the study area are *Garuga floribunda, Swintonia acuminata, Gomphia angustifolia, Alstonia macrophylla and Vitex parviflora.*

The lowland evergreen type of forest and the forest over ultramafic soils are representative of the forests in the study area. The distribution of the latter type coincides with major fault lines in the country. In the study site, the species found exclusively representing the lowland evergreen rainforest were *Aglaia sp., Artocarpus blancoi, Arctocarpus heterophyllus, Evodia ternata, Leucaena leucocephala, Lunasia amara, Mallotus philipinensis, Pittosporum sp., Planchonella sp., Polyscias nodosa, Radermachera pinnata, Trema orientalis* and *Polyalthia sp.* The indicator species of forest over ultramafic soils is *Mallotus philippinensis.* Other species confined to the forest over ultramafic soils in the study site are *Alstonia scholaris, Antidesma bunius, Dinochloa luconiae, Dracaena angustifolia, Ficus balete, Ficus nota, Flacourtia sp., Guettarda sp., Harpullia arborea, Leucosyke caputata, Melia azedarach, Morinda bracteata, Polyalthia sp., Psychotria luzoniensis, Pterospermum niveum, Schefflera actinophylla, Szygium alcinae* and *Wikstroemia polyantha.* The two forest types have been extensively altered and appear now as secondary forests indicated by the presence of *Antidesma bunius, Mallotus philippinensis, Homalanthus popolneus, Macaranga bicolor, Macaranga tanarius* and *Trema orientalis.* The reserve area also contains reforestation species such as ipil-ipil (*Leucaena leucocephala*), mahogany (*Swietenia macrophylla*), *Albizzia falcata* and fruit trees such as nangka (*Arctocarpus heterophyllus*) and lubi (*Cocos nucifera*) indicating the high level of disturbance in the area.

3.1.6 Fauna

A diverse fauna both wild and domesticated was observed within the vicinity of the study site in Corella. The mammalian species that were identified included the flying lemur (*Cyanocephalus volans)*, three species of bats: short-nosed fruit bat (*Ptenochirus jagorii*), dog-faced fruit bat (*Cynopterus brachyotis luzoniensis*), Philippine leaf-nosed bat (*Hipposideros diadema griseus*), the only other primate species in the area, Philippine macaque, (*Macaca fascicularis philippinensis*), Philippine field rat (*Rattus mindanensis mindanensis*), Philippine palm civet (*Paradoxuros philippinensis*) and a variety of domesticated pig, cat, dog, water buffalo, cow and horse.

Feral cats are abundant within the reserve area and local field guides reported to me that they are the main predators of the tarsiers. Snakes are also possible predators and four species of snakes were observed and identified during the course of the study: Philippine Blunt-headed Tree Snake (*Boiga angulata*), Brahminy Blind Snake (*Typhlops braminae*), Paradise Snake (*Chrysopelea paradisi*) and Northern Triangle-spotted Snake (*Cyclocorus lineatus*). Feral cats and snakes have also been reported to be predators of *T. bancanus* and *T. spectrum* (MacKinnon and MacKinnon, 1980; Niemitz, 1984; Gursky, 1997).

The most probable competitors for food of the tarsiers in the study site are the insectivorous bats (i.e. *Hipposideros diadema griseus*) and birds. A nocturnal and insectivorous bird species observed was the Philippine frog-mouth (*Batrachostomus septimus*). It was found to be widespread in the reserve area. Contrary to some descriptions (Heaney and Regalado,

1998) I have heard this species make distinct calls at dusk specifically before hunting for food and also during mating season. Other bird species identified were the serpent eagle (*Spilornis holospilus*), small skylark (*Alauda gulgula wolfei*), little crow (*Corvus enca sierramadrensis*) and the Philippine bulbul (*Hypsipetes philippinus philippinus*).

3.1.7 ***Human Population***

The 4,117 square kilometre land area of Bohol carries *c.* 1.2 million people. As a result, the island has been heavily deforested. Rice and coconut are the major agricultural products but demand is always higher and the province at times needs to import additional rice supply from the nearby province of Negros. People also depend on fishing which is a year round activity.

Most of the people that live around the reserve area are subsistence farmers. A recent study show that their level of awareness about biodiversity and tarsier conservation is significant (Gesite, 1999). However, they have negatively affected the various parts of the reserve areas by cutting trees. It is important to note that the reserve area has no designated buffer zone and within its vicinity is an abandoned Integrated Social Forestry project (a reforestation livelihood program) leaving patches of overgrown rattan (*Calamus sp.).* The absence of buffer zones and the fact that trees are being cut are factors that are putting pressure on the remaining population of tarsiers in the area. It is evident that there is a need for active community involvement around the reserve area instead of the current limited and passive awareness.

3.1.8 Tourism

Bohol is becoming a leading tourist destination in the Philippines. The reserve area in Corella is being promoted as a major tourist attraction with the main funding for infrastructures coming from the Department of Tourism and Philippine Tourism Authority. The figures for 1997 reveal that 61,766 international and domestic tourists visited Bohol (DOT, 1998). Ecotourism can contribute revenues to the province and generate tourism-related livelihood. From a conservation standpoint, nature tourism can provide an economic justification for conservation of areas that might not otherwise receive protection (Boo, 1990).

3.2 METHODS

3.2.1 Mapping

In the complex and dense geomorphology of the study site, a system of reference points from which animal locations can be plotted was necessary. An attempt was made to fix reference points using a Global Positioning System (GPS II Plus) (manufactured by Garmin Inc., Olathe, KA). However, satellite access was limited by the >50% canopy cover, and even in open areas excessive time was required for satellite acquisition. Although taking the average of repetitive fixes at a single location can increase accuracy and precision (Johnston, 1998), the inherent error of +/- 10m was deemed unacceptable for the study of a relatively small home range. For these reasons, the technique was abandoned and reference points were fixed using a technically simple system.

A starting point was identified utilizing an existing footpath in the study area. New trails were also cut and compass bearings were taken from one tree to the next farthest visible tree with every interval forming a straight line. Their distances were measured using a field measuring tape. Trees that were used as reference points were marked with reflective flagging tapes and assigned an individual identification number. This process was continued after individuals were captured and further flagged points became necessary as the animals were tracked.

The end of the process of establishing the reference points defined the limits of the core study site, which then covered an area of *c*. 70 ha. As no aerial photographs of the area were available, the core study site was represented on paper as a grid on a scale of 1: 1,000 and used to plot the locations of the animals. Later, the grid was entered into a geographic information systems program Arcview 3.2 (manufactured by Environmental Systems Research Institute Inc./ESRI, Redlands, CA).

3.2.2 Geographic Information Systems (GIS)

Geographic Information Systems (GIS) have been increasingly used in natural resources management. The technology comprise a set of tools for collecting, storing, retrieving, transferring and displaying spatial data from the real world for a particular set of purposes (Burroughs, 1987). Its current application includes management of forested, agricultural and coastal lands and fish and wildlife planning (Bernhardsen, 1992). It also involves the study of animal populations, particularly in the protection of endangered species and their natural habitats (Aronoff, 1989; Morain, 1999). This application further encompasses the determination of the species' home range sizes and configurations, extent of overlap, density structure and distribution. Frequently, a Global Positioning System (GPS) is used to collect locational data and these in turn are integrated into GIS for spatial and/or temporal analyses (Johnston, 1998). Among the recently developed Arcview extension program is the Animal Movement Analysis (Hooge and Eichenlaub, 1997). Arcview is a fully functional GIS program that is capable of analysing geographic data in interactive maps called Views (ESRI, 1996). The Animal Movement Analysis is an Arcview program extension that works in multiple projection systems, uses the selected records (enabling complex queries or selections) and will integrate with many types of spatial data (Hooge and Eichenlaub, 1997).

There are two major approaches in representing the spatial components of geographical data: the vector and raster data models (Chrisman, 1997). The vector data model defines an area as a set of lines. Among the advantages of its use are its ability to precisely position features in space as point lines and polygons, and its ability to support graphics closely resembling hand drawn diagrams. The raster divides the entire area of interest into a regular grid of cells, and each grid square, or pixel, is defined by its row and path number; for example , 1 for forest, 2 for shrub, 3 for grassland, etc. In the raster format, overlay operations are easily implemented and high spatial variability is efficiently represented (Aronoff, 1989; Burroughs, 1987). These two data models were used for the analyses of habitat use by *T. syrichta*. **Figures 3.7 and 3.8** show the flowcharts used for Geographic information System (GIS) procedure and analysis, respectively.

3.2.3 Mistnetting and Hand Capture

Initially, mistnetting was chosen as the only capture method of choice because it has been used in four field studies of other tarsier species without mortality or injury (Fogden, 1974; MacKinnon and MacKinnon, 1980; Crompton and Andau, 1986; Gursky, 1997). There was no mortality during capture to any of the tarsiers in this study. A total of 8-15 polyester mist nets (2.5 x 12 m; 1.5 inch mesh) were randomly set up on ground level up to 2.5m above the ground around sleeping sites or in areas where tarsiers were heard vocalizing (**Figure 3.9**). Nets were opened an hour before dusk and rolled down at sunrise. The nets were initially monitored every hour. I have observed that the presence of people monitoring the nets drives

Figure 3.7. Geographic Information System Procedure Flowchart.

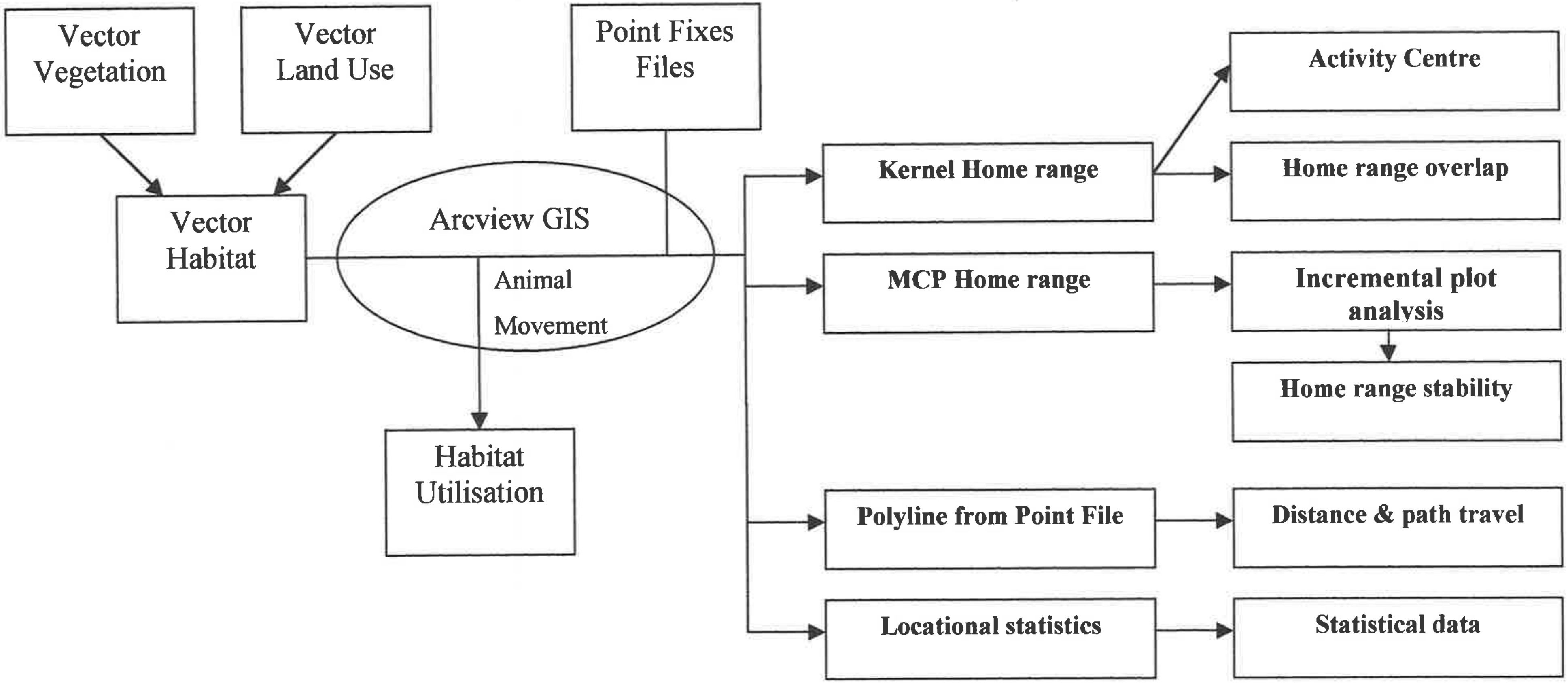
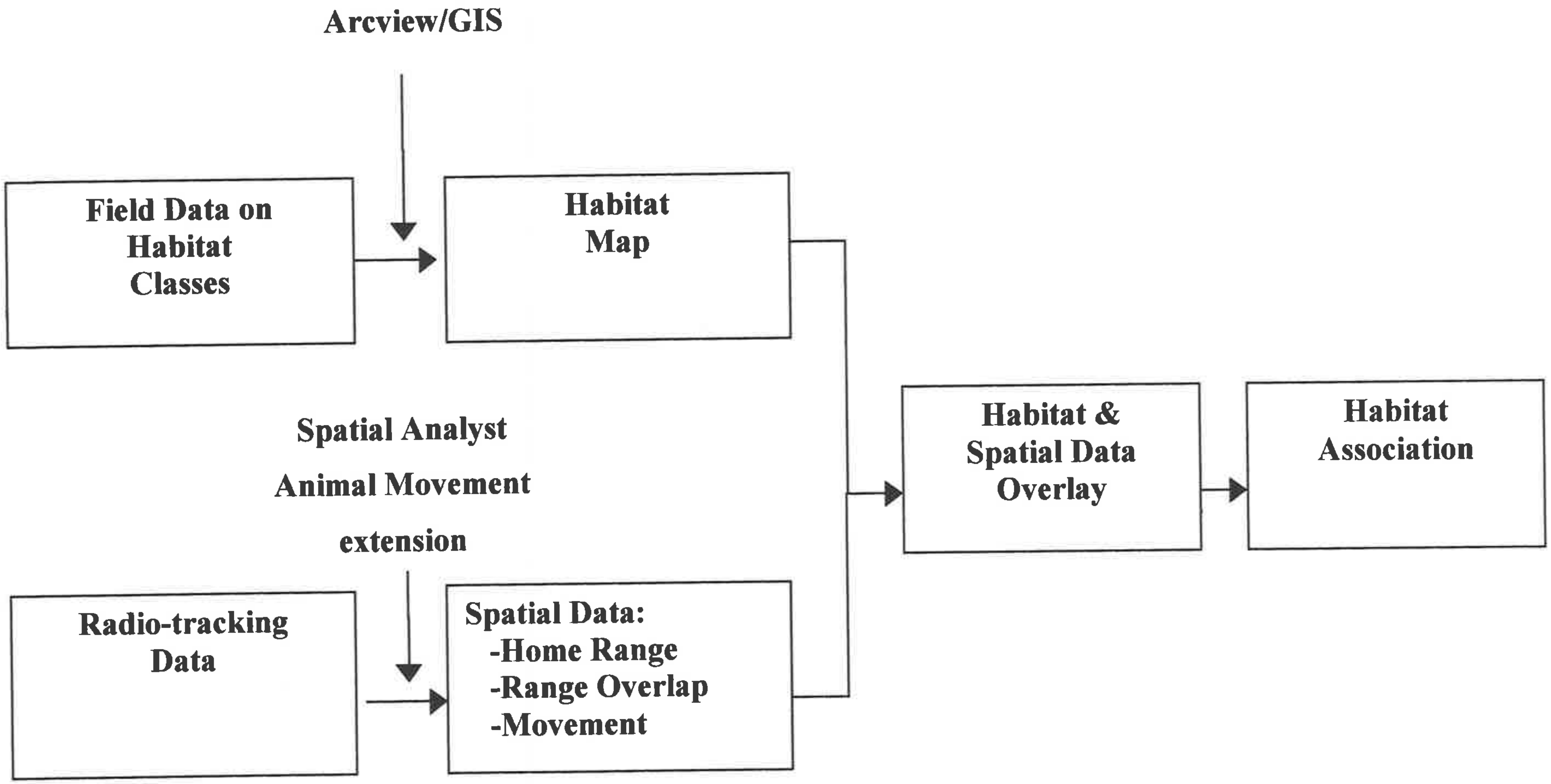


Figure 3.8. Geographic Information System Analysis Flowchart.



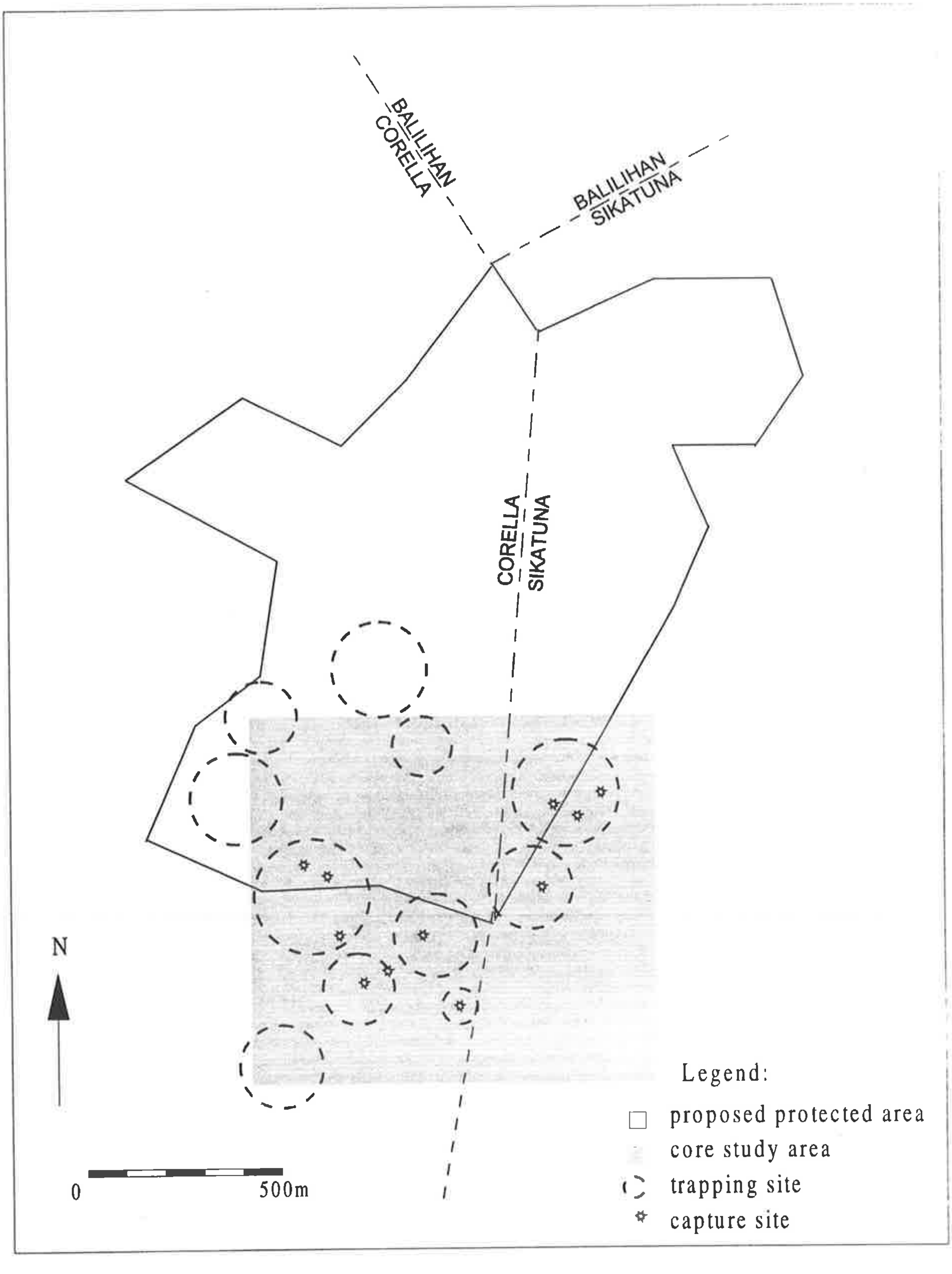


Figure 3.9. Locations of trapping sites in Corella and Sikatuna, Bohol.

away tarsier individuals, which never came near the nets again. I decided to check the nets every 3-4 h instead. However, a longer interval caused more stress to the animal as they unsuccessfully struggled to get out of the nets. Mist nets were continually transferred to other prospective locations when no animals are caught for 3-10 nights. Alternatively, hand capture was utilised to capture associated untagged individuals that evaded the nets. No association was observed between capture rate and phase of the moon or rainfall. This was tested for a total of 98 mistnetting nights.

A summary of animals caught during the study is given in **Table 3.1**. It is important to note that we never captured more than one individual in a single mist net in one night. Some captured and radio collared animals were sighted with untagged companions. However, further mistnetting within the range of these collared animals did not yield associated untagged individuals. Although study animals were never heard to elicit alarm calls as had been recorded for other tarsier species (MacKinnon and MacKinnon, 1980; Gursky, 1997) subsequent radiotracking revealed that they do avoid their capture sites for several days or even weeks. In order to catch associated individuals, I have decided to adopt an alternative method which is hand capture. Hand capture is a relatively safe and straightforward process. It is best done by an experienced tarsier handler and during daytime when the animals are resting and relatively immobile in their sleeping sites. This method has also been used on other field studies of tarsiers (Crompton and Andau, 1986; Dagosto and Gebo, 1997). Among my 11 study animals, 5 were hand captured. Retrapping 7 of my study animals was also done by hand as all attempts to recapture by mistnets were unsuccessful. Three animals lost their signals (two of the three were occassionally seen in their sleep sites) and one died (possibly due to predation) at the end of the study.

Table 3.1. Trapping records at Corella, Bohol 1999.

Animal ID	Sex/Age	Weight (gm)	Date captured	Height captured (m)	Method of capture	Recapture
4505	female/adult	132	25-Feb-99	Ground	mistnet	by hand
2730	female/adult	125	25-Feb-99	0.25	mistnet	by hand
2943	male/sub adult	105	14-Mar-99	0.50	mistnet	died
2956	male/adult	128	1-May-99	2.00	by hand	lost signal
4511	female/adult	125	1-May-99	1.75	by hand	lost signal
2843	male/adult	143	1-May-99	1.50	by hand	by hand
2963	male/adult	133	1-May-99	1.50	by hand	lost signal
2996	female/adult	107	13-Jul-99	1.50	mistnet	by hand
4523	female/adult	112	18-Jul-99	1.50	mistnet	not recaptured
4533	male/adult	138	17-Aug-99	2.00	by hand	by hand
2967	female/adult	116	28-Aug-99	1.20	mistnet	by hand

MacKinnon and MacKinnon (1980) reported similar difficulties in retrapping and were not able to recapture through mistnets any of their thirteen individuals. Crompton and Andau's (1986) field study included nine individuals and recapture records were as follows: three individuals were recaptured by mistnets, two individuals were recaptured by hand, one was lost and three were never recaptured. Similarly, out of eighteen individuals initially trapped, Gursky (1997) only managed to recapture five despite changing the position of the mistnets as well as setting the mist nets at different heights. Two of her animals removed their loop radio collars shortly after attachment. The remaining animals that had not been recaptured were each observed to leave and enter their respective sleeping sites.

3.2.4 Morphological Measurements

Upon removal of each tarsier from the mist net, captured individuals were placed in a calico bag and weighed with a Salter spring scale providing an accuracy of +/- 2 g . Physical examination through visual assessment and palpation was done to determine gender, reproductive condition (pregnant, lactating, non-pregnant, descended testes) and any possible injuries that might have been incurred during capture. The morphological measurements were taken using a flexible measuring tape and digital caliper. The measurements taken were: (1) total length; (2) tail length; (3) body length; (4) hindlimb length; (5) thigh length; (6) leg length; (7) foot length; (8) big toe length; (9) arm length; (10) forearmlength; (11) forelimb length; (12) hand length; (13) thumb length; (14) testes length; (15) testes width and (16) ear length. Definitions of these measurements are given in **Table 3.2** (Glander, 1992). Morphometric data are presented in Chapter 5: Social Organization and Reproductive Behaviour.

Table 3.2. Description of the morphological measurements taken on captured*T. syrichta* Individuals.

Measurement	Definition
Total length	was measured from the tip of the tail to the most anterior point on the head with the head in its normal position (i.e. chin near the chest).
Tail length	was measured at the ventral side of the tail from the tip of the tail to the junction of the base of the tail with the perianal region.
Body length	was the total length minus the tail length.
Hindlimb length	was measured from the groin to the end of the longest digit.
Thigh length	was measured from the groin to the center of the knee.
Foot length	was measured from the tip of the heel to the end of the longest digit
Leg length	was measured from the center of the knee to the end of the longest digit.
Big Toe length	was measured from the junction between the big toe and the second toe, to the end of the big toe, excluding the nail.
Forelimb length	was measured from the axillary region to the tip of the longest digit, excluding the nail.
Arm length	was measured from the axillary region to elbow
Forearm length	was measured from the elbow to the tip of the longest digit
Hand length	was measured from the junction of wrist and hand to the tip of the thumb
Thumb length	was measured from the junction between the first and second digits to the tip of the thumb, excluding the nail.
Testicle width	was measured from the right bottom to the left bottom of both testicles.
Testicle length	was measured from the right top testicles to the bottom of the right testicles.
Testicular volume	was calculated by 4/3 pi (.5L) $(.5W)^2$ where L=length and W=width.
Ear length	was measured from the center of the ear at its base near the skull to its longest point.

3.2.5 Radiotelemetry

Radiotelemetry has been increasingly used to study the behavioural ecology of a number of nocturnal prosimian primates, including the lesser bushbabies (*Galago senegalensis*) (Bearder and Martin, 1979); *Galago zanzibaricus* (Harcourt and Nash, 1986); aye-aye (*Daubentonia madagascariensis*) (Sterling, 1993; Ancrenaz *et al.*, 1994). This method has allowed the collection of ecological data on what otherwise would have been difficult to gather due to the cryptic behaviour of the species and the complex structure of the rainforest habitat.

My study utilised radiotelemetry or radio tracking to determine size of home range, degree of home range overlap, movements and habitat preferences of the Philippine tarsier, *Tarsius syrichta.* The principle of radiotelemetry basically involves the use of a radio receiver that is connected to a hand- held directionally sensitive antenna that traces the bearing of the source of pulsed signals coming from a battery powered radio transmitter attached to an animal. The frequency from the mounted radio transmitters allow identification of a particular individual's location (Mech, 1983; Kenward, 1987; White and Garrot, 1990).

There are two major classifications of techniques used to obtain locations of radio collared animals: triangulation and non-triangulation procedures. Triangulation method involves estimating the location of a transmitter by using two or more directional bearings obtained from known locations remote from the transmitter's position. It comes with the assumption that the radioed animal is near the point at which the bearings cross. The non-triangulation procedure is a simple and effective technique of obtaining positional data by following the transmitted signal's increasing strength until the radio collared animal is actually observed (Mech, 1983; White and Garrot, 1990). Both methods were used in this study.

The radio equipment used consisted of Biotel TX1- LD radio collar transmitters (manufactured by Biotelemetry Tracking Australia, Norwood, SA) of different set frequencies within a 150 MHz band and a pulse rate of 60 bpm. Silver oxide button- sealed 1.5 v batteries were used with an average life span of 3.7 months. The transmitter was fitted using a brass loop collar that also served as the antenna and was coated with smooth Polyvinyl chloride (PVC). Securing its two ends around each tarsier's neck with miniature brass bolts and nuts activated the transmitter. The collar had several holes to allow for easy adjustment to the neck circumference of the animal. The attachment procedure took approximately ten minutes and did not require the use of any immobilizing drug. The radio collar was ensured to have the right fit by moving it freely around the animal's neck and briefly inserting a pen through the space in between the tarsier's neck and the collar. None of my study animals were able to remove their collars after attachment. Radio collared animals were kept in confinement overnight after collar attachment. This is to allow observation on any effects the collar may have on activities such as feeding. To facilitate animal identification in the field, colored Scotchlite reflective tapes (3M Australia Pty, Ltd, Vic) were attached on the surface of the transmitter batteries on the ventral side of the animal's neck. Each individual was assigned a distinctive color or color combinations.

A hand-held RX 5 radio receiver (manufactured by Biotelemetry Tracking Australia, Norwood, SA) powered by Nickel Cadmium rechargeable batteries and alternatively 4 rechargeable 'AA' standard 1.3 v torch batteries was used for the receiving system. The receiver was tuned to a frequency band of 150-151 MHz. The small size and light weight of this particular receiver proved to be of high advantage when working in dense vegetation. The radio receiver was attached by a coaxial cable to a folding hand-held portable Yagi antenna The maximum effective reception distance at the site was 300-400 metres. The schedule of radiotracking for each individual and other relevant details for this methodology are further discussed in Chapter 4 on Home Ranges.

3.2.6 Habituation

Prior to collection of behavioural data, focal individuals were followed for a number of nights to habituate them. The animal is described as habituated when it allows an observer to approach within 1-2 m while it conducts its normal pattern of activity. Varying degrees of habituation among study individuals was evident. One adult male (ID No.= 2963) allowed close proximity observation without undergoing a distinct habituation phase. Another adult male (ID No.= 2843) would still flee even after being homed in for several sampling shifts. It eventually was habituated. An adult female (ID No.= 4508) allowed itself to be observed after 3-4 nights of habituation.

3.2.7 Informal Behavioural Observation

Study animals were tracked commencing at dusk, 17h30-18h00 hr. A focal individual was homed in on its sleeping site and observation was conducted for as long as possible or until the animal was out of sight. A standard flashlight powered with 2 rechargeable D 1.5 v batteries was used to facilitate observation. A night vision scope was found to be of limited use when observing detailed sequence of changing behavioural activities on a very small animal. Initially, a 15-minute focal behavioural sampling was utilised but the periods when the tarsiers can be clearly observed are too short, fast and very spaced out. The first alternative method used was informal or *ad libitum* behavioural sampling (Altmann, 1974).

The method of Crompton and Andau (1986, p. 339) was then utilised for behavioural counts where a single postural observation or movement served as a unit of observation. "Chained" movements were treated as multiple displacements; postural records were taken once only for each sighting of uninterrupted postural activity. Observations using five-minute intervals were also used for the activities grooming, feeding and resting when the animal could be observed for a sustained period of time.

Behavioural observations were conducted not only at dusk but also within sampling shifts at night when my field assistant and I visually encountered tracked animals while we move from one flagged reference point to another to get our bearing measurements. Visual fixes were also obtained at dawn when animals went back to their sleeping sites. Behavioural data that were collected included foraging; feeding; resting; travelling, grooming, autogrooming. The description of these behavioural activities (Gursky, 1997) is presented in **Table 3.3**. Additional data were also gathered on: substrate type, support orientation, support diameter, height from the ground and locomotor styles such as vertical cling and leap, quadrupedal walk, bipedal hop, climb, sit (Fleagle, 1988).

3.2.8 Population Density

The accuracy of estimating population density is influenced by factors such as species and habitat characteristics. *Tarsius syrichta* in particular is a nocturnal, cryptic, solitary-living species. Although the animal has a distinct call, it is generally silent (pers. observ.). In order to estimate population density of *T. syrichta*, I utilised home range data based on systematic tracking in an intensive study area.

3.2.9 Vegetation Survey

In order to characterize the vegetation of the study site, vegetation sampling in four randomly chosen locations within the 172 ha reserve area was conducted (see **Figure 3.10**). For each location, four 100 m transects were plotted giving a total number of 16 transects in the four randomly chosen sites. The point quarter sampling method was used to sample the trees in the study area (Brower *et al.*, 1991). The height and diameter at breast height (dbh) of each tree were recorded. All trees were identified to the lowest possible taxonomic unit.

Table 3.3. Definition of behavioural states of tarsiers.

Behaviour	**Definition**
Forage	Actively searching the ground or leaves or air for a moving prey item. This also involves ear twitching while trying to locate prey auditorally, but primarily involves active scanning behaviour. Head may not be in normal position, turned from 0 degrees. Also includes travel movements while searching for food.
Feed	The animal is actively eating a prey item. This includes all handling time of prey such as putting the prey into the mouth.
Rest	The animal is motion less. Its ear and head are not moving. Its head is not rotated from the normal position. Its eyes may be closed and the animal may be sleeping.
Travel	Actively moving from one support to another via various locomotor styles such as vertically clinging and leaping, quadrupedal walkism and climbing. Exclude movements while actively foraging.
Social	Grooming others, vocalizing play grappling (running and jumping and tail pulling).
Transport	Infant is located within the mouth or clinging on to the fur of an individual who is travelling.
Miscellaneous	Grooming self (scratching with the grooming claw or toothcomb, may include marking own body with scent glands), cleaning body with tongue or hands like a cat and or toothcomb).

In order to quantitatively describe the tarsier's habitat, additional indices were calculated (Brower *et al.*, 1991), these were: Relative Species Coverage, Relative Species Density, Relative Species Frequency and Importance Value Index. Relative Species Density (RD_I) is

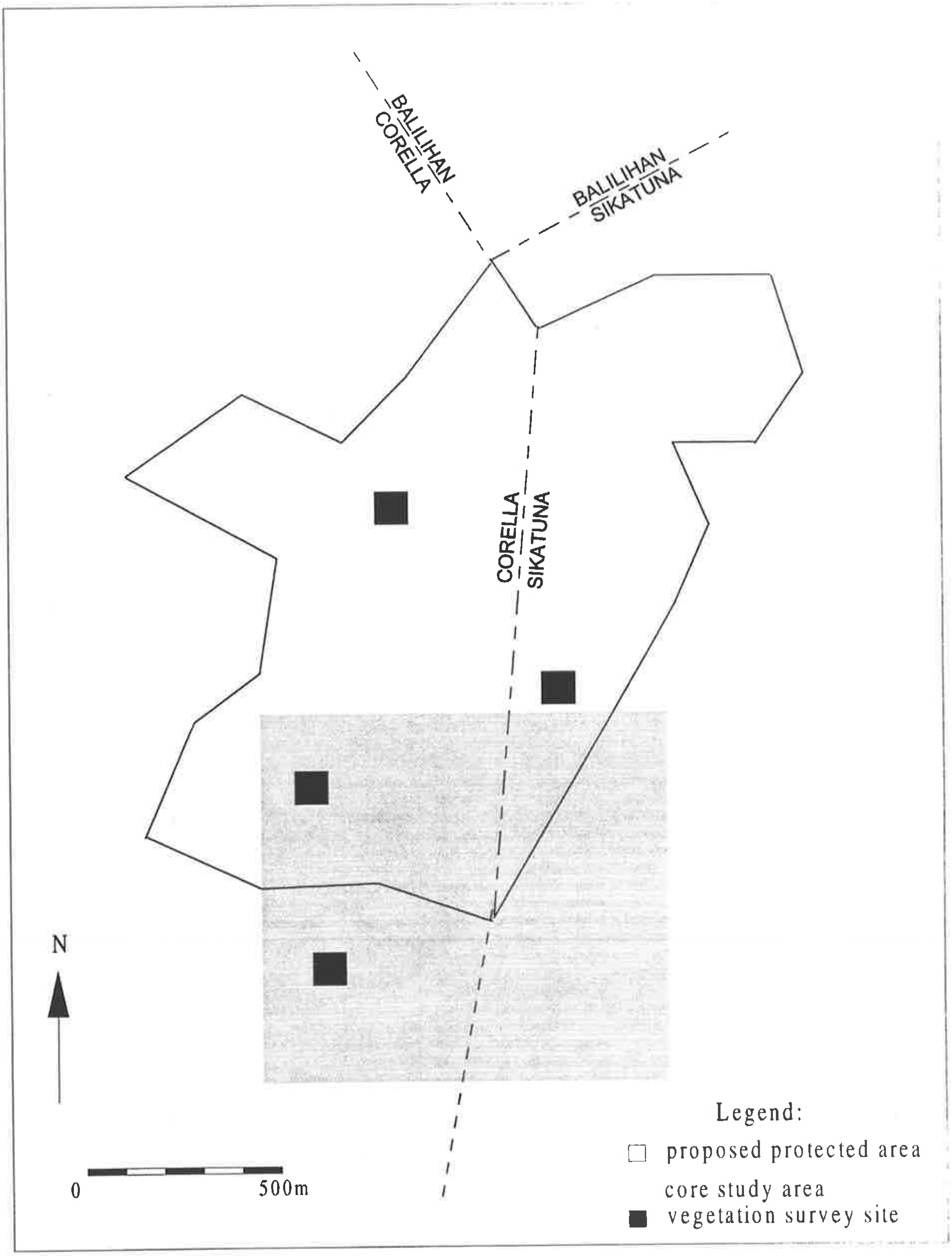


Figure 3.10. Locations of vegetation survey sites in Corella and Sikatuna, Bohol.

the number of individuals of a given species (n_I) as a proportion of the total number of individuals of all species (ΣN): $Rdi = n_I / \Sigma N$. Relative frequency (R_f) is the frequency of a given species (f_I) as a proportion of the sum of the frequencies for all species (Σf): $Rf_I = f_I / \Sigma f$. Coverage is the proportion of the ground occupied by a vertical projection to the ground from the aerial parts of the plant. The relative coverage (RC_I) for the species *i* is the coverage for that species (C_I) expressed as the proportion of the total coverage (TC) for all species: (C_I) expressed as the proportion of the total coverage (TC) for all species: $RC_I = C_I / TC$. The sum of the above three relative measures for each species is called the Importance Value (IV_t): $IV_I = RD_I = RF_I + RC_I$ (Brower *et al.*, 1991).

3.2.10 Rainfall Data Collection

Daily rainfall was recorded to the nearest millimetre from February 1999-December 1999 using a Nylex standard rain gauge with a capacity to collect a maximum of 250 mm of rain at one time.

Chapter 4:

Home ranges, spatial movements and habitat associations

CHAPTER 4: HOME RANGES, SPATIAL MOVEMENTS AND HABITAT ASSOCIATIONS

4.1 INTRODUCTION

Since the late 1960s, there has been a marked decrease in tropical rainforest cover in the Philippines (Collins *et al.*, 1991; Kummer, 1992; Kummer and Turner, 1994, Whitmore, 1997). The resultant loss of habitat has been of major concern as a factor contributing to the population decline of several endemic mammalian species such as *Tarsius syrichta* (Heaney, 1993, Wildlife Conservation Society of the Philippines, 1997). Prior to this study, there is very little known on the behaviour and ecology of *T. syrichta*. The species has been described to occupy a wide variety of habitat which included coastal bamboo forests (Fulton, 1939); secondary and third growth forests in coastal areas and valleys (Wharton, 1948), mixed secondary forest and agricultural land between 50 and 100 m elevation, and primary lowland and montane forests between 300 and 700 m elevation (Rickart *et al.*, 1993). However, most of these descriptions were based on informal encounters and anecdotal reports and no systematic sampling was done to determine the size of the tarsier population and the extent of range use within the habitats described.

A preliminary survey provided data on male home range size only (n=2) (Dagosto and Gebo, 1997). This study was conducted to fill this gap. In order to implement an effective conservation plan, it is important to understand the spatial and habitat requirements of the animal in an increasingly fragmented landscape of small forest patches. To achieve this, a radio-tracking study was conducted to determine the spatial behaviour and habitat use by free-ranging Philippine tarsiers in Corella, Bohol. The principal objectives of this chapter are: 1) to determine home range sizes and configurations; 2) to describe movements and activity patterns of the animal; 3) to examine habitat associations using vegetative cover and land use patterns.

4.2 METHODS

4.2.1 Radiotelemetry

The tarsiers were tracked on foot using hand-held RX 5 radio receivers and portable 3-element Yagi antennas that were described in detail in Chapter 3. The radiocollared animals were tracked using a combination of continuous and discontinuous monitoring. A single sampling shift can be equivalent to 12 hours: dusk (18h00) to dawn (06h00) or 6 hours: dusk (18h00) to midnight (24h00) or midnight (24h00) to dawn (06h00). Continuous tracking involved following the movements of an animal through an entire sampling shift and taking bearings at 15-minute intervals. This allowed one animal to be tracked at a time. Discontinuous tracking involved taking locational bearings at one-hour intervals. This allowed tracking of as many as three animals in one night.

Two types of location estimate were obtained. 'Exact" fixes were obtained by homing in on the collared individual. This was usually done during continuous tracking when only one animal was followed within an entire sampling shift and behavioural observations made possible. 'Bearing' fixes were obtained by simultaneous triangulation from identified reference points (e.g. trees tagged during mapping) and animal positions were estimated. Simultaneous triangulation was made possible with my assistant and I having synchronised timers. The hilly terrain, dense vegetation and small size of the transmitter required directional bearings to be made within 50 m of the tarsier. The discontinuous tracking involved 2-3 individuals being tracked sequentially on an hourly interval within a single sampling shift. Data derived from both continuous (four 15-minute interval readings treated as a single fix) and discontinuous tracking were used for the home range and habitat utilization analysis. Nightly travel distance was calculated using only points from the 15-minute interval tracking.

All home range calculations were done using the Geographic Information Systems (GIS)/ Arcview 3.2 (Environmental Systems Research Institute Inc./ESRI, Redlands, CA) program extension Animal Movement Analyst (Hooge and Eichenlaub, 1997). I chose non-parametric methods to calculate the home-range size and centre of activity of the animals: the minimum convex polygon, MCP (Mohr, 1947; Southwood, 1966) and the Kernel Home Range method of analyses, KERNEL (Worton, 1989) using the 95% and 50% isopleths. The MCP is the simplest and most common method used and provides a good basis of comparison with related studies. The Kernel method was chosen for calculating utilization distribution instead of the more widely used Harmonic Mean HMM (Dixon and Chapman, 1980) for the following reasons. The HMM: 1) is highly dependent on grid origin and spacing (Worton, 1987, 1989, White and Garrot, 1990); 2) The reciprocal kernel function on which the method is based results in the central observations having an unduly large influence on outer areas (Worton, 1995). For these reasons, the Animal Movement Analyst program does not directly output an area measurement and does not calculate the utilisation distribution for the Harmonic Mean. The merits of the Kernel method include the following: 1) It is highly flexible and able to fit nonconvex, multimodal irregularly shaped distributions; 2) It can produce a density estimate directly; 3) Grid size or placement (Silverman, 1986; Worton, 1987; Seaman and Powell, 1996 and Seaman *et al.*, 1998) does not influence it. A significant difficulty with the Kernel method is its sensitivity to the choice of an appropriate smoothing parameter *h* (Wray *et al.*, 1992; Seaman *et al.*, 1998). However, using least squares cross validation (LSCV), a jackknife method which uses an iterative approach in selecting the smoothing width, minimizes the estimated error for a given sample (Silverman, 1986; Seaman *et al.*, 1998). The limitation of the LSCV is that it does not work acceptably for datasets with multiple observations at identical locations such as trap grid data, and animals in dens or nests (Silverman, 1986; Tufto *et al.*, 1996; Seaman *et al.*, 1998). Since my study animals did not fall into any of these categories, I considered my choice of the Kernel method to be valid. The Animal Movement Analyst program automatically calculates the LSCV for the smoothing parameter *h*. Hooge and Eichenlaub (1997) found this method to provide a less biased Kernel estimator. The stability of home ranges and sufficiency of number of fixes were checked by incremental plot of home range area against fixes which were added sequentially by increments of five location points (Harris *et al.*, 1990). The animals with stable home ranges are expected to reach an asymptote, while floaters should increase their ranges progressively. Differences in home range between sexes were tested with two-way analysis of variance (ANOVA). The point to point distance travelled by a study animal was computed using the Create Polyline from Point File option under the Animal Movement program.

4.2.2 Radiotelemetry Bearing Accuracy

It is very important for every radiotracking study to test for the accuracy of the procedure being conducted. This holds especially true in cases wherein estimates of position of a focal individual are done through remote triangulation from pairs of fixed or mobile receiving stations (**Figure 4.1**) (Mech, 1983, White and Garrot, 1990) instead of homing in and obtaining visual fixes. Several factors influence the accuracy of collecting locational data through triangulation: landscape topography, weather, vegetative cover, inter observer reliability and behavioural traits of the study animal (MacDonald and Amlaner, 1980; Hupp and Ratti, 1983; White and Garrott, 1990). My study utilised both homing

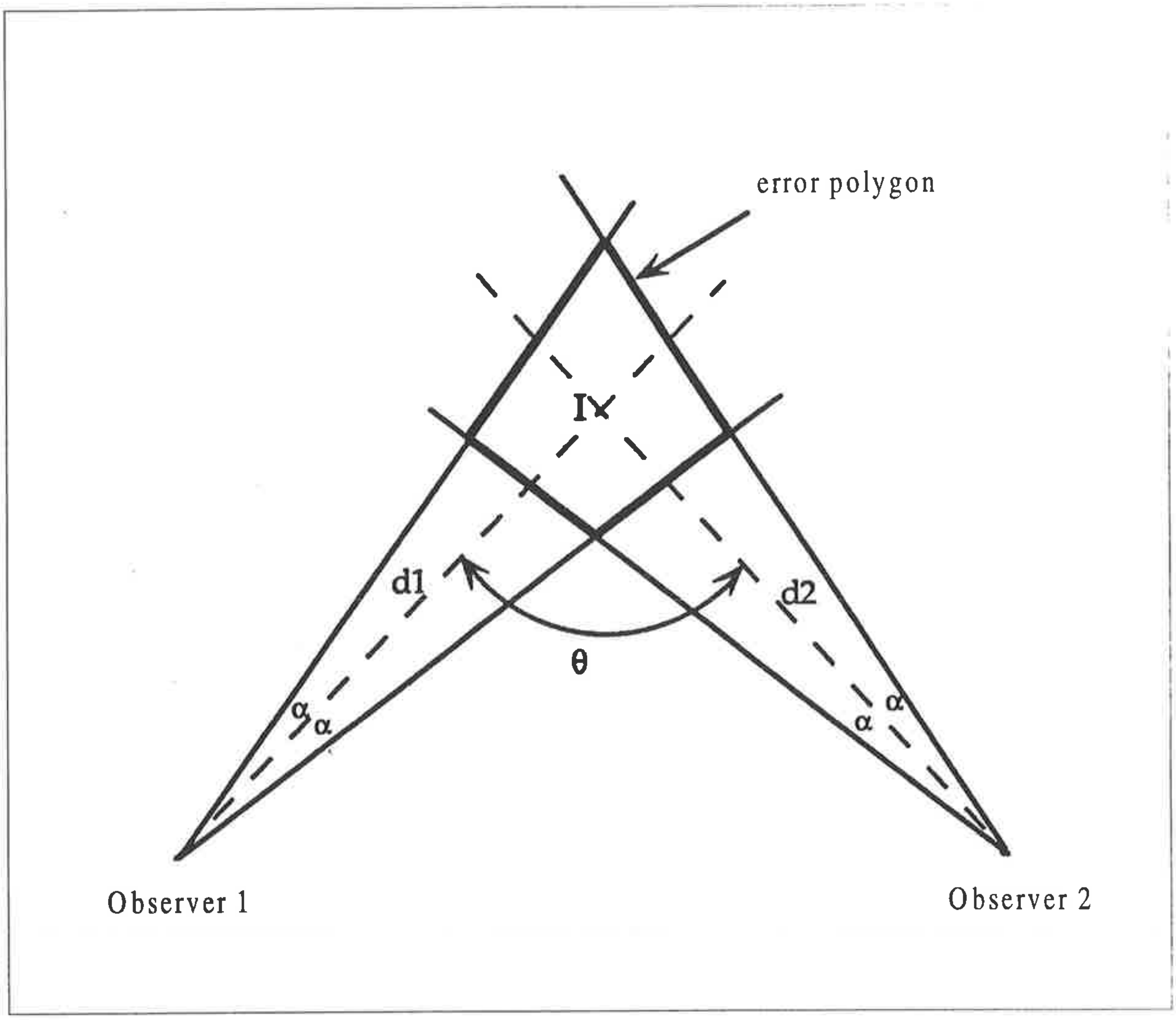


Figure 4.1. Bearing triangulation geometry.

in and triangulation methods. I conducted a series of accuracy tests between a field assistant and myself for the triangulation method.

Accuracy tests were done within the 70-ha core study site, on the second month of radiotracking study thereby allowing time to identify strengths and weaknesses and make further improvements. The equipment used were the same ones previously described under Radiotelemetry. One person placed a transmitter on a tree branch 1-1.5 m above the ground and marked the branch with a colored flagging tape. A measuring tape was used to form a straight line from the flagged tree branch to a known receiver location. After the distance has been measured, the true bearing of the planted transmitter was taken using a compass and the flagging tape was removed. The other person stood on the known receiver location and took estimated bearings, using a hand- held compass from positions where the strongest signal is coming from. If the strongest signal cannot be sharply discerned, we alternatively used the 'null-average' technique (Kenward, 1987). The person taking the bearings was always unaware of the true location of the transmitter.

In order to estimate overall system precision (s_p) and observer bias ($bias_{obs}$) we used twelve different receiving stations and 24 transmitter locations. The transmitter locations covered an area most regularly used by two of my study animals. Each observer took bearings of 12 transmitter locations from six of the twelve stations. Measurements were recorded from stationary collar as it was difficult to simulate active and moving signals in dense tropical forest vegetation. At each site, error was measured as the degree of deviation between the true transmitter bearing and the bearing determined by monitoring the radio signal. The tests were conducted during the period April 15-16, 1999. To investigate variation in sampling error, we took three sets of repeated measurements for each different transmitter location.

Each set of repeated measurements was performed consecutively by one person within a given morning or afternoon.

4.2.3 Independence of Movements

The problem of autocorrelation in serial fixes (Swihart and Slade, 1985; 1986; 1997) was taken into account to ensure independence of locational observations. I calculated the Schoener's ratio t^2/r^2 (Schoener, 1981; Swihart and Slade, 1985) for each individual (**Table 4.2**) and have taken into consideration the body weight of the animal (Harestad and Bunnell, 1979; Swihart *et al.*, 1988). Based on these parameters, a 40-75 minute-interval was determined to ensure independence of fixes. For computational simplicity, I have rounded it to 60-minute intervals.

4.2.4 Habitat Classifications

The core study area was traversed by foot and mapped according to vegetation type. Areas were classified as (1) secondary lowland evergreen forest; (2) shrubland; (3) grassland; (4) bamboo clumps; (5) agricultural land; (6) residential and (7) water/swamp. Any patch larger than approximately 10 m in diameter was mapped. The classifications were assigned based on physical characteristics and land use pattern.

Secondary lowland evergreen rainforest' was defined as canopied woods with thick understorey vegetation. This was further subdivided into late succession forest – trees more than 15 m in height and early-mid succession forest – trees with height ranging from 5.0–15 m. 'Shrubland' consisted of open, dense sapling growth, generally from 1.0–5.0 m in height. 'Grassland' areas contained weeds, short and tall grasses with height from ground level up to 1.0 m. 'Agricultural' areas were comprised of rice fields and coconut plantation. 'Bamboo clumps' were scattered patches of native bamboo species. 'Clearings' were formerly vegetated areas but are now mainly bare ground with few patches of grasses. 'Residential' areas were comprised of *c.* 10 houses and their immediate surroundings. Finally, 'swamp' was used to describe the only body of water found on the study site. **Figure 4.2** illustrates the vegetation and land-use map of the study site. **Figures 4.3 a and b, 4.4 – 4.6** show portions of the study site that represent the habitat classifications described above.

4.3 RESULTS

4.3.1 Triangulation Bearing Accuracy

The bias and precision of triangulation bearings obtained during tarsier tracking were estimated based on the results of our accuracy test. Bias was 0.5 ° (bearings too far anti-clockwise) and precision ± 3.2 ° (1 SD) ($P < 0.05$, n = 72), mean locational error was 0.4m ± 1.6m (1 SD) ($P < 0.05$, n = 72) at a mean working distance of 23.1 m (Mean working distance = average for several bearings taken for one fix). This is within the distance (3-50 m) that my field assistant and I used during actual radiotracking.

4.3.2 Home Ranges

Home ranges were estimated over an 8-month period for four adult males and six adult females. A total of 642 radiotracking hours was spent collecting field data (**Table 4.1**). Since the wet and dry seasons are not pronounced, it was not possible to discern a seasonal effect on home range size. For purposes of comparison, home range sizes were calculated during months of least and highest rainfall. There were no observed differences in home range sizes among individuals in relation to monthly rainfall patterns (Simple linear regression, range: $P = 0.118\text{-}0.977$, $n = 9$). An attempt was also made to examine the effect of breeding season on

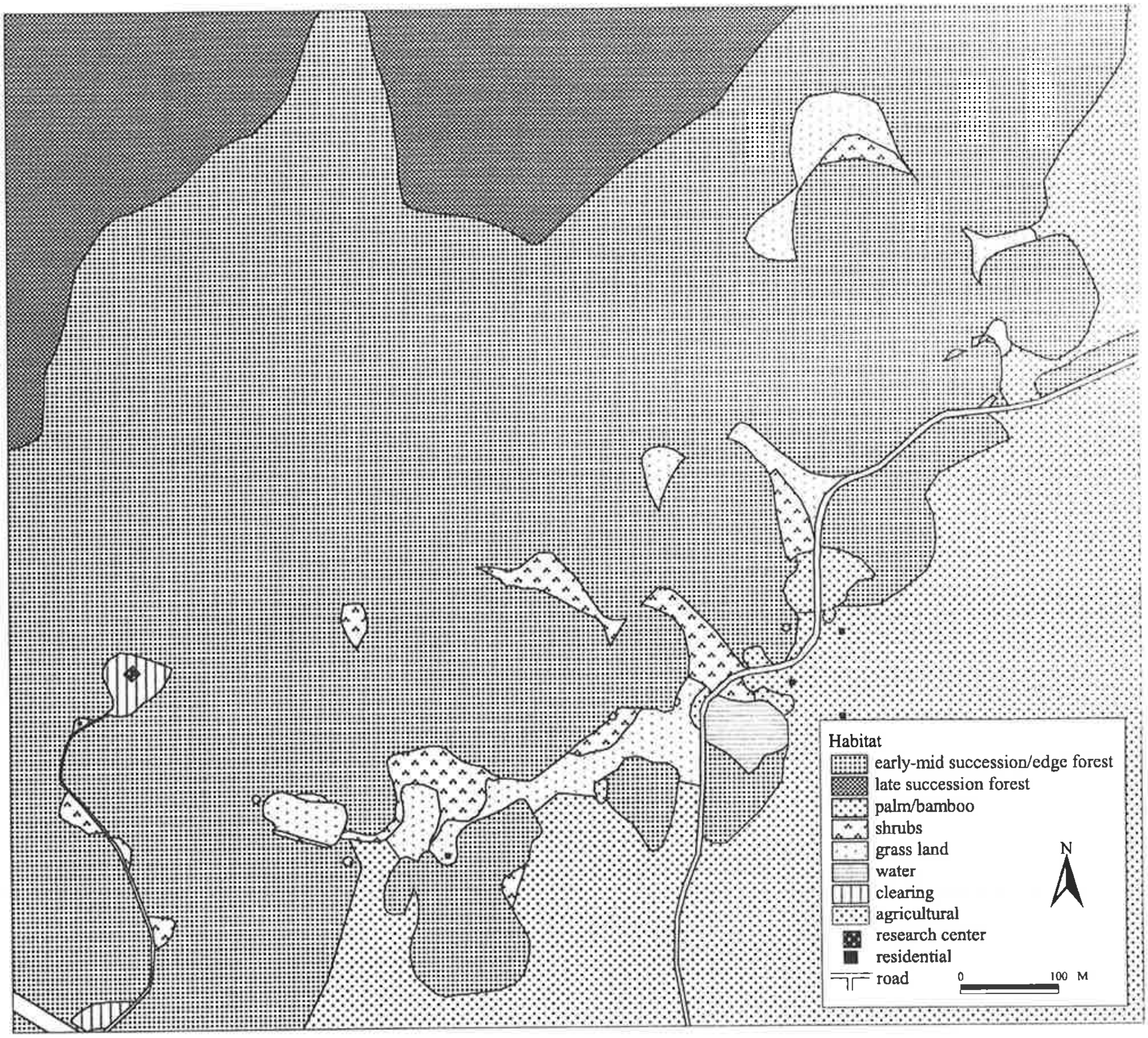


Figure 4.2. Habitat map of the study site.

Figure 4.3 a and b. Habitat gradient showing grassland, shrubland, early-mid succession forest and late succession forest.

Figure 4.4. Open grass corridors flanked by patches of native bamboo species.

Figure 4.5. Agricultural land comprised mainly of rice and coconuts

Figure 4.6. The swamp representing the only body of water in the study site

home range size. Based on the birthing patterns observed within the duration of the study (**Figure 4.7**) and the available literature on average gestation length of tarsiers: 180 days for captive *T. syrichta*, 191 and 178 days for wild *T. spectrum* and captive *T. bancanus* respectively (Izard *et al.*, 1985, Roberts, 1994, Gursky, 1997), the breeding season was estimated to fall in the months from November to January. Unfortunately, access to the study area was limited to the months February to October. Therefore, all fixes were combined to examine the overall home range of each individual during the period of the study.

The number of fixes required for an incremental plot of home range area (using MCP) of fixes to asymptote was 71.3 (+/- 21.4) for adult males and 42.5 (+/- 18.6) for adult females. Subadult male 2943 did not have a stable home range as indicated by its progressively increasing area plot (**Figure 4.8**). The average home range area was 6.86 ha for males and 2.76 ha for females using MCP, and 6.03 ha for males and 2.14 for females using Kernel 95% Home Range estimate. The average home range area using both MCP and Kernel 95% was 6.45 ± 1.68 ha (n = 4) for adult males and 2.45 ± 1.43 ha (n = 6) for females (**Table 4.2**) (**Figure 4.9, Appendices 4 and 5**). There were no significant differences between the estimated home range areas using either MCP or KERNEL 95% (Two-sample t-test: t = -0.60, d.f. – 18, P = 0.553). However, between sexes, male individuals had significantly larger home ranges than females (Two-way ANOVA, P < .001). The subadult male had a mean home range of 13.4 ha (13.6 ha and 13.1 ha for MCP and Kernel 95% respectively). This subadult male individual was considered to be dispersing as indicated by its progressing incremental plot of home range area which did not asymptote. Hence, it was not included in the over-all analysis of home range data. It eventually died after the second month of tracking, possibly due to predation by a stray cat. The radio-collar was recovered from the

Table 4.1. Basic information on radio-tracking for estimation of home range of tarsiers.

Individual number	Sex	Age	Date of Capture	Total no. of fixes taken	Tracking Period
2730	female	adult	25/02/99	97	3 mos, 15 days
2967	female	adult	26/08/99	93	1 mo , 13 days
2996	female	adult	13/07/99	123	2 mos, 21 days
4505	female	adult	25/02/99	84	3 mos, 21 days
4511	female	adult	01/05/99	100	4 mos, 4 days
4523	female	adult	13/07/99	76	2 mos, 28 days
2843	male	adult	01/05/99	109	4 mos, 0 day
2956	male	adult	01/05/99	64	1 mo , 21 days
2963	male	adult	01/05/99	99	3 mos, 24 days
4533	male	adult	17/08/99	90	1 mo , 11 days

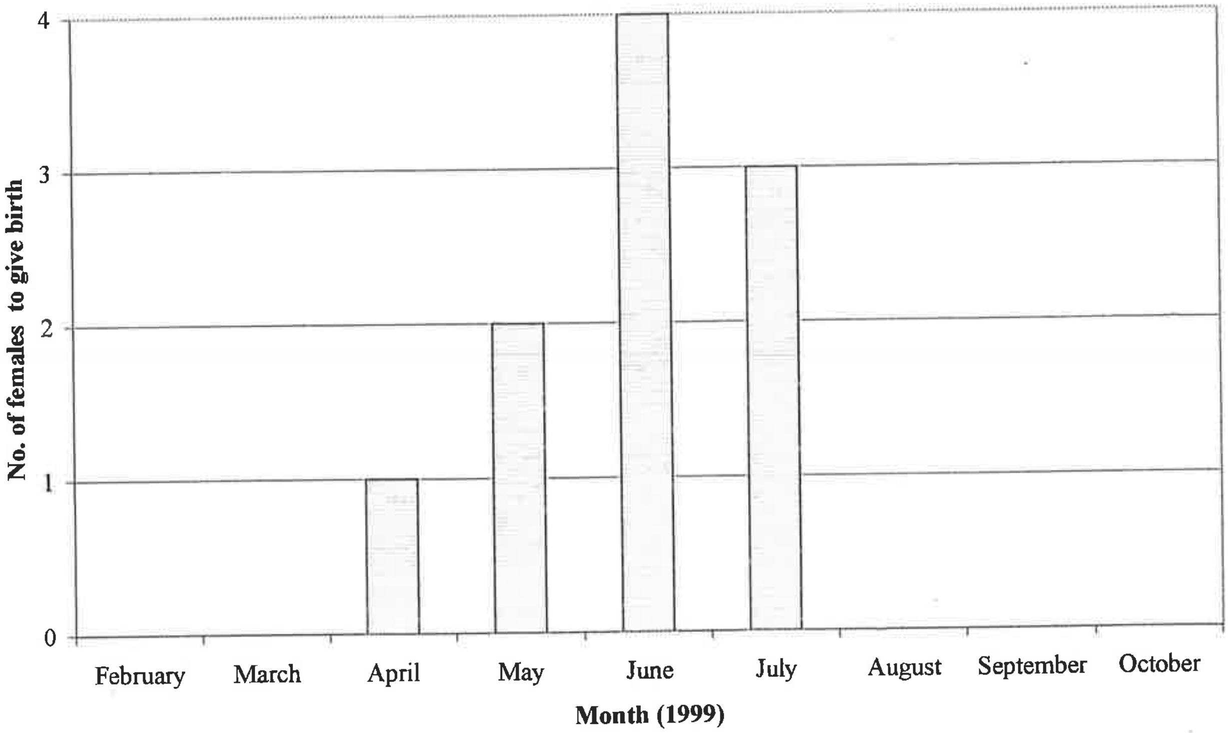


Figure 4.7. Birth months for the collared and other non-collared females.

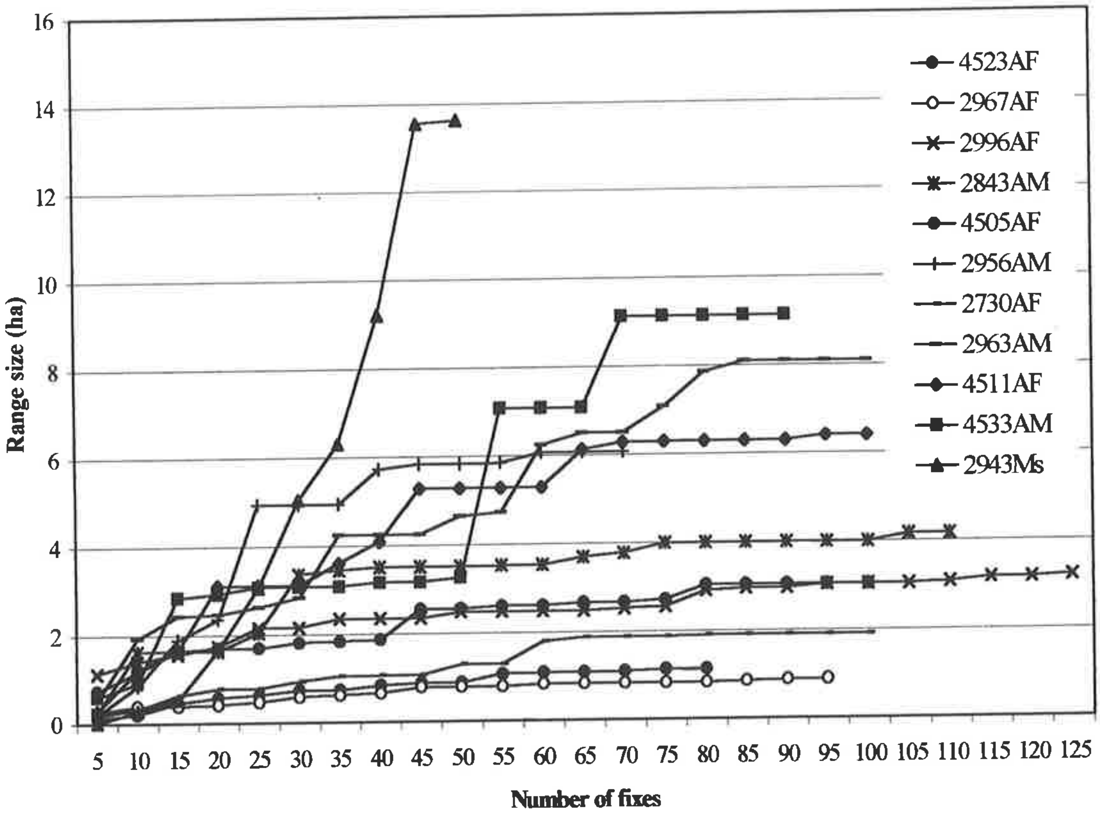


Figure 4.8. Incremental area plot of the radio tagged tarsiers. Range size calculated by MCP.

Table 4.2 Philippine tarsier home range estimates calculated for minimum convex polygon (MCP) and Kernel analysis (KER) 95%, determined by radio-telemetry locations.

ID No.	Age/Sex	Body	Home Range (ha)			Schoener's ratio
			MCP 100%	KER 95%	Mean MCP & 95%	
2730	AF	125	1.90	1.39	1.65	1.17
2967	AF	116	0.89	1.12	1.01	1.19
2996	AF	107	3.21	2.83	3.02	0.83
4505	AF	132	3.04	3.72	3.38	1.36
4511	AF	125	6.40	2.41	4.41	1.57
4523	AF	112	1.14	1.35	1.25	1.39
2843	AM	143	4.16	4.06	4.11	1.26
2956	AM	128	6.07	6.68	6.38	0.76
2963	AM	133	8.09	7.56	7.83	0.80
4533	AM	138	9.13	5.83	7.48	0.89

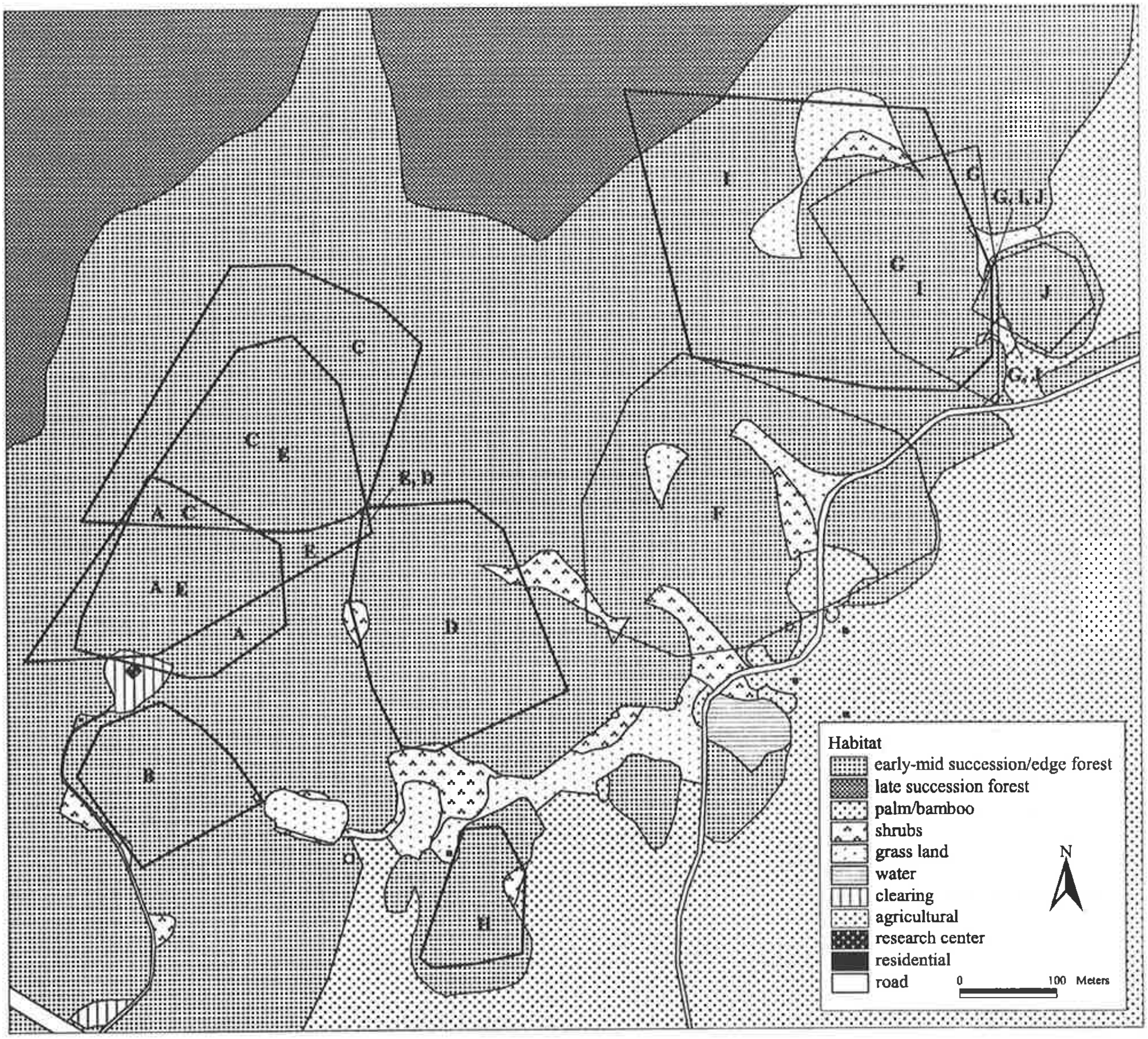


Figure 4.9. Minimum convex polygon (MCP) home ranges. The letters represent tarsier individuals (A=4505; B=2730; C=4511; D=2843; E=2956; F=2963; G=2996; H=4523; I=4533).

remnants of the carcass, which was partially buried under leaf litter. Habitat configurations using MCP and Kernel 95% and 50% are shown in **Appendices 3, 4 and 5**. The patterns of range overlap are discussed in Chapter 5 as they relate to the social organization of the species.

4.3.3 Sleeping Sites

Radio collared individuals were observed to utilise 1 primary and several alternative sleeping sites. Males tended to move from one sleeping site to another on a more frequent basis than the females. Males utilised an average of 7-8 sleeping sites while females tended to limit their sleeping sites to 3-4 different locations over the entire duration of the study. Females returned to their most favoured sleeping sites on a more frequent basis (almost every night) compared to males. All the collared females in this study were at one stage either pregnant, gave birth, carried and nursed an infant. These different physiological stages definitely influenced patterns of movements. Each study animal was observed to be solitary in its sleep sites and while foraging at night. The closest distance noted between sleep sites was approximately 5 m between a male and a female with a baby. Strictly speaking, these individuals were not sharing the same sleep site. **Table 4.3** lists identified tree species utilised as sleeping sites. **Figure 4.10** shows the use of *T. syrichta* of different types of sleeping sites. The sleep sites of *T. syrichta* were highly variable. They ranged from rock crevices near the ground, to vine tangles, dense thickets of *Pandanus*, palms, tree trunks and fork branches of trees, 5 m above the ground. Individuals were observed to cling on tree trunks while sleeping. Trees used for sleeping sites included species such as *Ficus*, *Pterospermum*, *Szygium*, *Pisonia*, *Gnetum*, *Trema*, *Evodia*, *Arenga* and *Colona*. Some sleep sites were located on the periphery of the forest near houses, although tarsiers were never observed to foray into residential areas.

Table 4.3. List of identified sleep trees.

Genus	Species	Tree Height (m)	Height use of tarsier from ground (m)
Arenga	*pinnata*	5.29	1.25
Colona	*serratifolia*	5.18	2.75
Ficus	*benjamina*	8.02	1.75
Ficus	*chrysolepis*	12.50	1.5
Ficus	*cumingii*	10.15	1.0
Ficus	*gigantifolia*	12.32	1.5
Ficus	*pubinervis*	5.46	2.5
Evodia	*ternata*	4.96	1.75
Gnetum	*gnemom*	8.25	1.38
Pisonia	*umbellifera*	4.18	1.63
Pterospermum	*obliquum*	10.34	1.0
Pterospermum	*niveum*	7.13	1.75
Syzgium	*claviflorum*	5.76	1.5
Trema	*orientalis*	5.84	1.5

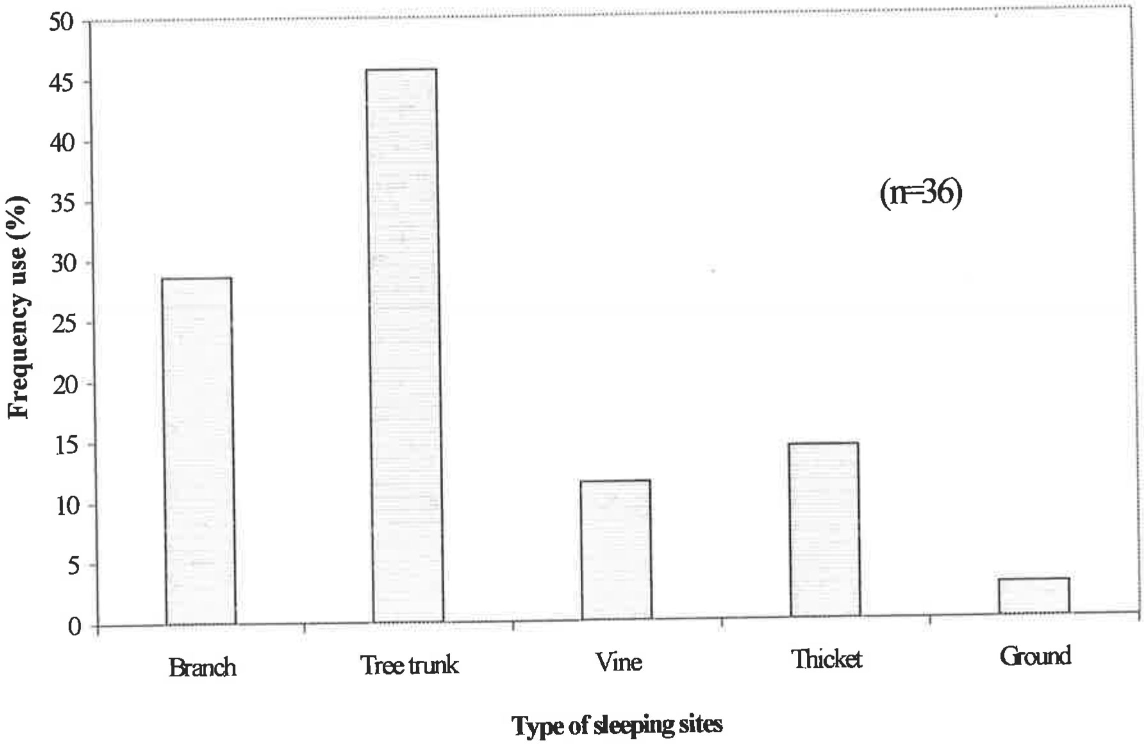


Figure 4.10. Types of sleeping sites used by individual tarsiers, based on a total of 36 observations of 10 individuals.

4.3.4 Movements and Activity Patterns

Nightly activity patterns (**Figure 4.11**) show that tarsiers were most active at dusk, with a peak of activity between 18h00 hours and 19h00 hours, although these patterns may vary between individuals (**Figure 4.12 and 4.13**). Results of continuous monitoring were obtained for individual tarsiers for a total of 21 twelve-hour shifts (dusk to dawn; **Table 4.4**). The mean distance travelled during a single night was 1,636 m for adult males (4 tarsiers followed for a total of 8 nights) and 1,119 m for 6 adult females (13 nights). The most extensive movement in one 12-hour shift (point to point distances summed) was by an adult male ID No. 4533 who travelled 2,284 m (with 336.4 m between the most distantly separated points) (**Figure 4.14**). The greatest distance between two succesive points during a 15-min interval was 336.4 m by an adult male ID No. 2956. The shortest recorded distance travelled in a 12-hour shift was 659 m by an adult female ID No. 2730 (**Figure 4.15**). This observation was taken 15 days before female ID No. 2730 gave birth. Casual observations during the day revealed that individuals were almost totally inactive. Aside from sleeping and resting, grooming for brief periods were the only other activity observed.

T. syrichta did not use their entire home range area on a per night basis (12-hour, dusk to dawn shift). Males on an average utilised a larger percentage of their home range per night than females. For example, a male individual ID No. 2843 used 74% of its range area on June 18. Male individual ID No. 4518 used only 18% of its home range on June 25, while female individual ID No. 4511 used only 6% of its area on June 26. A non-random pattern of range use was observed among the tarsiers during the study. The pattern of range utilisation in tarsiers suggests searching for food items and exploratory movements. Males tended to traverse the periphery of their range frequently and travel from one end to the other end, often using a different sleeping site from that used the previous night (**Figure 4.16**).

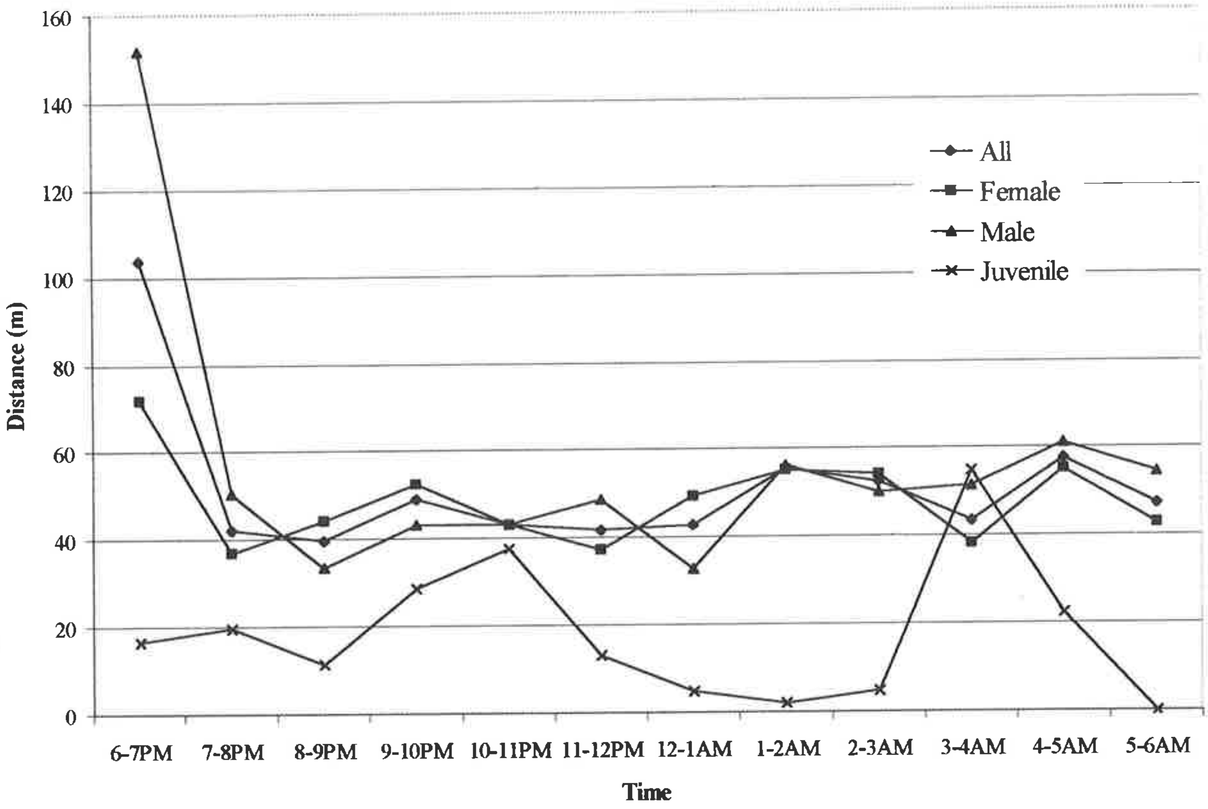


Figure 4.11. Nightly activity patterns of 11 tarsier individuals. Shows hourly average distance travelled from 18h00 to 06h00.

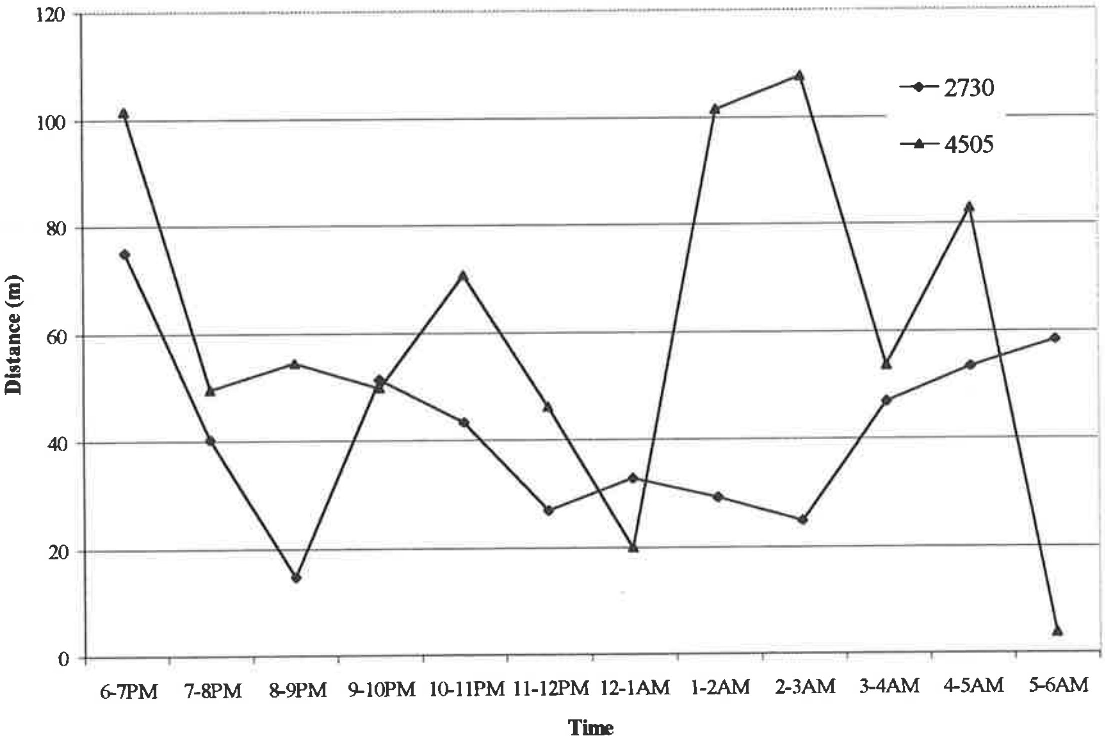


Figure 4.12. Nightly activity patterns of individuals 2730 and 4505. Shows hourly average distance travelled from 18h00 to 06h00.

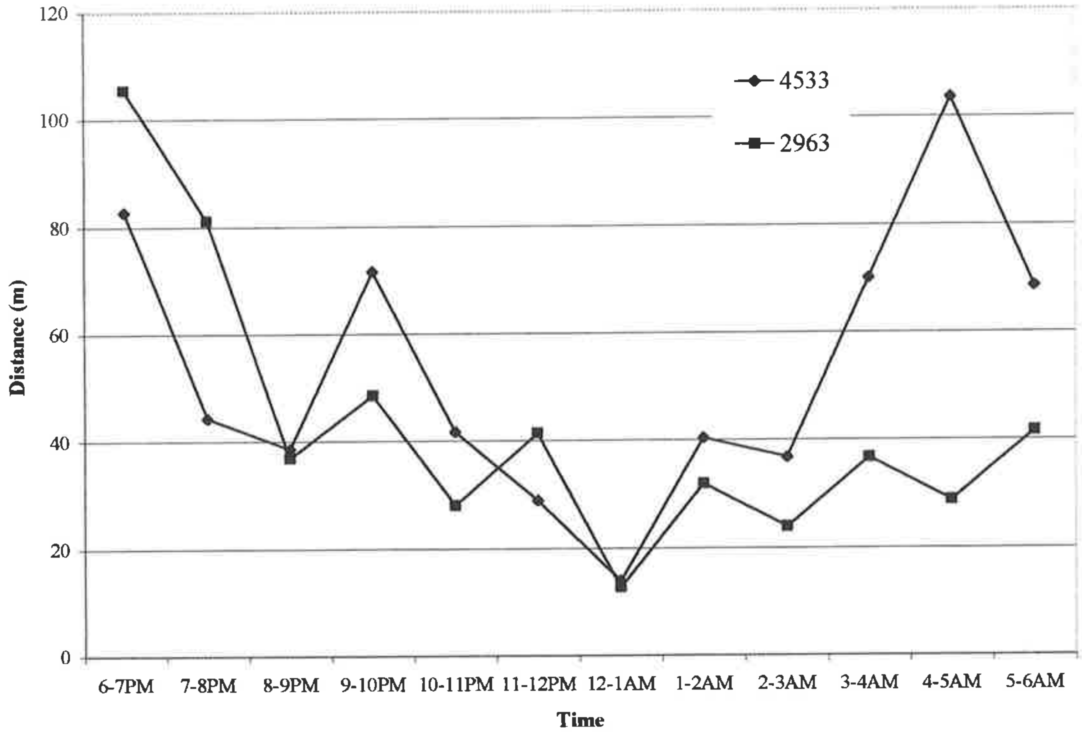


Figure 4.13. Nightly activity patterns of individuals 4533 and 2963. Shows hourly average distance travelled from 18h00 to 06h00.

Table 4.4. Summary of continuous (15-min) tarsier tracking results for 12-hour shifts. Distance traveled is sum of distances between consecutive fixes.

Tarsier No.	Age/Sex	No. of shifts	Distance traveled (m/12-hour shift)	
			range	mean
4505	AF	3	1,103-1,369	1,199
2730	AF	3	659-973	820
4511	AF	2	693-1,605	1,149
2843	AM	2	1,309-2,055	1,682
2956	AM	2	1,710-1,912	1,811
2963	AM	2	707-1,758	1,233
2996	AF	1	965	965
4523	AF	2	1,212-1,335	1,274
4533	AM	2	1,350-2,284	1,817
2967	AF	2	1,121-1,487	1,304

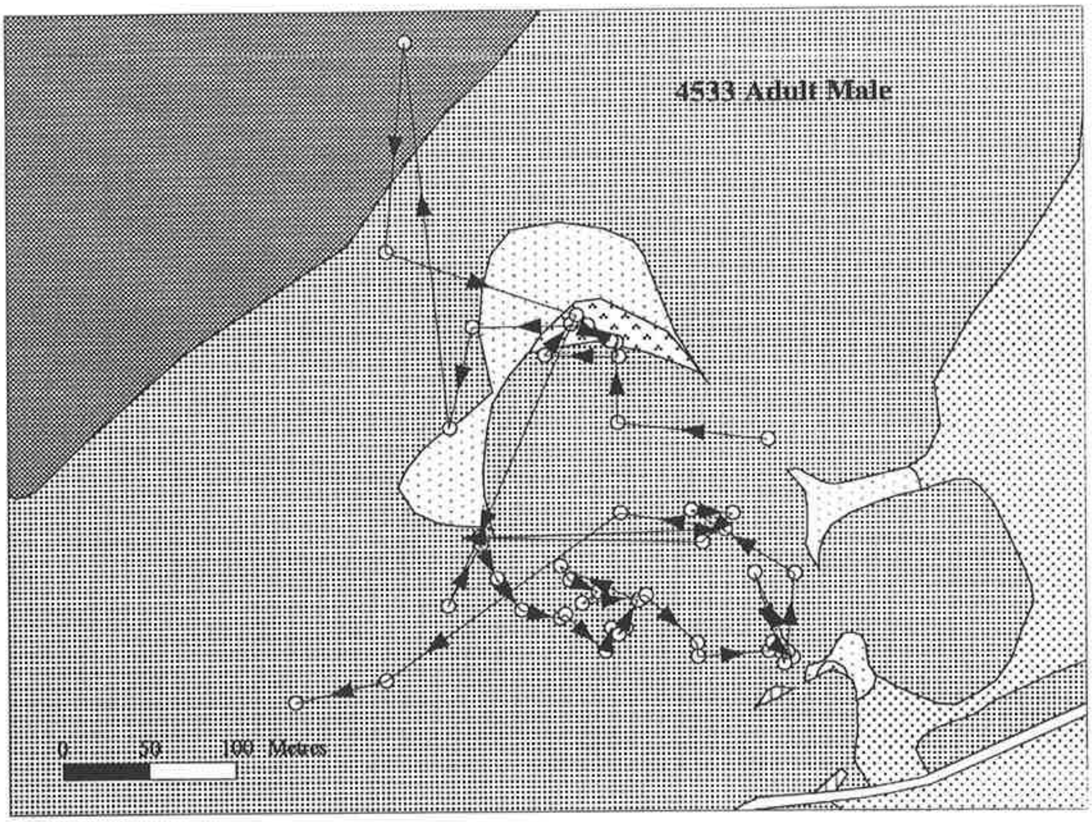


Figure 4.14. Polyline of adult male 4533 showing longest distance travelled within a 12-h shift (18h00-06h00), open circle indicate location points at 15-min intervals.

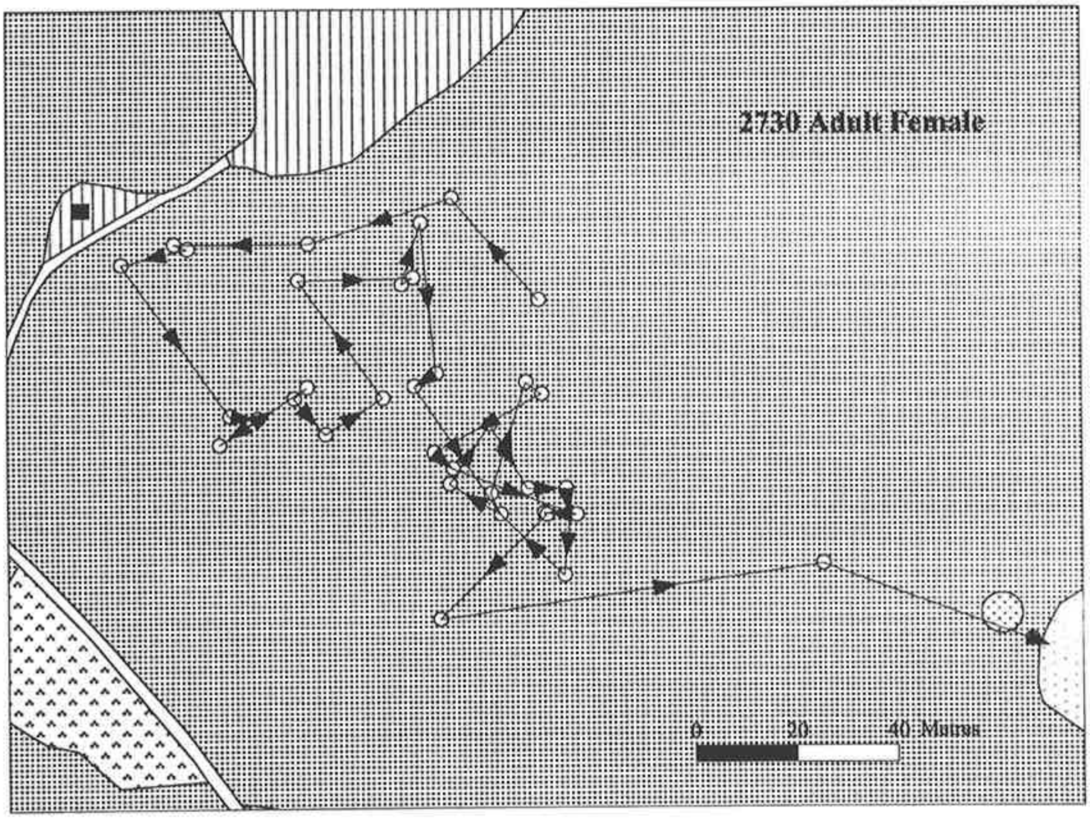
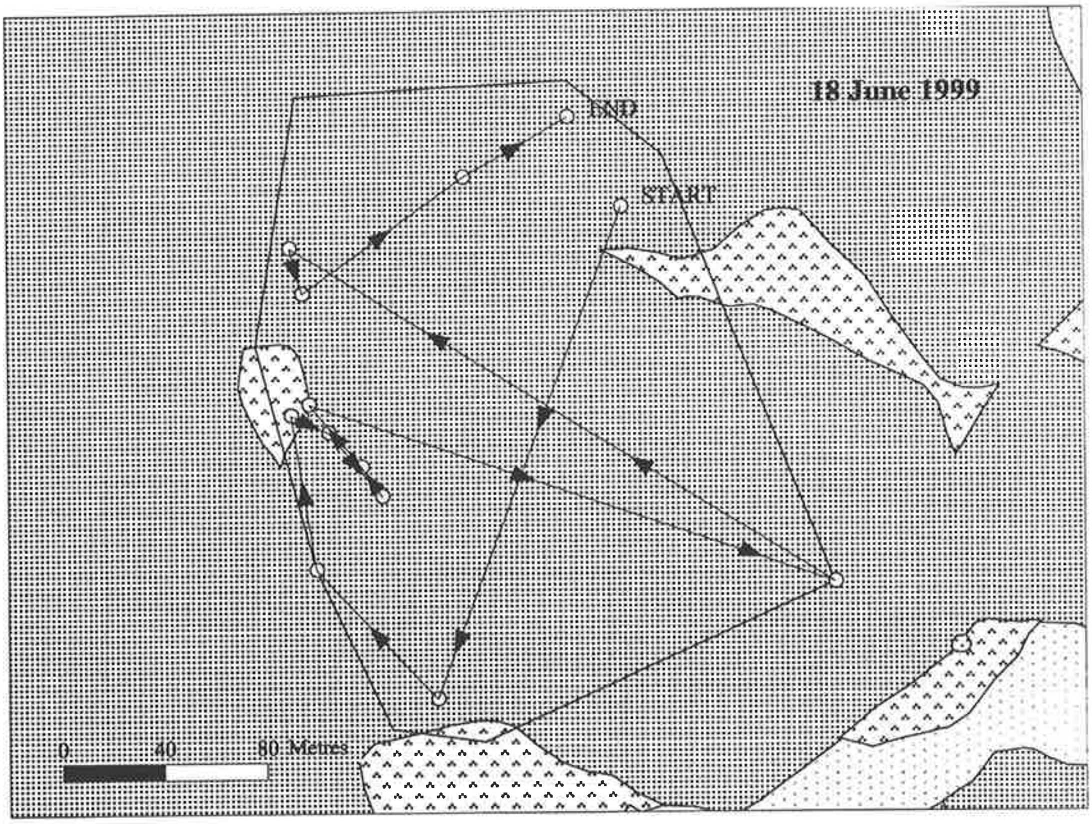


Figure 4.15. Polyline of adult female 2730 showing shortest distance travelled within a 12-h shift (18h00-06h00), open circle indicate location points at 15-min intervals.



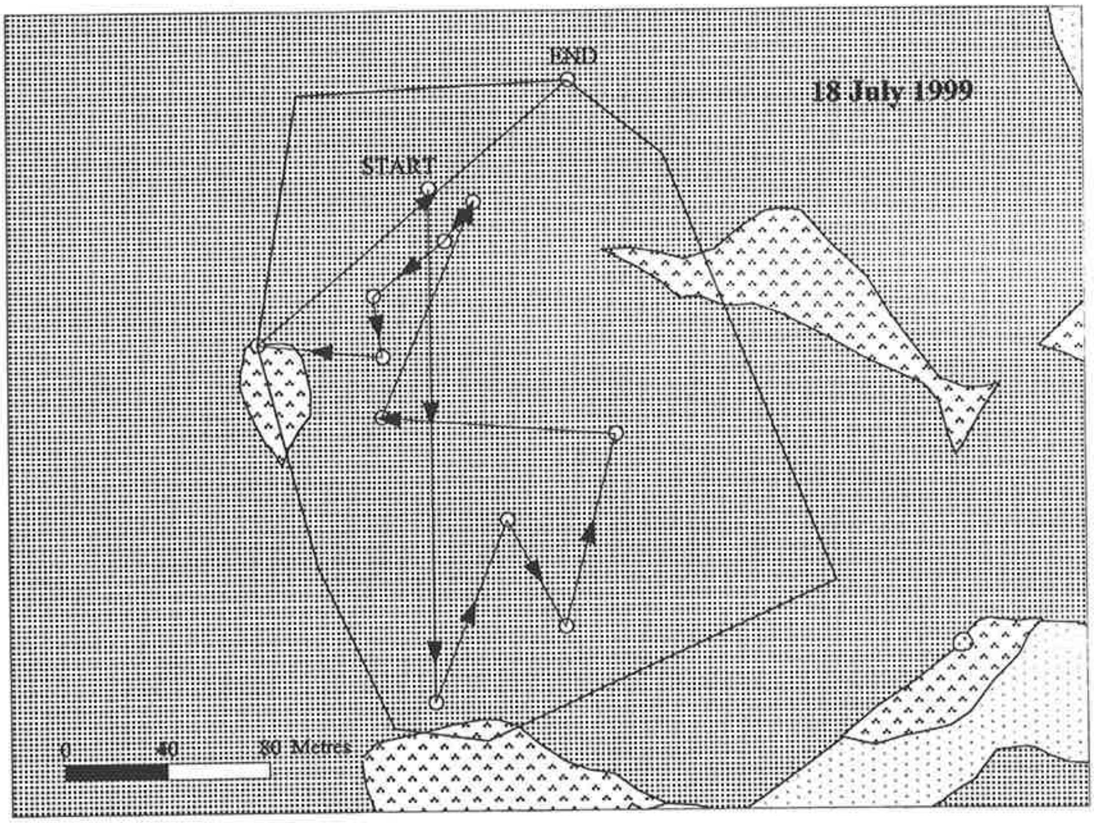


Figure 4.16. Characteristic movement patterns of male individuals as represented by adult male 2843.

Females followed a habitual path for several nights and changed to a new travel path subsequently. Females used their activity centres more than males and they also tended to limit their movements just before giving birth and until they had weaned their infants (**Table 4.5**) (**Figure 4.17**). Females appeared to maintain a range only large enough to provide food for themselves and any offspring. Tarsiers moved quickly across narrow breaks of open grass areas and utilised these to move from one forest patch to another. All in all, data on percentage use of home range show males used 3%-74% while females utilised 6%-57% of their home range within a 12-hour (dusk to dawn) period (**Table 4.6**). However, in 62% of continuous (12-hr) monitoring, males and females, on average, used 21%- 50% of their home range (**Figure 4.18**).

Table 4.5. The mean distance travelled per hour by females in varying reproductive states.

Individual	Mean Distance Traveled (m)	Pregnant	Lactating	Non-Reproductive
4511	61.08	57.38 m	47.91m	73.18 m
2730	40.66	41.07 m	39.02 m	-
4505	60.93	65.41 m	57.09 m	-
2996	48.96	-	-	48.96 m
2967	36.06	-	36.06 m	-
4523	50.45	-	-	50.45 m
Mean Distance Travelled (m)	49.69 (n=6)	54.62 m (n=3)	45.02 m (n=4)	57.53 m (n=3)

4.3.5 Habitat Associations

The data for the habitat use of the *T. syrichta* are presented in **Figure 4.19**. In every case the early-mid succession stage forest was the most preferred habitat type, having an average observed utilisation of 96.8% (total number of pixel counts for all tarsiers per habitat class) by all study individuals. The preference for the early to mid succession forest was followed by (in order of preference) shrubland, palm/bamboo, late succession forest and grassland.

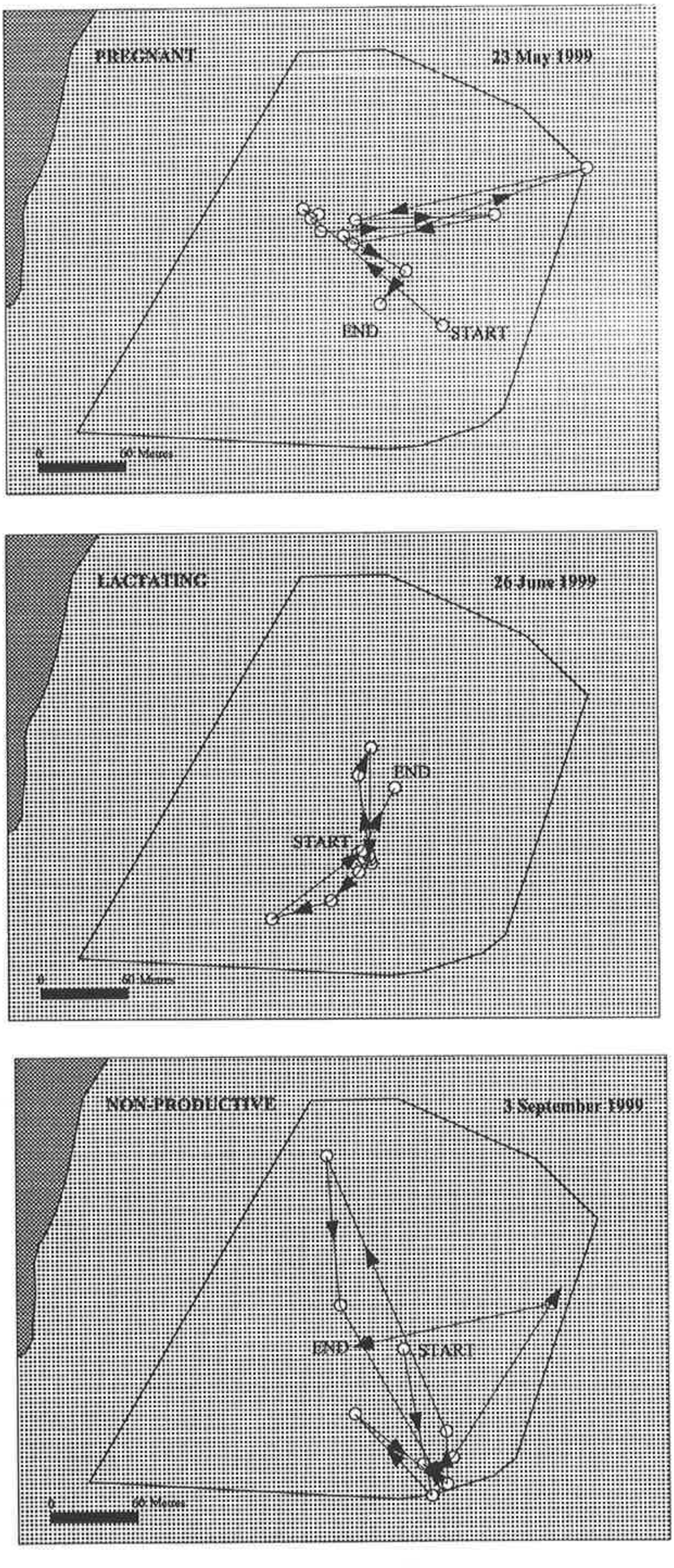


Figure 4.17. Characteristic movement patterns of female individuals in different reproductive stages as represented by adult female 4511.

Table 4.6. Range use of individual tarsiers using continuous 12-h tracking.

Individual	Date	Area (ha)	MCP (ha)	use/night (%)
2963	25-Jun-99	1.469	8.091	18
	21-May-99	0.231	8.091	3
4533	09-Sep-99	0.449	9.127	5
	05-Oct-99	4.289	9.127	47
2956	23-May-99	1.990	6.070	33
	16-May-99	1.763	6.070	29
2843	05-May-99	1.627	4.159	39
	18-Jun-99	3.098	4.159	74
4523	07-Oct-99	0.650	1.136	57
	08-Sep-99	0.494	1.136	44
2967	12-Sep-99	0.200	0.891	22
	04-Oct-99	0.307	0.891	34
4511	26-Jun-99	0.375	6.399	6
	23-May-99	1.037	6.399	16
2730	08-Mar-99	0.531	1.900	28
	13-Mar-99	0.579	1.900	30
	12-Mar-99	0.652	1.900	34
4505	04-Mar-99	1.529	3.035	50
	25-May-99	1.222	3.035	40
	10-Mar-99	1.642	3.035	54
2996	10-Sep-99	0.380	3.205	12

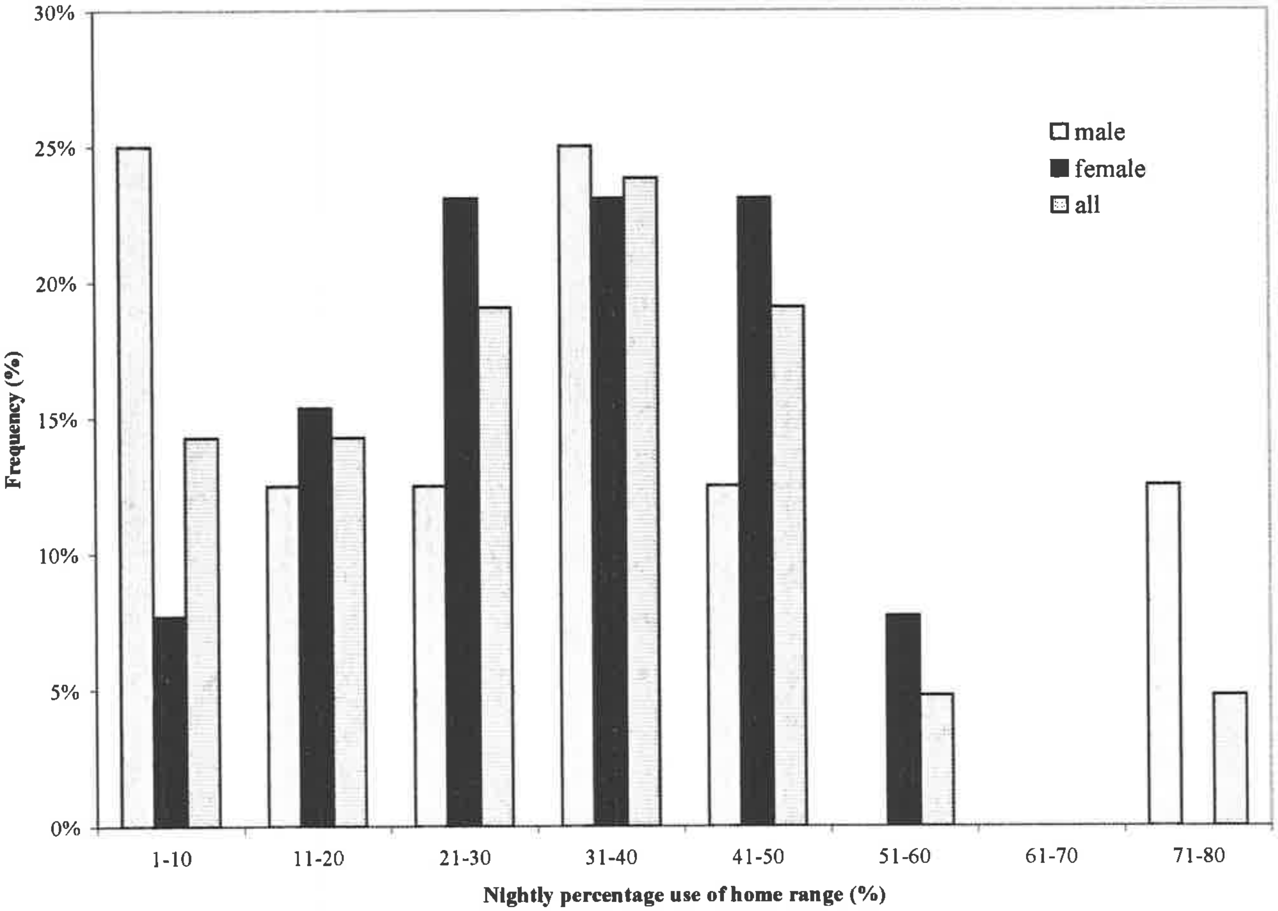


Figure 4.18. Nightly range use of the Philippine tarsier.

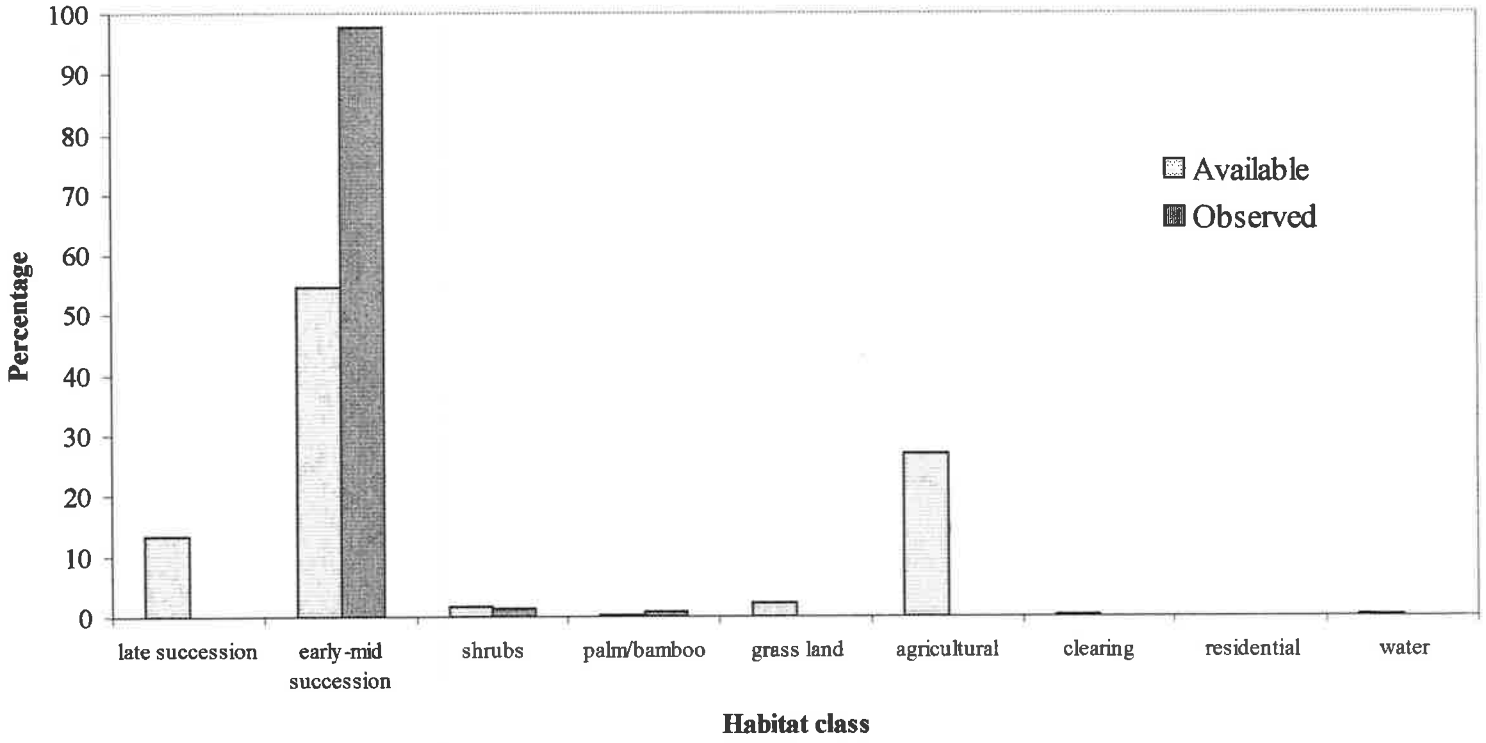


Figure 4.19. Observed utilisation versus available proportions of habitat classes. Available proportions are equivalent to the number of pixel counts per habitat class over total pixel counts of the entire study area. Observed values are total pixel counts for all tarsiers per habitat class

The last type was mainly used when traversing from one forest patch to another. The other habitat types found within the study area that tarsiers never utilised were: clearings, agricultural, residential houses and water/swamp. No further statistical analyses were done to verify the proportion of habitat used, as data showed tarsier locations were tightly clustered within the early to mid succession type of forest and illustrated the strong preference of the tarsiers for this habitat class over other habitat types available within the study area. It is important to note that the early-mid succession type had the highest available proportion (55%) among the different habitat classes and this was likely to have had an influence on the animals' choice and usage of habitat. However, when the next three most available habitat types are compared: agricultural (27%), late succession forest (13%) and shrubland (2%), the observed utilisation was highest in shrubland, even though it had the lowest available proportion among the three habitat classes. This implies that proportion of availability alone is not a strong factor in dictating habitat preference. It should be accompanied by suitability, such as having an abundance of substrates used by the animal. Small-diameter sized substrates are abundant in early-mid succession forest (Zou *et al.*, 1995; Franklin *et al.*, 1997). The predominant use of these substrates (**Table 4.7 and 4.8**) by the tarsiers may account for their preference for the early-mid succession habitat.

Table 4.7 Support diameter (cm) used for foraging.

Substrate	Minimum	Maximum	Mean
Tree trunk	2	15	7.067
Sapling Trunk	0.2	4	2.482
Ground	NA	NA	NA
Others	1	2	1.553

Table 4.8 Support diamcter (cm) used for travelling.

Substrate	Minimum	Maximum	Mean
Tree trunk	3	15	6
Sapling Trunk	0.5	3	1.931
Ground	NA	NA	NA
Others	1	1	1

4. 4 DISCUSSION

4.4.1 Home Ranges

This study provides new information on the ecology and behaviour of *Tarsius syrichta* in the wild. The home range sizes of *T. syrichta* were larger relative to *T. spectrum* and *T. dianae* in Sulawesi but smaller or equal to that of *T. bancanus* in Borneo (**Table 4.9**). Home range overlap was distinct between sexes but there was minimal overlap within sexes. Male home ranges overlapped those of more than one female. However, individuals were always solitary, as was observed with tarsiers in Leyte (Dagosto and Gebo, 1997) and in Borneo (Crompton and Andau, 1986, 1987). The patterns of males having larger home ranges than females and exhibiting spatial overlap between sexes albeit foraging solitarily have also been observed in other nocturnal prosimians such as *Microcebus murinus* and *M. rufus* (Pages-Feuillade, 1988; Radespiel, 2000; Atsalis, 2000). Factors such as small body size and complexity of the rainforest habitat contribute to the solitary foraging strategy of these nocturnal species as they rely on crypsis as defence against predation (Charles-Dominique, 1977; Atsalis, 2000).

Vocalisation and scent-marking by urinating are recognised as an important component of tarsier behaviour (Niemitz, 1979b, 1984, Wright *et al.*, 1986, 1987). Vocalisation was observed to be the main mode of contact between conspecifics during this study. Although I did not directly observe scent-marking behaviour, trees that had been urine marked were

Table 4.9. Reported home range sizes of different wild tarsier species in various habitat types from radiotelemetry studies.

Species	Mean Home range (ha)	Habitat	Study location	Source
T. bancanus	males = 8.75-11.25 females = 4.5-9.5	1° and 2° lowland rainforest	Sabah, Borneo	Crompton and Andau (1986)
T. spectrum	males = 3.07 females = 2.32	lowland rainforest, sea level	Tangkoko Nature Reserve, North Sulawesi	Gursky (1997)
T. syrichta	male = 0.6-2.0	2° lowland rainforest 100 m asl	Mt. Pangasugan,Leyte	Dagosto and Gebo (1997)
	males = 6.45 female = 2.45	2° lowland rainforest 100-200m asl	Corella, Bohol	**present study**
T. dianae	males &females = 0.5-0.8	1° and 2° rainforest 1,000m asl	Kamarora, Lore Lindu, Central Sulawesi	Tremble *et al.* (1993)

discernible (by smell) within the home ranges of the study animals and this implies territorial behaviour. There are similarities between the observed pattern of range overlap of *T. syrichta* and those of *T. bancanus* and *T. spectrum*. Fogden (1974) determined large areas of overlap between sexes and smaller areas of overlap within each sex in *T. bancanus*. Crompton and Andau's (1986, 1987) data on *T. bancanus* indicated that the ranges of individual females were visited by multiple males. The implications of range overlap to the social structure of *T. syrichta* are further discussed in Chapter 5 on Social Organization.

4.4.2 Movement Patterns

Distances travelled per night by *T. syrichta* in Bohol (x = 1,636 m for males; x = 1,119 m for females) were comparable with those of *T. bancanus* (x = 2,081.6 m for males and x = 1,448.1 m for females) (Crompton and Andau, 1986, 1987) and *T. spectrum* (1,500-2,000 m) (Gursky, 1997, 1998). However, it does not compare with the results of Dagosto and Gebo's (1997) preliminary study of tarsiers in Leyte (x = 301 m for two males) despite utilising the same 15-minute interval in continuous tracking. It is most likely that Dagosto and Gebo's (1997) result is a consequence of tracking only two animals in short and intensive periods.

The percentage of range utilisation (12 h, dusk to dawn shift) of *T. syrichta* (range: 3-74% for males; 6-57% for females) differs to that of *T. bancanus* with 50-75% and 66-100% of their range utilised by males and females respectively. However, Crompton and Andau (1986, 1987) noted that in 45% of the observations, only 10% of the range was utilised by the study animals. The percentage of range utilisation of *T. syrichta* varied each night among males and females. Females tend to remain in one corner of their home range especially when they are near parturition or foraging with their offspring. Gursky (1997) reported that pregnant and lactating female *T. spectrum* have limited mobility and moved significantly shorter distances than females in other reproductive phases. The same observation holds true for *T. syrichta*.

4.4.3 Habitat Associations

This study shows that *T. syrichta* utilised early to mid succession regrowth forest to a much greater extent than late succession secondary growth forest. This could relate to the abundance of small-diameter vertical supports that the tarsiers used in the former vegetation type. *T. bancanus* (Niemitz, 1984; Crompton and Andau, 1986), *T. spectrum* (MacKinnon and MacKinnon, 1980; Gursky, 1997) and *T. dianae* (Tremble *et al.*, 1993) similarly preferred these small-diameter vertical supports (**Table 4.10**). Smaller substrates can be beneficial in providing a more secure grip while foraging as was observed with the slow loris *Nycticebus sp.* (Dykyj, 1980) and may also explain the preference of tarsiers for these substrates (Roberts and Cunningham, 1986).

T. syrichta seemed to have a propensity towards the forest's periphery (**Figure 4.9**). This can possibly be correlated to the 'edge effect' where higher resource availability is found along forest edges. Insects often increase in diversity and abundance near edges usually as a result of elevated numbers of edge and generalist species (Brown and Hutchings, 1997; Didham, 1997). Resource abundance can further be attributed to microclimatic factors such as greater light intensity brought about by lateral exposure to direct solar radiation along edges (Andren, 1994; Baldi, 1999). The fact that tarsiers utilised open corridors to move from one forest patch to another further maximises their ability to use forest edges effectively. The same ability makes *T. syrichta* susceptible to predation and these aspects of *T. syrichta*'s ecology clearly warrant further investigation.

Table 4.10. Most preferred substrate types and sizes of different free ranging tarsier species.

Species	Activity	Substrate types	Substrate sizes (diameter, cm)	Source
T. bancanus	foraging	vertical tree trunks	1-4	Niemitz, 1984
		sapling trunks	<2	Crompton & Andau, 1986
T. spectrum	hunting & travelling	- -	<4	MacKinnon & MacKinnon, 1980
	resting & marking	-	4-8	
	infant transport	-	3	Gursky, 1997
	infant parking	vertical	1	
T. syrichta		-	<5	Dagosto & Gebo, 1997
	foraging and travelling	vertical tree trunks	5.0-15.0	**present study**
		vertical sapling trunks	0.2-4	
T. dianae	foraging	sapling trunks	2.1-3	Tremble *et al.*, 1993

Field studies on other tarsier species have reported use of a wide variety of habitat types. Primary forest, secondary forest, shrub, mangrove, coastal areas and areas bordering plantations were inhabited by *T. bancanus* (Niemitz, 1979b). Tremble *et al.* (1993) observed *T. dianae* to prefer dense tangle of liana vines and a tree cavity for sleeping sites, and these sites were located in early successional habitat near secondary forest with vegetation comprised mainly of bushes, ferns and small trees. Wild *T. spectrum* was reportedly found in almost all habitat types (Leksono *et al.*, 1997) and sleeping sites varied accordingly. They slept in hollows of large trees particularly *Ficus sp.* in primary forest. Bamboo was a preferred sleeping site in secondary forest, riparian or gallery forest, villages and cultivated areas. Dry branches and dead leaves that had accumulated among the exposed roots of the mangrove and base of grass clumps in grassland had also been used as sleeping sites. Areas of dense human population and intensive agriculture were two habitat types that reportedly showed local extinction of *T. spectrum* population on Sulawesi (Leksono *et al.*, 1997). Wild

T. syrichta had not been observed to utilise residential areas and land cultivated for agriculture.

Early observations on *T. syrichta* found 'lowland, coastal regions in primary and secondary forests' as the habitat type where the species was most common (Fulton, 1939; Wharton, 1948). A survey on the distribution and ecology of mammals in Leyte, Biliran and Maripipi (Rickart *et al.*, 1993) found tarsiers on Leyte in a wide variety of habitat types: mixed secondary forest and agricultural land between 50 to100 m elevation and primary lowland and montane forests between 300 and 700 m elevation. Dagosto and Gebo's (1997) study in Leyte was conducted in secondary forest at 100 m elevation. They reported that *T. syrichta* were absent from areas that lacked large trees (>40 cm dbh) which is contrary to what we observed in Bohol where tarsiers were distributed in early to mid succession forest with abundant sapling growth and trees having ≥ 5 cm dbh. Large trees (≥ 50 cm dbh) were present in the late succession forest within the study site in Bohol and tarsiers were heard vocalising in these areas. However, random trappings yielded more individuals inhabiting early-mid succession forest. There is a possibility that tarsiers can be habitat generalist and thrive in different stages of tropical rainforest growth at varying elevations. However, it is not known which among these different habitat types support significant populations of Philippine tarsiers other than what is provided by the results of this study.

4.4 SUMMARY

Home ranges, spatial movements and habitat utilisation patterns were determined during a radiotracking study on four male and six female Philippine tarsier *T. syrichta* in Corella, Bohol from early March-October 1999. Home ranges averaged 6.45 ha. for males and 2.45 ha. for females (MCP and Kernel 95%), allowing for a density of 16 male and 41 female tarsiers per 100 hectares. The utilised habitats are primarily located in secondary lowland rainforest in early to mid-succession stage, but individual tarsiers readily traversed open narrow grass areas to move in between forest patches. However, the tarsiers avoided adjacent clearings, residential areas and agricultural plantation. The home range of one male overlapped extensively with that of one female and to a lesser extent with a second female. Home ranges of males showed little overlap (2.71%) and the same was observed among the females (3.35%). Nightly travel distance averaged 1,636 m for males and 1,119 m for females. Individuals were observed to forage and sleep solitarily.

Chapter 5:

Social Organization and Reproductive Behaviour

CHAPTER 5: SOCIAL ORGANIZATION AND REPRODUCTIVE BEHAVIOUR

5.1 INTRODUCTION

Within the order Primates, there is a diverse array of social organization and mating systems (Bearder, 1987). The variations in social structure include fission-fusion such as found in *Ateles geoffroyi* (Klein and Klein, 1977), *Pan troglodytes* (Wrangham, 1977) and *Pongo pygmaeus* (Mitani *et al.*, 1991); polyandry in *Saguinus fuscicollis* (Terborgh, 1986); harem in *Aloutta sp.* (Terborgh, 1986); a variant of noyau in *Galagos sp.* (Bearder, 1987); and multi-male such as found in *Macaca sp.* (Van Schaik *et al.*, 1983). A mere 15% of all primate species are classified as monogamous (Rutberg, 1983). Nocturnal primates were originally thought to differ in their social systems from their diurnal counterparts, with the latter being more gregarious (Bearder, 1977). However, subsequent research has revealed that nocturnal species are less dispersed and less solitary than previously thought (Bearder and Martin, 1979; Bearder, 1987). They have quite complex and varied social organization (Harcourt and Nash, 1986; Bearder, 1999).

Several factors influence variations in primate social structure: predation risk (Janson, 1986; Terborgh, 1986); abundance and spatial and temporal distribution of food (Wittenberger, 1980; Chapman, 1990; Morland, 1991); patterns and frequency of births, deaths, immigration and emigration (Digby and Barretto, 1993); and body weights and reproductive behaviour (Clutton-Brock and Harvey, 1977). Intra-specific variations have been suggested for the social organization of tarsiers (Gursky, 1995, 1997) with facultative polygamy aptly describing the social structure of both *T. spectrum* and *T. bancanus*. The primary aim of this chapter is to describe the social structure of *Tarsius syrichta* and discuss the variables that interrelate with it, such as patterns of range overlap, body weights, spatial distribution of resources and parental care. A secondary aim of this chapter is to present some aspects of the reproductive behaviour of *T. syrichta* and correlate it with the species' social structure. The chapter compares the results of this study with those of previous studies on *T. bancanus*, *T. spectrum* and addresses directions for further research.

5.2 METHODS

Morphometric data together with body weights were among the parameters used to determine the social strucuture of *T. syrichta*. Different morphological measurements were taken upon capture of the animals. The methods were discussed in detail in Chapter 3. Other parameters used included patterns of night range length and home range overlap, which have previously been discussed in Chapter 4. Methods for collecting behavioural data have been described in Chapter 3.

5.3 RESULTS

5.3.1 Morphometrics and Body Weights

The mean capture weight of adult male *T. syrichta* ($n = 4$) was 135.5g (± 6.45, range: 128 - 143). Females ($n = 6$) weighed 120 g (± 9.4, range: 107-132). There was a significant difference between male and female body weights, with males being larger than females (Two-sample t-test, $P = 0.019$) (**Figure 5.1**). These confirm the results of Kappeler (1990, 1991) on captive *T. syrichta*, showing males to be significantly larger than females. For purposes of comparison, we considered only the initial capture body weights of both females and males, although body weights were also taken during recapture and final capture to check on possible effects of the collar on the animal. In general, males did not appear to be affected

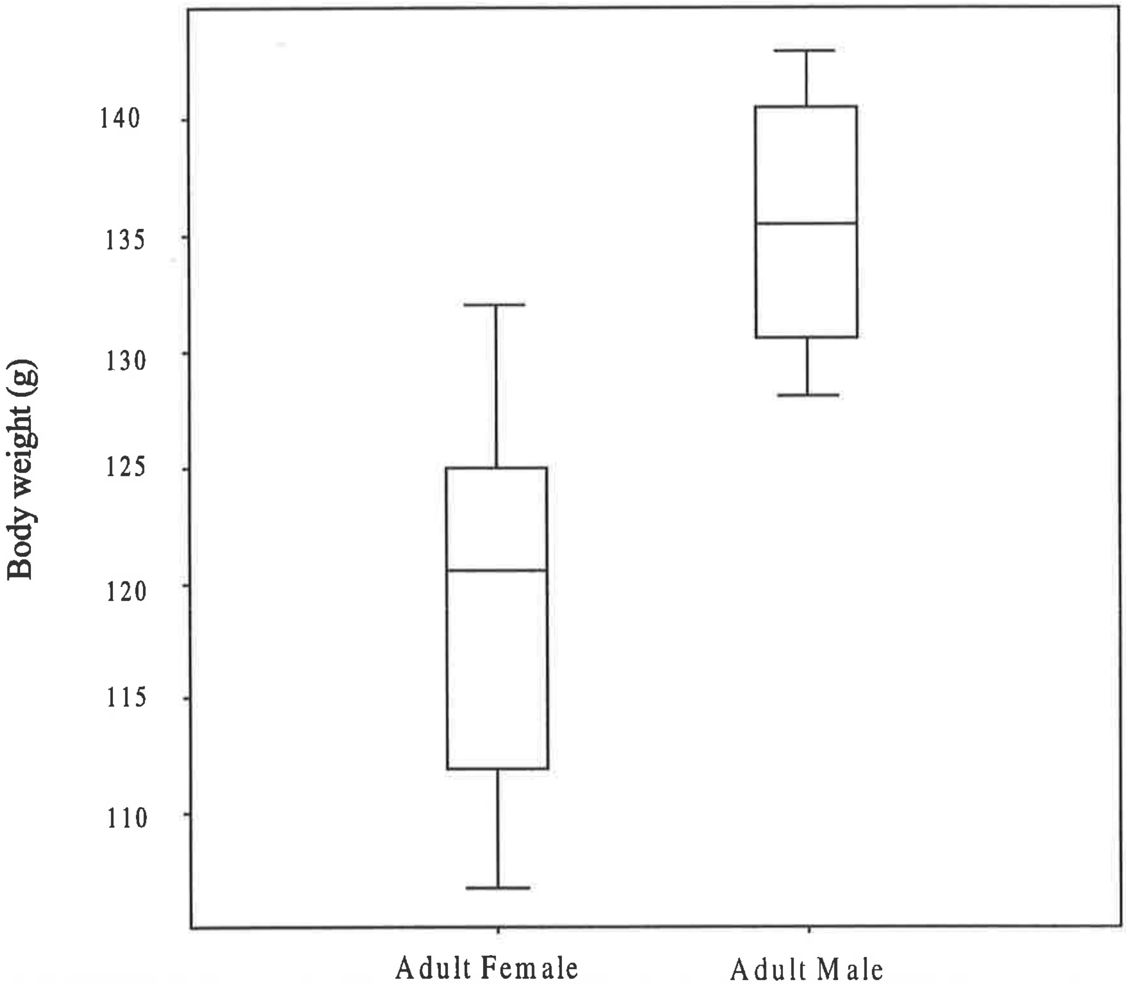


Figure 5.1. Box plot of adult male and female body weights, showing mean and standard deviation of males: x = 135.5 g ± 6.45, range 128-143 g and females: x = 120 g ± 9.4, range 107-132 g.

by the weight of the collars, with recorded body weight gains during final capture ($x = 3.1$ g). The effect of the collars on the females cannot be ascertained because body weights varied depending on their reproductive status. During the study, females were either pregnant, lactating or non-reproductive. Females gradually gained weight as their pregnancy progressed (+ 8 g for ID No. 2730) and during post-weaning period (+ 8 g for ID No. 2996) but weight loss was recorded when females were lactating ($x = -14.0$ g for ID Nos. 4505, 2967, 4511 and 2730). The variations in body weight during different stages of capture (initial, repeat, and final) are presented in **Table 5.1**. The only other morphological measurement which showed significant difference between males and females was hindlimb length (two-sample *t*-test, $P = 0.024$) with males having longer hindlimbs. The arithmetic mean and standard deviation of different morphological measurements for each adult sex category are presented in **Table 5.2.**

Appendix 6 presents morphological measurements taken on all tarsier individuals captured during this study. Data include measurements taken on four infants who have been carried by their mothers either during initial capture or recapture. Data on mother-infant morphological measurements are discussed in this chapter's Reproductive Behaviour section.

5.3.2 Home range overlap

Home range overlap was computed using KERNEL 95%. There was a moderate level of overlap (average of 38.5%) in the home ranges of males and females, suggesting that they form social pairs. There were apparently two male/female pairs with overlapping activity centres. In contrast, the degree of overlap of males with other females (secondary partner) only averaged 14.5%. I would like to emphasise that my data are preliminary and the stability

Table 5.1. Relative weight of the transmitter package for each individual and changes in body weights during capture.

ID No.	Age/Sex	Initial body weight (g)	Collar weight (g)	Collar-body weight ratio(%)	Recapture body weight (g)	Final capture body weight (g)	Weight loss/gain (g)	Comments
2730	AF	125	8	6.40	133	105	-20*	pregnant (IC & RC), nursing (FC)
2967	AF	116	10	8.62	110	110	-6*	nursing (IC, RC & FC)
2996	AF	107	10	9.35	n/a	115	8*	nursing (IC), non-reproductive (FC)
4505	AF	132	8	6.06	132	123	-9*	pregnant (IC & RC), nursing (FC)
4511	AF	125	8	6.40	112	n/a	-13**	pregnant (IC), nursing (RC)
4523	AF	112	10	8.93	n/a	n/a	n/a	nursing (IC)
2843	AM	143	9	6.29	143	154	11*	n/a
2956	AM	128	8	6.25	127	n/a	-1**	n/a
2963	AM	133	9	6.77	134.5	n/a	1.5**	n/a
4533	AM	138	10	7.25	n/a	139	1*	n/a

* final capture weight - initial capture weight
**recapture weight - initial capture weight
IC-initial capture
RC-recapture
FC-final capture

Table 5.2. Sex differences in numerous morphological measurements.

Measurement	Male mean	Male S.D.	N	Female mean	Female S.D.	N	Mean Difference	T	P
Body weight	135.5	6.45	4	119.5	9.4	6	16	-2.95	0.019
Total length	353.8	4.79	4	336.7	18.62	6	17.1	-1.76	0.116
Body length	121.2	10.31	4	116.7	6.06	6	4.5	-0.9	0.396
Tail length	232.5	9.57	4	219.2	14.97	6	13.3	-1.56	0.157
Hindlimb length	185	4.08	4	172.5	8.22	6	12.5	-2.78	0.024
Thigh length	56.25	4.79	4	56.67	7.53	6	-0.42	0.1	0.925
Lower leg length	62.5	6.45	4	55.83	4.92	6	6.67	-1.86	0.099
Foot length	66.25	2.5	4	60	6.32	6	6.25	-1.85	0.101
Big toe length	22.81	1.21	4	21.44	0.98	6	1.37	-1.97	0.084
Forelimb length	111.2	2.5	4	105	11.4	6	6.2	-1.06	0.321
Arm length	30	0	4	31.67	5.16	6	-1.67		0.545
Forearm length	37.5	5	4	36.67	2.58	6	0.83	-0.35	0.735
Hand length	42.5	2.89	4	38.33	4.08	6	4.17	-1.75	0.117
Thumb length	11.77	1.51	4	11.94	0.87	6	-0.17	0.24	0.819
Ear length	24.89	2.3	4	22.13	4.34	6	2.76	-1.15	0.283

of these pair bonds can only be confirmed through a long-term field study. Females' ranges were not observed to overlap with that of more than one male. Two radio-collared females in the study site did not have associated radio tagged males. There was very little overlap within sexes, 2.71% and 3.45% for males and females respectively (**Table 5.3 and Appendix 7**).

Table 5.3. Percentage overlap of home ranges of adjacent individuals using the 95% Kernel home range (%).

Overlap	Mean ± s.d.	Range
male with female partner	38.5 ± 7.4	33.27-43.68
male with other female	14.5 ± 14.2	4.49-24.60
non-partner female with other males	n/a	n/a
male with other males	2.71 ± 0	2.71
female with other females	3.45 ± 3.8	0.64-6.05
male/female groups with other groups	n/a	n/a

The Philippine tarsiers were observed to forage and sleep solitarily, except for females carrying their infants. There was never an instance, throughout the duration of the study, of an adult individual being seen in close proximity (< 10 m) with a conspecific during nocturnal activity. A single observation was made of male 4533 and female 2996 having sleeping sites *c.* 5 m apart.

5.3.3 Resource Distribution

The study site was a mosaic of forest fragments with adjacent flat areas cleared for agriculture (**Figure 4.9**). Random trappings around sleeping sites or in areas where tarsiers were heard vocalizing (**Figure 3.9**) yielded individuals living along the forest periphery (**Figure 4.9**). The forest was comprised by suitable (early-mid succession forest) and bounded by less suitable (late succession forest) and non-suitable (agricultural) habitat areas for the tarsiers. The distribution of the tarsiers (see **Figure 4.9**) suggests that resources are more abundant along the forest periphery.

5.3.4 Communication

Both males and females vocalised from a distance (a high pitch single whistle *c.* 3-5 s apart was the most common sound and they also used a bird-like melodious trill), although there were no observed patterns of call periodicity or frequency. Calls were rarely responded to, with a response being heard on only three occasions. In general, tarsiers moved about in the forest in almost total silence.

5.3.5 Reproductive Behaviour

5.3.5.1 Birth months and Parental care

Observations of birthing patterns are very preliminary as this study lasted for 8 months. However, the initial trend suggests that *T. syrichta* breeds seasonally with at least one birth peak from June to July (**Figure 4.7**). Nursing infants had a mean weight of 36.75 g. The ratio between mother and infant weights is presented in **Table 5.4**. Figures show infants being carried even if they weighed as much as 40.18% of their mothers' body weight. The weaning age was *c.* 78 days, determined when infants were not observed to share a sleeping site with their mother. This observation was based on 4 of the 6 radio-collared females with infants.

It is of interest to note that males were never observed in contact with infants and were not seen to have any role in rearing the young *i.e.* infant transport. This is despite the fact that during lactation, when the mother has to forage to meet the nutritional demands of both herself and her offspring, the added burden of carrying a heavy infant greatly limits movement and foraging rate (**Table 4.5**). Gursky (1997), in her study of *T. spectrum*, observed limited forms of paternal care such as grooming and playing with infants. However, this was not the case in my study.

Table 5.4. Infant-mother weight ratio.

ID No.	Age/Sex	Mother's body weight (g)	Infant's body weight (g)	Infant to mother weight ratio (%)
2996	AF	107	39	36.45
4505	AF	123	34	27.64
4511	AF	112	29	25.89
4523	AF	112	45	40.18

5.3.5.2 Testicular size

Data on the testicular size of *T. syrichta* show that testes weight was on average 3.65 g. The testes to body weight ratio is presented in **Table 5.5.** Data were taken from the 4 adult radiocollared males and the only radiocollared subadult male, during initial capture.

Table 5.5. Testis-body weight ratio.

ID No.	Body weight (g)	Testes weight (g)	Testes to body weight ratio (%)
2943	105	2.54	2.41
2956	128	4.15	3.24
2843	143	4.19	2.93
2963	123	1.65	1.24
4533	133	5.73	4.15
Mean	129	3.65	2.79

5.4 DISCUSSION

The social structure of *T. syrichta* appears to be non-monogamous with significant overlap between home ranges of individual males and females. The male's range overlapped with two females whose ranges overlapped, albeit minimally. Paired males and females foraged apart and did not share the same sleeping site. Therefore, opportunities for extra pair matings were available. Intra-specific variation in the social organization of *T. bancanus* had been implied (Gursky, 1995), from pair bonding (Niemitz, 1984) to a variant of the noyau social system (Crompton and Andau, 1986; Fogden, 1974). In *T. spectrum*, the home range of a male overlapped that of one or more females whose ranges also overlapped (Gursky, 1995, 1997). It has been suggested that facultative polygamy may best describe the social structure of both *T. bancanus* and *T. spectrum* (Gursky, 1995).

Parental care in *T. syrichta* was solely provided by the mother until weaning (*c.* 78 days), and males were never observed to transport young (pers observ.). Gursky (1997) concluded that male care in *T. spectrum* was very limited, which can be attributed to a relatively low paternity certainty that is a consequence of overlapping home ranges. The same can be said for *T. syrichta*. In species where parental care duties are delegated to one of the partners, the partner not investing in parental care duties can expend increased time and energy on intrasexual competition for resources and mates (Emlen and Oring, 1977); polygamy had been found to be more prevalent in such species.

Morphometric data indicate dimorphism in body size between males and females, with males having significantly larger body sizes than females. Sexual dimorphism in body weight has been linked to social structure (Kay *et al.*, 1988) and suggests polygyny (Kleiman, 1977). It has been predicted that sexual dimorphism is distinct in single-male polygynous species (Harcourt *et al.*, 1981), with larger males increasing their reproductive success by defending a larger territory that overlaps with that of multiple females, thereby maximizing the frequency of matings. Although individuals appear dispersed and solitary all the time, overlapping home ranges further indicate the maintenance of a family structure and an active breeding unit (Eisenberg *et al.*, 1972). This 'solitary' yet polygynous pattern is also exhibited by other nocturnal prosimians such as *Perodicticus potto* (Charles-Dominique, 1977, 1980). *T. syrichta* in captivity have been observed to scent-mark, allogroom, play with and sniff partners (Haring *et al.*, 1985). However my observations in the field found individuals to forage and sleep alone.

Testicular size relative to body weight has been associated with the breeding system in primates (Harcourt *et al.*, 1981). It has been hypothesised that relatively large testis size might be associated with sperm competition (Dixson, 1998) and that selection will favour males who can deposit the largest number of sperm especially in a multi-male breeding system (Harcourt *et al.*, 1981; Moller, 1998). In the case of *T. syrichta*, preliminary data on testicular size showed that it has a large mean testis to body weight ratio of 2.79% relative to other primates (*sensu* Harcourt *et al.*, 1981). However, no definite conclusion can be drawn from these data as there is no significant information on testes weight of other free-ranging prosimians much less that of tarsiers which can serve as point of comparison. Gursky's (1997) data on *T. spectrum* showed an even higher mean testis to body weight ratio of 5.51%. However, the difference in the testes to body weight ratio between the two species is not significant ($p = 0.197$) and therefore could not be used as a basis to determine any form of interspecific variation in mating system. In order to further correlate relative testes size of tarsiers to their sexual behaviour and mating system, further studies involving more individuals during varying seasons must be conducted.

The mating system can also be influenced by the spatial distribution of resources (Emlen and Oring, 1977). Five feeding bouts were observed during the duration of the study and arthropods comprised all food items consumed. Although quantitative sampling of food items was not done, *ad hoc* observations in the field showed that arthropods were abundant in the study area. However, the fragmented nature of the forest and the observed propensity of the tarsiers towards the periphery of the forest suggest that resources were patchily distributed. Emlen and Oring (1977) suggested that uneven spatial distribution of resources encourage polygamy as some individuals gain control over a larger quantity or better quality of resources.

From the above discussion on the social organization of *T. syrichta*, factors such as the pattern of overlapping home ranges, absence of paternal care, sexual dimorphism and spatial distribution of resources in the study area suggest that the species is most likely polygynous. *T. syrichta* form family groups of one adult male and one or two adult females and their offspring.

5.5 DIRECTIONS FOR FUTURE RESEARCH

There is a need to further confirm the social structure of *T. syrichta*. The study of the relationship between social structure and population genetics in mammals has increasingly gained interest (Vanstaaden, 1995; Dobson, 1998). The past decade has seen a wide range of applied genetic testing not only in the field of behavioural ecology but also in the related field of conservation biology (Obrien, 1994; Scheffrahn, 1998). In primates, genetic testing has recently been used in conducting paternity analyses, necessary in interpreting patterns of social organization and mating systems (Martin *et al.*, 1992). Several techniques have been utilised to determine paternity in primate species, such as the use of DNA markers in chimpanzees (*Pan troglodytes*) (Ely *et al.*, 1998) and blood protein electrophoresis and DNA fingerprinting in barbary macaques (*Macaca sylvanus*) (Menard *et al.*, 1992). These methods could be used to further confirm the social organization of *T. syrichta* as well as that of other tarsier species.

Chapter 6:

Foraging and Travelling Behaviour

CHAPTER 6: FORAGING AND TRAVELLING BEHAVIOUR

6.1 INTRODUCTION

In order to understand the relationships between animal populations and their environments, it is necessary to determine how individuals that comprise those populations use various microhabitats or substrates within those environments (Rotenberry and Wiens, 1998). Information about an animal's preferred substrate for its daily/nightly activities such as foraging and feeding can make a significant contribution to the management of the species. Removal of substrates most often used by the animals can lead to isolation of habitat patches and consequently genetic collapse (Pearl, 1992). In order for a specific population to survive, critical habitat features used by the animals need to be maintained including preferred level of the forest strata, substrate orientation and size (Harris and Silva- Lopez, 1992). The aims of the work reported in this chapter were therefore threefold: (1) to determine what activities tarsiers performed most often; (2) to determine in what substrate they performed these activities; and (3) to ascertain the most common postural behaviour or mode of locomotor for a particular type of activity. This information is required to establish the association between the substrate types preferred by *T. syrichta* for each observed activity and the corresponding locomotor mode used.

6.2 METHODS

6.2.1 Behavioural Observations

This study involved observing the behaviour of *T. syrichta* within an eight-month period. Ten individuals were tracked at various times and the activities they performed, types of substrate used, height used from the ground and preferred mode of locomotor or posture were recorded (**Table 6.1**). The different activities were measured in three ways due to the difficulty of observing the small-sized tarsier at night. The first method used was informal or *ad libitum* behavioural sampling (Altmann, 1974). The second was the method of Crompton and Andau (1986, p. 339) which was utilised for behavioural counts where 'a single postural observation or movement served as a unit of observation'. Movement actions such as travelling, foraging and carrying infants were recorded as the number of times continuous movement was observed. "Chained" movements were treated as multiple displacements; postural records were taken once only for each sighting of uninterrupted postural activity. Third, observations using five-minute intervals were also used for activities such as grooming, feeding and resting when the animal can be observed for a sustained period of time. The activity types have been described in **Table 3.3** of Chapter 3. This chapter summarises the results of foraging and travelling data, as these are the two activities for which the data facilitate statistical analyses.

Table 6.1. The range of information collected for each factor of interest: the type of activity, the substrate used and locomotor mode recorded for every individual.

Type of Activity	Substrate	Mode of Locomotor
Autogrooming	Ground	Vertical Cling & Leap
Grooming infant	Tree Trunk*	Quadrupedal walk
Resting	Branch**	Cling
Travelling	Sapling Trunk***	Bipedal Stationary
Foraging	Bamboo	Bipedal Hop
Feeding	Bush	Climbing Down
Vocalising	Twig	Climbing Up
	Climber Vine	Sitting
		Cantilever

*Tree trunks are vertical supports from the ground and have dbh of >2.5cm.
**Branches are either diagonal/oblique, angled or horizontal supports from tree or sapling trunks and
measure 1.0-4.0 cm in diameter
***Sapling trunks are vertical supports from the ground with a dbh of 0.5-2.0 cm.

6.2.2 Data Analyses

For the travelling data, the response for each individual was the number of continuous active movements that involved multiple displacements from one particular substrate to another and utilised various locomotor styles such as clinging and leaping (VCL), quadrupedal walk and climbing. In comparison, the response for the foraging data primarily involved scanning behaviour and included the number of times an individual moved its head in a particular substrate and posture. It also included travel movements while searching for food. Travel while searching for food was differentiated from purely travelling behaviour, in that it involved intermittent scanning when moving between substrates. Data are in the form of counts; therefore a log-linear model assuming a Poisson distribution was considered an appropriate modelling approach. This is one form of a generalised linear model (GLM) analysis. It involves transforming the response with the appropriate link function, in this case the logarithmic link, given by $\log(\mu)$, to ensure that the mean is positive. This is a necessary condition when dealing with count data. The model included categorical factors for substrate and locomotion. A factor for individual was also included to ensure that the number of times each animal was seen foraging or travelling is fixed (*i.e.* marginal totals are fixed equal to their observed values). The first model used for foraging data is as follows:

MODEL 1

The maximal model fitted to the data had the following form:

$$\log(\mu_{ijk}) = \lambda + (Individual)_i + (Substrate)_j + (Locomotion)_k$$
$$+ (Substrate.Locomotion)_{jk}$$

where $i=1 \ldots 10; j=1,\ldots,8; k=1,\ldots,9$ $(Individual)_i$ is a parameter for the ith individual; $(Substrate)_j$ a parameter for the jth Substrate, etc.

λ is an intercept parameter

μ_{ijk} expected mean number is the movement (for the relevant response) for the *i*th individual with substrates=*j* and locomotion=*k*

Dropping terms from the model and assessing the change in residual deviance assesses the importance of each term in explaining the response. This test is approximately chi-squared distributed. The residual deviance is analogous to the residual sum of squares in analysis of variance, in that it is a measure of the lack of fit between the observed and fitted values. To be confident there are no inadequacies with the model, the dispersion parameter was calculated, which was estimated by the ratio of the Residual Deviance to its degrees of freedom. Essentially a goodness-of-fit test, this ratio should be approximately 1.

Other model fitted for foraging data:

MODEL 2 = Model 1 – Substrate.Locomotion

$$\log(\mu_{ijk}) = \lambda + (Individual)_i + (Substrate)_j + (Locomotor)_k$$

Model 2 is the final model.

Other models that were fitted in order to test each main effect separately were:

MODEL 3 = Model 2 – Substrate

Given by:

$$\log(\mu_{ijk}) = \lambda + (Individual)_i + (Locomotor)_k$$

MODEL 4 = Model 2 – Locomotion

Given by:

$$\log(\mu_{ijk}) = \lambda + (Individual)_i + (Substrate)_j$$

6.3 RESULTS

6.3.1 Activities Recorded by 5-minute Interval Sampling

Autogrooming, grooming baby, resting, feeding and vocalising were the activities recorded at 5-minute intervals. Branch was the main type of substrate that was associated with these activities, except for feeding which was observed to occur while individuals were using sapling trunks and tree trunks (**Table 6.2**). All the counts for the 5-minute behavioural sampling were considered low and could not be analysed statistically.

Table 6.2. Instances of selected activities in relation to substrate used, recorded by 5-minute behavioural sampling.

Substrate	**Activity** **AG**	**Feed**	**G/B**	**R**	**V**	**Total**
Branch	45		10	38	1	94
Sapling trunk		28		1		29
Tree trunk		4		1		5
Thicket				1		1
Total	45	32	10	41	1	129

SG-Autogrooming G/B -Grooming baby Feed–Feeding R-Resting V- Vocalizing

6.3.2 Foraging

Tarsiers were observed in the following substrates while foraging: tree trunk, sapling trunk, branch, thicket and ground. The mode of locomotor and postural behaviour observed while foraging were: climbing up, climbing down, sitting, bipedal hop, clinging, leaping and quadrupedal walk. Not all combinations of substrate and locomotion were recorded in the foraging data. Counts of the number of times individuals spent time foraging in the branch and thicket were very low. Therefore, the information from these substrates was combined and formed a new substrate referred to as 'others'. The number of recorded observations of some activities was also small and so it was decided to combine climbing up and climbing down to form the locomotor type 'climb'. The activities: bipedal hop, quadrupedal walk and sitting were combined into a single locomotor type referred to as 'others'. The data are presented in **Appendix 8** and the models fitted in are presented in **Appendix 9**. **Table 6.3** summarises the models fitted for the Foraging data.

Table 6.3. Summary of models fitted for foraging data.

	Model	Residual Deviance	d.f.	Dispersion Parameter	Change in Dev. (allowing for disp)	p-value
1	Full	237.198	27	8.78		
*2	1 - Substrate:Locomotion	241.474	30	8.05	0.160	0.92
3	2 - Substrate	338.687	33		4.03	0.02
4	2 - Locomotion	468.000	33		9.38	0

**Final Model*

The Residual Deviance obtained from the full model, Model 1 is 237.2 on 27 degrees of freedom. The estimated dispersion parameter for this model is 8.78. The data is clearly overdispersed (as the dispersion parameter is much greater than 1) indicating that there may be other factors not included in this model which could be influencing the response. The results should therefore be treated with caution.

To determine if there is an interaction between substrate and locomotor, this term (substrate·locomotion) was removed from the full model and by calculating the change in deviance and allowing for the overdispersion, its importance was assessed. The change in deviance between Model 2 and Model 1 is 0.16 on 3 and 27 degrees of freedom and is compared to an F distribution (p=0.92). It can be concluded that there is no significant interaction between substrate and locomotion at the 5% level and so this term was permanently removed from the model.

Next, substrate and locomotion were removed in turn (Model 3 and Model 4). It can be concluded that both the main effect of substrate and the main effect of locomotion are statistically significant, $p = 0.02$ and $p = 0$ respectively. The final model is therefore given by Model 2. It can be concluded that there is no interaction between substrate and locomotion, but differences are present in foraging activity between substrates and in foraging activity between locomotion. The expected mean number of foraging actions in each substrate is presented in **Table 6.4**, with the expected mean number of foraging actions for each postural behaviour presented in **Table 6.5**.

Table 6.4. Expected mean number of foraging actions for each substrate used.

Substrate	Exp. Acts	Approx SE
Tree Trunk	32.59	1.72
Sapling Trunk	13.66	0.99
Ground	4.88	0.71
Other	12.68	1.62

Table 6.5. Expected mean number of foraging actions for each locomotor type used

Locomotor Type	Exp. Acts	Approx SE
Cling	30.99	1.43
Climb	1.25	1.42
VCL	7.6	0.94
Other	6.82	0.79

Based on actual counts (representing the total number of times all individual were observed foraging) and expected number of foraging actions shown in **Table 6.4**, it can be concluded that individuals are more likely to be observed foraging in tree trunks (counts = 434, exp. Acts = 4.88) than in any other substrate. They were rarely observed foraging on the ground (counts = 50, exp. Acts = 488). **Figure 6.1** further summarises the substrates used during foraging. Frequency on the y-axis was calculated based on actual counts (see**Appendix 8**).

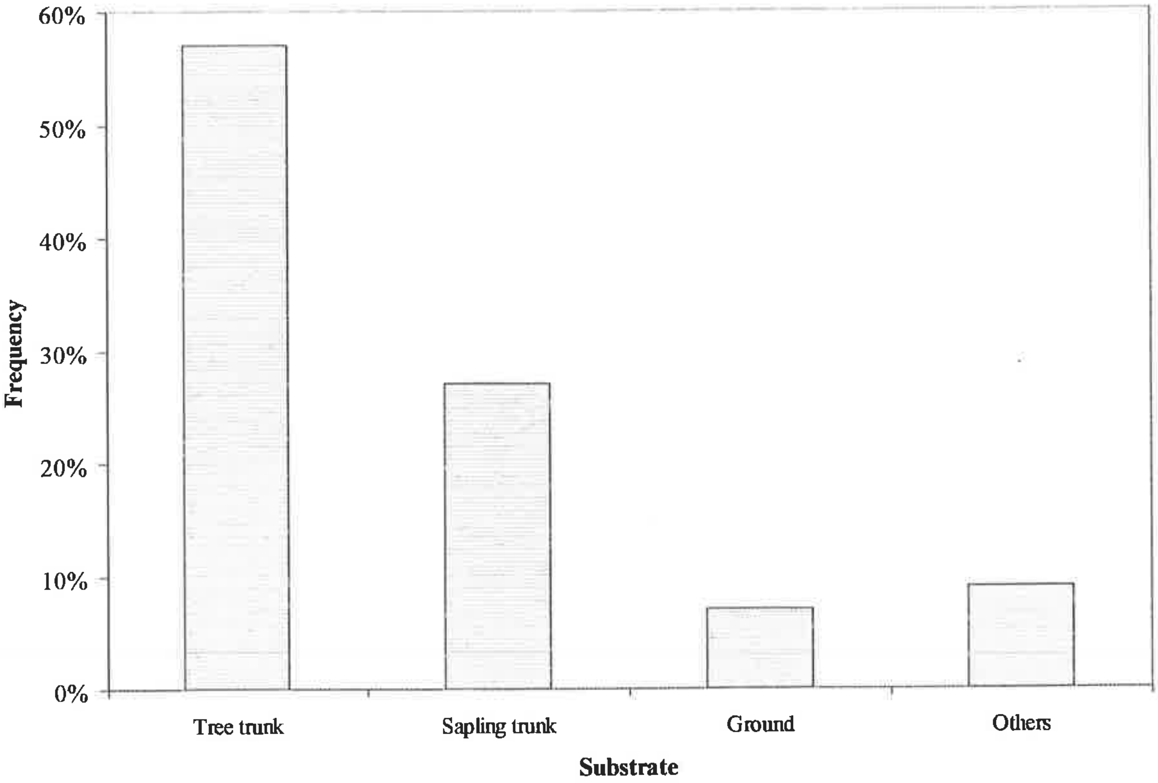


Figure 6.1. Preferred substrate used for foraging.

Based on data presented in **Table 6.5**, it can be concluded that when foraging, individuals are more likely to be clinging than performing any other behaviour (**Figure 6.2**). This can be attributed to the fact that foraging behaviour was primarily observed and recorded while the animal was scanning its surroundings looking for prey. Tarsiers are known to utilise the ambush-capture or sit and wait method of catching prey (Niemitz, 1979a, 1979b) and this method is associated with scanning as the behaviour primarily involved in foraging (Fogden, 1974; Roberts and Cunningham, 1986, Gursky, 1997).

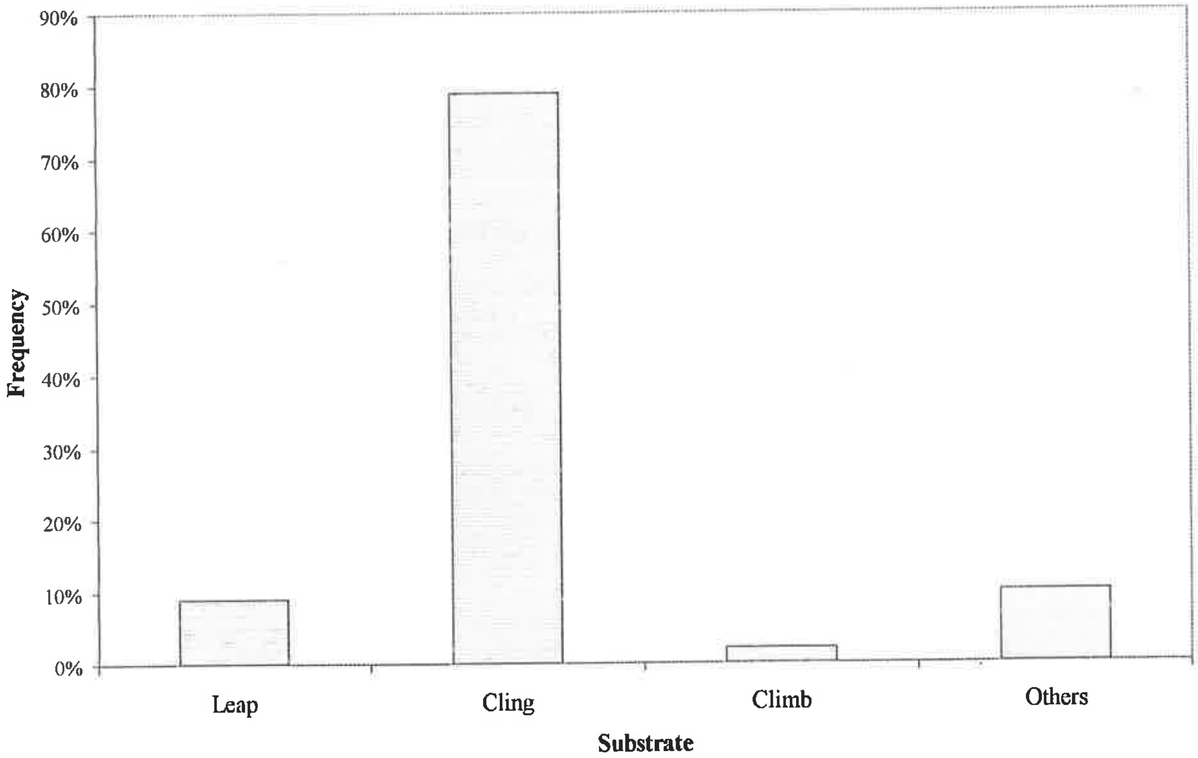


Figure 6.2. Locomotor mode and postural behaviour used for foraging.

Data on height use of the animal while foraging on different substrates are presented in **Table 6.6.** Tarsiers were observed to forage on tree trunks at a mean height of 1.618 m. An individual was observed to use a tree trunk at 7 m above the ground, however, this only accounted for a single observation. The mean height used when foraging on sapling trunks was 1.390 m, slightly less than that when using tree trunks. Radiocollared individuals foraged very near the ground at a mean height of 0.46 m when using other substrates.

Data on the height use of tarsiers when using different modes of locomotor while foraging are presented in **Table 6.7.** The mean height use when clinging was 1.653 m. compared to 1.167

m and 1.422 m when climbing and doing vertical cling and leap respectively. Individuals foraged relatively higher when performing other modes of locomotion.

Table 6.6. Mean height used by *T. syrichta* while foraging as influenced by substrate.

Substrate	Minimum	Maximum	Mean
Tree Trunk	0.3	7	1.618
Sapling Trunk	0.2	2.5	1.390
Ground	NA	NA	NA
Other	0.2	1.3	0.46

Table 6.7. Mean height used by *T. syrichta* while foraging as influenced by locomotor type.

Locomotor Type	Minimum	Maximum	Mean
Cling	0.2	7	1.653
Climb	0.5	2	1.167
Leap	0.25	3	1.422
Other	1.5	2.5	1.931

6.3.3 Travelling

Tarsiers were observed in the following substrates while travelling: tree trunk, sapling trunk, ground, branch, twig and bush. The types of locomotor observed while travelling were: leaping, climbing down, climbing up, bipedal hop and quadrupedal walk. Not all combinations of substrate and type of locomotor were recorded for the travelling data. Adult female (ID No. 4523) was the only individual not visually observed travelling over the course of the study.

Counts of the number of observed continuous travelling movements were very low for branch, twig and bush. These three types of substrate were combined to form the level 'others', and this was subsequently used in the analysis. The numbers of recorded travelling actions were low for climbing down and climbing up. These two levels were combined to form the locomotor mode 'climb'. Similarly, the bipedal hop and quadrupedal walk were combined and this level called ‘others’.

Data are presented in **Appendix 8** and the fitted models presented in **Appendix 9**. **Table 6.8** summarises the models fitted for the Travelling data.

Table 6.8. Summary of models fitted for travelling data.

	Model	Residual Deviance	d.f.	Dispersion Parameter	Change in Dev. (allowing for disp)	p-value
*1	Full	74.09	25	2.96		
2	1 - Substrate:Locomotion	122.89	29		4.12	0.01

**Final Model*

The Residual Deviance obtained from the full model, Model 1 is 74.09 on 29 degrees of freedom. The dispersion parameter is 2.96, again indicating that the data is overdispersed. The results should again be treated with caution.

To determine if there is an interaction between substrate and locomotion, this term was removed from the model and its importance assessed by calculating the change in deviance (divided by the dispersion parameter). The change in deviance between Model 2 and Model 1 is 4.12 on 4 and 25 degrees of freedom, and was compared to an F distribution ($p = 0.01$). It can be concluded that there is a significant interaction between substrate and locomotion. The final model is therefore given by Model 1. The expected mean number of travelling actions for each combination of substrate and locomotion is presented in **Table 6.9**.

Table 6.9. Expected mean number (and standard error) of travelling movements for substrate by locomotor type interaction.

	Substrate				
Locomotor Type	**Tree Trunk**	**Sap. Trunk**	**Ground**	**Branch**	**Other**
VCL	14.96 (1.36)	16.16 (1.42)	1.05 (0.74)	1.036 (0.46)	2.09 (1.04)
Climb	14.26 (1.38)	7.92 (1.73)	NA	5 (2.24)	NA
Other	1	NA	NA	5.76 (1.66)	6 (1.73)

NA refers to combinations not present in the data.

Based on results shown in **Table 6.9**, it can be concluded that tarsiers are most likely to be observed moving by leaping in either a tree trunk or sapling trunk, but rarely observed using this behaviour in other substrates. Climbing is also most likely to be observed on a tree trunk. In comparison, the other modes of locomotor which include bipedal hop and quadrupedal walk, are most likely to be observed in branch or other substrates (includes bush and twig). Tarsiers observed in this study were rarely seen travelling on the ground. **Figures 6.3** and **6.4** give the summary of substrate and mode of locomotor used during travelling.

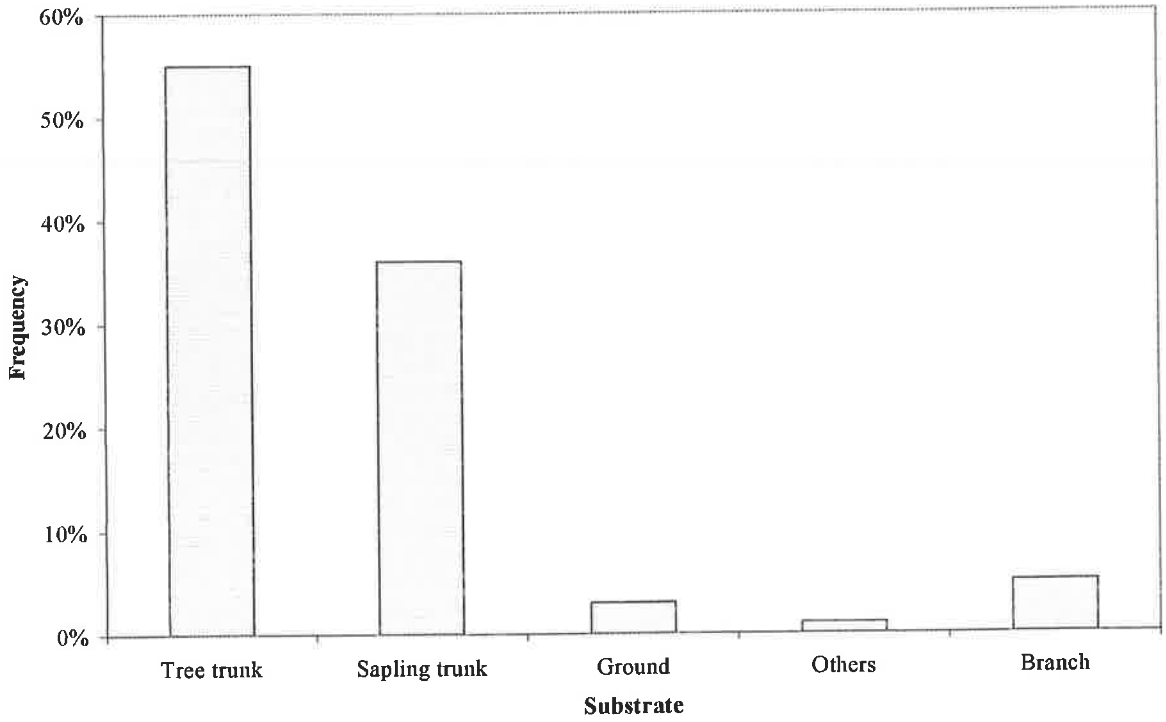


Figure 6.3. Substrate used for travelling.

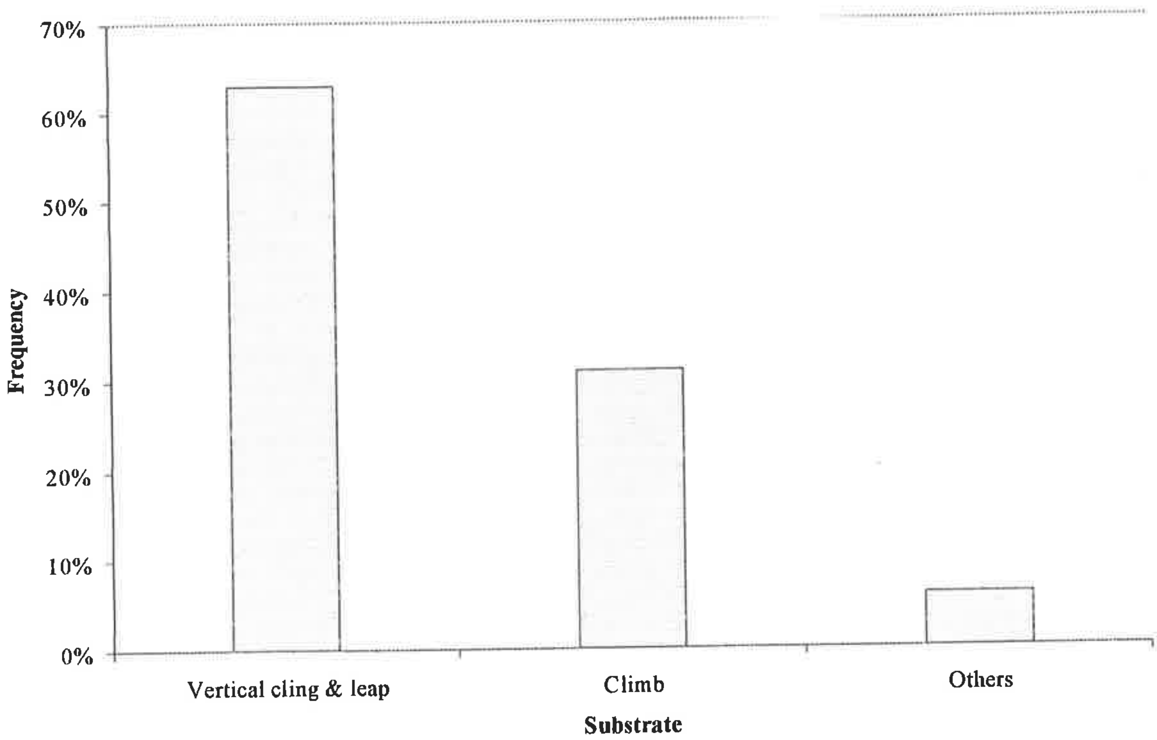


Figure 6.4. Locomotor used for travelling.

Data on height use of radiocollared tarsiers while travelling as influenced by substrate and locomotor type interaction are presented in **Table 6.10**. The highest mean height used while travelling was 1.873 m while leaping and using tree trunk as initial substrate. The lowest mean height was 0.775 m while leaping and using other types of substrates such as twigs and bush.

Table 6.10. Mean height used by *T. syrichta* while travelling as influenced by substrate and different modes of locomotor.

Mode of Locomotor – vertical cling and leap

Substrate	**Minimum**	**Maximum**	**Mean**
Tree Trunk	0.15	3.5	1.873
Sapling Trunk	0.2	3.5	0.961
Ground	NA	NA	NA
Branch	0.5	2.5	1.36
Other	0.5	1	0.775

Mode of Locomotor - Climb

Substrate	**Minimum**	**Maximum**	**Mean**
Tree Trunk	0.3	4.8	1.434
Sapling Trunk	0.7	2.2	1.262
Ground	NA	NA	NA
Branch	1	1.4	1.2
Other	NA	NA	NA

Mode of Locomotor - Other

Substrate	**Minimum**	**Maximum**	**Mean**
Tree Trunk	1.5	2	1.708
Sapling Trunk	NA	NA	NA
Ground	NA	NA	NA
Branch	1.5	2	1.708
Other	NA	NA	NA

6.4 DISCUSSION

The analysis of the travelling and foraging behaviour of *T. syrichta* presented in this chapter has found that, both type of substrate and mode of locomotion are important predictors when establishing the occurrence of both foraging and travelling activities. It should be noted that the models fitted for each response were overdispersed indicating that other factors may be influencing the response. The results should therefore be treated with caution. The analysis has further shown that tarsiers perform each activity in different substrates and with different modes of locomotion, although the tree trunk was the substrate observed most often for both activities. While foraging, clinging is the postural behaviour most often observed. In contrast, leaping in a tree trunk or sapling trunk was most commonly observed when tarsiers were travelling. The strong correlation between substrate use and locomotion as it influences the animal's activities has been attributed to the unique limb structure of the species. The characteristic low intermembral index (ratio of forelimb length and hindlimb length) of tarsiers highly indicate their specialization for vertical clinging and leaping and with the small body size consequently influence their use for small diameter-sized substrates (Fogden, 1974; Niemitz, 1979a, Roberts and Cunningham, 1986). Based on results from modelling morphometric data, Niemitz (1979a) hypothesized that tarsiers vary in the degree to which they use different locomotor and postural modes and consequently substrate use.

The results of this study did not support the prediction of Niemitz's (1979a) model that *T. syrichta* would utilise predominantly oblique supports, but they confirmed that *T. syrichta* is not strictly arboreal and utilises the ground as a substrate, albeit rarely (**Table 6.4**). This observation is similar to that made of wild (Niemitz, 1979a) and captive (Roberts and Cunningham, 1986; Roberts and Kohn, 1993) *T. bancanus* rarely using the ground. It has been suggested that ground was avoided because locomotion was difficult to perform on such substrate (Roberts and Cunningham, 1986). In the case of *T. syrichta,* there is a possibility that ground utilisation is also a behavioural adaptation in the absence of a more contiguous habitat. This is taking into consideration that movements in between habitat patches are important for a certain population to survive (Burkey, 1989).

Field data indicate that activities of *T. syrichta* were concentrated within a specific height range. Observations of the average height use of 0.46 m to 1.931m for foraging and 0.775 m to 1.873 m for travelling indicate propensity for the lower forest stratum. The same has been observed with *T. bancanus* (Crompton and Andau, 1986; Roberts and Cunningham, 1986) and *T. dianae* (Tremble *et al.*, 1993). The varying altitudinal range of habitat (Tremble *et al.*, 1993) possibly influenced the differences in the frequency of height use between *T. bancanus* and *T. dianae* were. Distribution of food resources also dictates the height use and consequently support-use and locomotion of species such as *Galago senegalensis* (Crompton, 1984 as cited by Crompton and Andau, 1986). The risks of predation in the wild have been pointed out to possibly dictate the use of tarsiers for a specific height range within the lower to middle forest strata. Avoidance of the canopy and ground lessen the risk of exposure to arboreal and terrestrial predators respectively (Roberts and Cunningham, 1986). Further studies on factors (*i. e.* predator-prey relationships, forest architecture/phylogeny) that influence microhabitat selection in tarsiers will definitely yield interesting and useful information.

The behavioural observations in this study have similarities with those of Dagosto and Gebo's (1997) behavioural observations of *T. syrichta* in Leyte, and that of MacKinnon and MacKinnon (1980); Crompton and Andau (1986); Tremble *et al.* (1993) on *T spectrum, T.*

bancanus and *T. dianae* respectively (see **Table 2.1**). The similarities among the tarsiers in Bohol and those of the four above-mentioned studies include aspects such as VCL being the primary locomotor mode used. Foraging and travelling were the observed predominant behaviour during nocturnal activities. Vertical was the most preferred substrate orientation. Tree and sapling trunks were the principal substrate types used. However, quantitative comparison is not relevant, as the methods of handling and analysing the data are entirely different.

Chapter 7:

Population Viability Analysis

CHAPTER 7: POPULATION VIABILITY ANALYSIS

7.1 INTRODUCTION

Population viability analysis (PVA) is a process that involves predicting the probability that a species will become extinct in a specific region over a period of time in the future (Possingham, 1991; Boyce, 1992; Beissinger and Westphal, 1998). It is a mathematical modelling tool that evaluates the impact of certain processes such as natural catastrophes and loss of genetic diversity on the viability of a given population. PVA is specifically targeted towards threatened and endangered species or populations (Soule, 1980; 1987; Goldingay and Possingham, 1995), because the species' small population sizes make them highly susceptible to extinction (Terborgh, 1992). This brings into focus a closely related concept, minimum viable habitat area (MVHA). An MVHA has been described as an area of sufficient size capable of maintaining a viable population not only under normal conditions but also during chance events brought about by the environment (Shaffer; 1981, Beier, 1993). PVA does not constrain itself to merely defining a minimum habitat area and the viability of a population within that area (Thomas *et al.*, 1990) but provides insight into how to reduce the probability of extinction within some time frame (Boyce, 1992). These insights are best illustrated by the ability of PVA to predict the likely response of species to management actions such as reintroduction of captive-bred individuals (Bustamante, 1996; South *et al.*, 2000), prescribed burning (Possingham *et al.*, 1993), timber harvesting (Lindenmayer and Possingham, 1996), and the implementation of wildlife corridors (Norton and Nix, 1991).

PVAs have been performed on a wide range of species worldwide. These include: the spring chinook salmon *Onchorynchus tshavytscha* in Oregon, USA (Ratner *et al.*, 1997); the Florida manatee *Trichecus manatus latirostris* (Marmontel *et al.*, 1997); three species of butterflies in Europe *Cupido minimus*, *Melanargia galathea* and *Aporia crataegi* (Baguette *et al.*, 2000); the bearded vulture *Gypaetus barbatus* in the Austrian alps (Bustamante, 1996); the African elephant *Loxodonta africana* (Armbruster and Lande, 1993); the sooty shearwater *Puffinus griseus* in New Zealand (Hamilton and Moller, 1995); the yellow-bellied glider *Petaurus australis* in eastern Australia (Goldingay and Possingham, 1995); and the helmeted honeyeater *Lichenostomus melanops cassidix* in Victoria, Australia (Akcakaya *et al.*, 1995).

In Asia, PVA has not been widely used to assess the effects of demographic and environmental processes on the long-term viability of natural populations (Song, 1996). However, it is emerging as a useful tool for applied conservation biology in the region (Song, 1996; Li and Li, 1998; Horino and Miura, 2000). The literature on PVA for primate species is limited *i.e.* Tana river crested mangabey *Cercocebus galeritus galeritus* in Kenya (Kinnaird and O'Brien, 1991) and vervet monkeys *Cercopithecus aethiops* (Young and Isbell, 1994). This is despite the fact that some primates are considered to be keystone species and the viability of their populations contribute significant information in formulating sound forest management practices (Chivers, 1986; Mittermeier, 1986, Mittermeier and Cheney, 1987). A population viability analysis of the Philippine tarsier *Tarsius syrichta*, using the metapopulation model Analysis of the Likelihood of Extinction (ALEX) (Possingham and Davies, 1995) is presented in this chapter. The main aim of this work is to determine the area requirements and spatial configurations of habitat patches for viable populations of *T. syrichta*, in order to assess a sound conservation strategy for the species.

7.2 METHODS

7.2.1 The PVA Model

ALEX is a Monte Carlo simulation model that utilises pseudorandom numbers to simulate a scenario involving different stochastic processes. Each scenario is run several times to gather statistics on the likelihood of extinction. The user needs to specify the number of runs for each scenario and the length of the simulation in years (Harris *et al.,* 1987; Possingham and Davies, 1995). I chose to use this model because it has features that are applicable to *T. syrichta.* It simulates the dynamics of spatially structured populations and allows habitat selection through modelling movements between different patches. It accomodates environmental stochasticity at a subpopulation level. It was written to apply to any population that is under threat, and not just species that are extremely rare. It has a sensitivity analysis facility that helps the user identify parameters whose variance strongly influences the results – an especially important feature if existing data on a species are inadequate. However, the model has some important weaknesses that must be taken into account (Possingham and Davies, 1995): There is only one sex modelled in ALEX, which is usually the female. This is because for most species, the female limits the reproductive capacity of the population. The model ignores the possible effects of genetic structure on population viability. ALEX only allows for a simple age structure with only three classes of individual: newborn, juvenile and adult. The weaknesses of ALEX may limit its capability in working with very small populations. However, the model allows the user to specify a threshold population level (recommended is 5, at which the population is assumed to be extinct) in order to avoid the problems of modelling extremely small populations.

7.2.2 Data input into ALEX

7.2.2.1 Age classes and Mortality

ALEX models three age classes: newborn, juvenile and adult: newborns were described as individuals on their 1st year of life; juveniles are those that are on their 2nd year and adults are sexually mature and over 2 years of age. Different mortality probabilities can be assigned to each age class and are described on an annual basis.

The first year of a tarsier's life (newborn class in ALEX) involves an initial period of 2 months with infants being transported orally by their mothers. This period is relatively short due to the rapid post-natal development of the species (Wright, 1990; Roberts, 1994). Previous observations suggested weaning at 78-82 days (Roberts, 1994, pers. observ.), although independent foraging can be attained at 68 days (Haring and Wright, 1989). Infants were transported orally and parked on substrates when mothers were foraging. In the case of *T. syrichta*, an infant was generally left all by itself while the mother foraged hence risk of predation can be considered significant. The first year also involves very young individuals dispersing and establishing their own territory after weaning. Data from this study showed predation might have caused the death of a dispersing individual that was radiocollared. It was assumed that the estimated mortality rate on the first year would be relatively high at 35%.

Juveniles as described in this model are individuals who are in their 2nd year of life albeit sexually immature. Some individuals might already be in the final process of establishing their home range. The estimated mortality rate of this stage compared to that of the newborn stage is relatively lower at 20%.

Data on *T. bancanus* and *T. spectrum* indicated that beyond their second year, tarsiers are sexually mature and have generally established home ranges (MacKinnon and MacKinnon, 1980, Niemitz, 1984; Gursky, 1997). Based on these, the model was set so that *T. syrichta* will reproduce in its third year of life. Individuals over 2 years of age are modelled as adults in ALEX. No data are available on mortality or life span of wild *T. syrichta* and information on wild *T. bancanus* and *T. spectrum* is similarly lacking. The only record on the life span of *T. syrichta* is provided from a single captive individual that lived to the age of 12 years (Ulmer, 1960), although in general this species does not thrive well in captivity (Haring and Wright, 1989). If we assume that most tarsiers have the same life span (12 years) in the wild, if an adult died on its 12th year, it would have spent 10 years as an adult. With an estimated 65% mortality rate for the 10 years as an adult, this would correspond to an average annual mortality of 10% *i.e.* $\text{Mortality}_{(10\ \text{years})} = 1 - (1 - \text{Mortality}_{(1\ \text{year})})^{10}$.

7.2.2.2 Litter size and sex ratio

T. syrichta typically give birth to a single young (Catchpole and Fulton, 1943; Ulmer, 1963; Haring and Wright, 1989; Wright, 1990; Roberts and Kohn, 1993; pers. observ.). Preliminary data from this study suggest that *T. syrichta* reproduces seasonally with at least one birth peak from June to July (see **Figure 4.7**). The approximate gestation length recorded for *T. syrichta* was 180 days (Ulmer, 1963).

The data available for the sex ratio at birth are very limited. Among the four infants captured with their mothers, 3 were female and 1 was male thus giving a sex ratio of 3:1. On the other hand, assuming that there is no differential mortality between birth and the time an adult becomes trapped, the data on adults captured gives a sex ratio of 3:2 (6 females against 4 males). I calculated the 95% confidence intervals (Steel and Torrie, 1960) of each of these ratios (3:1 and 3:2) and a combination of both ratios (9:5) and found that the confidence intervals all included the even ratio of 1:1. I therefore considered 1:1 as a valid sex ratio. The same ratio was also observed when 26 *T. bancanus* individuals comprised by 13 males and 13 females were trapped in Sarawak, Borneo over a 23-month period (Fogden, 1974). The probability that a female young is produced was therefore assumed to be 0.50.

7.2.2.3 Home range size

This study is the first to provide data on the home range size of female *T. syrichta*. The mean range size was 2.45 ha per individual. Home ranges of females showed minimal overlap at 3.35% (**Table 5.3, Appendix 7**). Individuals were always observed to be solitary, except for a female with an infant. In the model, it is automatically assumed that a single adult female is able to occupy each home range.

7.2.2.4 Environmental variability

To simulate environmental stochasticity, ALEX uses an environmental variable drawn at random from a normal distribution with a user-specified mean and standard deviation. This variation influences the proportion of females in the population that breed each year. The model requires a value for the environmental variable to be specified at which all females in the population are able to breed (best condition) and a value at which no females can breed (worst conditions). The proportion of females that breed if the environmental variable is between the worst and best cases increases linearly from 0 to 1. If the environmental variable is greater than or equal to the best value, then the quality multiplier (proportion of breeding females) is set to 1 and if less than or equal to the worst value, the quality multiplier is zero. (Goldingay and Possingham, 1995).

Rainfall data were used to approximate the environmental variable because rainforest depends on it for growth and rainforest is the habitat type that the tarsiers utilised. The abundance of tarsier's main prey type, arthropods, is also sensitive to variation in annual rainfall. Data for annual rainfall totals supplied by the Philippine Atmospheric Bureau (PAGASA) for Bohol between 1961-1998 had a mean of 1,336 mm and standard deviation of 331.2 mm, demonstrating that there is little variability in rainfall on Bohol. The classification of the region's climate based on rainfall pattern falls under Type 4, wherein there is generally a uniform distribution of rainfall throughout the year (Morris and Rumbao, 1985). Environmental variation (*EV*) was modelled in this analysis by using a mean of 0.64± 0.16 (SD), calculated by dividing the mean rainfall for 1961 – 1998 which was 1,336 mm over the highest recorded annual rainfall within the same period equivalent to 2,087.5 mm. Based on the chosen environmental variable (rainfall), I estimated the best environmental level to be 0.5 and worst when 0.2.

7.2.2.5 Catastrophe

A catastrophe may be configured to affect population size by nominating the probability of occurrence of a catastrophe and extent to which a population is reduced if a catastrophe occurs (Southgate and Possingham, 1995). In the Philippines, forest fire has been one of the major causes of forest destruction together with logging and slash-and-burn agriculture. Pests and diseases are considered secondary causes (DENR/UNEP, 1997). Fire was chosen as the natural catastrophe to be modelled for this study. The catastrophe was set to be dependent on the biomass variable on a local scale (acts independently on each patch).

7.2.2.6 Biomass Function

'Biomass' is a habitat variable in the model that is intended to reflect patch quality, which can further be influenced by catastrophes, like fire or cyclone. The growth rate of a patch determines the annual increment in biomass. Biomass increases linearly until the maximum biomass is reached. The user can allow the biomass of a patch to affect the number of potential breeding females (Possingham *et al.*, 1992). The value for the growth of biomass in this study was determined based on the rate of regeneration of Southeast Asian secondary lowland rainforests, which was estimated to be 60 years (Gomez-Pompa *et al.*, 1991). The annual increment was therefore calculated to be 1.6%.

7.2.3 Analysis

7.2.3.1 Minimum viable habitat area

For the purpose of determining the minimum viable habitat area, the PVA was set up with a simple habitat configuration of a single patch of suitable habitat and did not include a catastrophic event. This approach was chosen in order to reduce the number of assumptions that are used in the model (Goldingay and Possingham, 1995). The baseline parameter values listed in **Table 7.1** were used to determine the minimum viable population for the Philippine tarsier. The population was considered viable when its probability of extinction was 5% or less within 100 years in a model without any catastrophe parameter included (Goldingay and Possingham, 1995). Simulations were run for different habitat area so that an assessment could be made of the minimum habitat area at which the criteria for viability will pertain.

7.2.3.2 Sensitivity Analysis

The baseline parameter values for mortality and probability of female being born used in this model were derived from limited data; therefore it was deemed necessary to test the

Table 7.1. Values of the life history and environmental parameters used in ALEX for the metapopulation analyses of the Philippine tarsier *Tarsius syrichta* (see Possingham and Davies, 1995).

Parameter	Value				
Probability of a baby is a female	0.5				
Maximum number of litter per year	1				
Maximum number of young per year	1				
Annual probability of litters					
0 litter per year	0.5				
1 litter per year	0.5				
Probability of young per litter					
0 young per litter	0				
1 young per litter	1				
Young per year					
0 female young	0.75				
1 female young	0.25				
Annual probability of death					
Newborn	0.35				
Juvenile	0.20				
Adult	0.10				
Quality/Biomass function					
Quality	0	0.1	0.8	1	1
Biomass	0	30	50	80	100
Number of Juvenile classes	2				
Best Environmental level	0.5				
Worst Environmental level	0.5				
Density in high-quality habitat					
Minimum living area	2.5				
Minimum breeding area	2.5				
Low patch population threshold	5				
Extinction threshold	5				
Patch characteristics					
Maximum quality of patch	1				
Maximum biomass of patch	1				
Initial population	1				
Initial biomass	1				
Growth rate of biomass (annual increment)	0.016				
Patch quality of environmental variable					
Mean	0.64				
Standard deviation	0.16				
Correlation of patch quality between patches	0.8				

sensitivity of these parameters. In order to allow an assessment of the sensitivity, deviations in these values were applied. The sensitivity analysis applied here was similar to that of Goldingay and Possingham (1995), wherein the population was simulated 100 times for a 200-year period. The probability of extinction within 100 years was expressed based on the results of each set of 100 simulations. A set of 100 simulations was done over a range of habitat sizes: (1) for different mortality values for newborn, juvenile and adult (**Figures 7.2, 7.3 and 7.4**) and (2) for different probabilities of female born (**Figure 7.5**).

7.2.3.3 Catastrophe and Patch variation

A catastrophe parameter of fire was introduced in the model, with the characteristics presented in **Table 7.2**. Different scenarios for patch characteristics, such as increasing the patch area, subdividing the patch equally into independent patches and introduction of a corridor between patches, were simulated and the probability of extinction within 100 years was noted.

Table 7.2. Values of the catastrophe and movement parameters used in ALEX for the metapopulation analyses of the Philippine tarsier *Tarsius syrichta* (see Possingham and Davies, 1995).

Parameter	Value			
Catastrophe characteristics				
Biomass dependence function				
Probability of catastrophe	0	0	0.01	0.02
Biomass variable	0	20	50	100
Biomass minimum effect	0.5			
Biomass maximum effect	1			
Population minimum effect	0.5			
Population maximum effect	1			
Probability of diffusion				
Newborn	0.2			
Juvenile	0.8			
Adult	0.2			
Effect of quality on diffusion	0.5			
Minimum proportion of population for diffusion	0.2			

7.3 RESULTS

7.3.1 Minimum viable population and habitat area

Given the values of the life history and environmental parameters (**Table 7.1**) used for the analysis, and in the absence of environmental catastrophe, the minimum habitat area that could attain a less than 5% probability of extinction within 100 years was 60 ha. (**Figure 7.1**). Therefore 60 ha can be considered as the minimum viable habitat area for the Philippine tarsier. Each female tarsier has home range of approximately 2.5 ha with little overlap thus the minimum viable habitat area of 60 ha contains 24 female individuals.

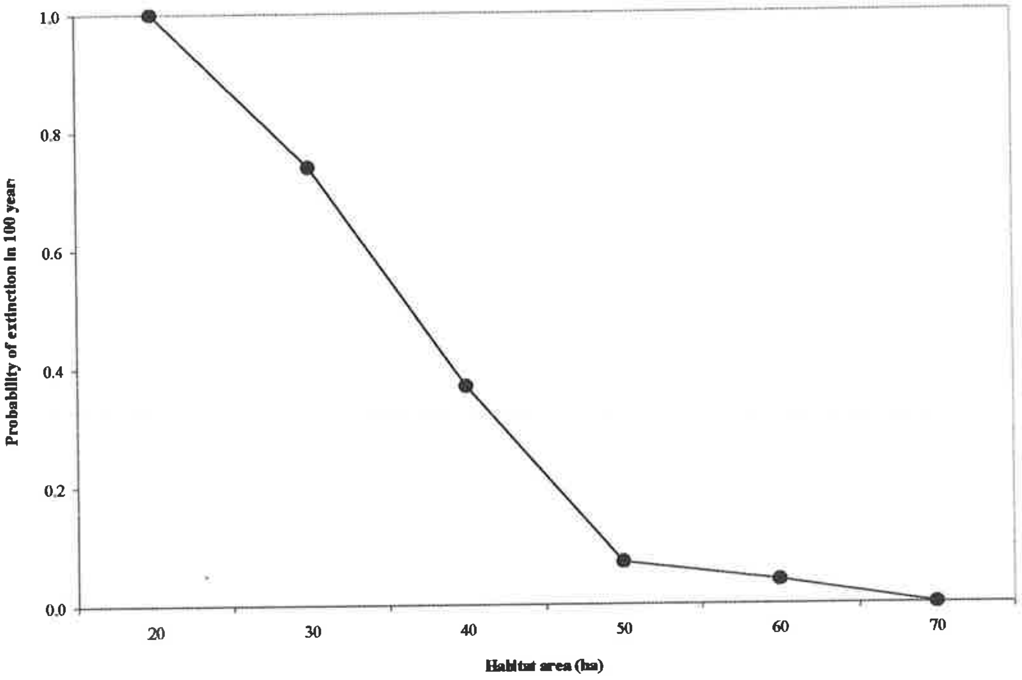


Fig. 7.1. Probability of extinction when the habitat area was increased.

7.3.2 Sensitivity Analysis

Varying the mortality rate of newborn, juvenile and adult tarsiers in the model generated different outputs. The output of the model was moderately sensitive to changes in the mortality rate for newborn and juvenile (**Figures 7.2** and **7.3**). However, sensitivity to varying adult mortality rate was very pronounced. A slight increase in adult mortality would make the population very unstable and causes a substantial increase in the probability of extinction (**Figure 7.4**).

The simulation also showed that when the habitat area was increase to 70 ha, variation in the mortality rate of newborn and juvenile resulted into similar probabilty of extinction within 100 years that approaches 0% (**Figure 7.2** and **7.3**). On the other hand, an increase in habitat area to 70 ha did not considereably reduce the extreme differences in probability of extinction for each variation of the adult mortality rate (**Figure 7.4**).

The model was also sensitive to changes in the probability of female born (**Figure 7.5**). An increase in the probability of a female being born also increased the viability of the population.

7.3.3 Catastrophe and Patch Variation

Different scenarios were run in the model to determine their effect on the viability of the population. The probability of extinction of 24 female tarsiers in a 60 ha patch did not increase in 200 years in a scenario were there is no catastrophic event considered. The probability of extinction within 100 years was 0% with a median extinction time of >200 years (Scenario 1) (**Figure 7.6**). When fire was introduced in to the model as a catastrophe, with values as listed in catastrophe characteristics in **Table 7.2,** the probability of extinction within 100 years increased considerably to 72% with a median time of extinction of 46 years (Scenario 2) (**Figure 7.6**). The patch area was increased four fold to 240 ha to test the effect on extinction. There was an improvement in viability; the probability of extinction within 100 years decreased to 42% and median time of extinction increased to 95 years (Scenario 3) (**Figure 7.6**). However, dividing the 240 ha patch into 4 equal independent patches of 60 ha further improved median time of extinction to 148 years and probability of extinction within 100 years decreased to 25% (Scenario 4) (**Figure 7.6**). Providing diffusion corridors of 100 m wide between the patches so that each patch is touching with two other patches and using the diffusion value in **Table 7.2**, showed no additional improvement in viabilty. The median time to extinction was 146 years and the probability of extinction within 100 years was 20% (Scenario 5) (**Figure 7.6**). Additional sensitivity simulations were done with Scenario 5 that included varying the width of diffusion corridors, minimum population for diffusion, effect of quality on diffusion and probability of diffusion (newborn, juvenile and adult). However, there were no significant changes obtained in probability of extinction with these variations.

In a hypothetical single patch with the parameters of catastrophe occuring as discussed, increasing the patch area improved the viability of the population (**Figure 7.7**). Subdividing the patch into 6 equal patches had different effects on viability that was greatly influenced by the size of the patches created. Subdividing a patch area into patches with less than 25 ha area resulted in instability, however when the area created was greater than 25 ha the viability improves. For example a patch area of 100 ha that has an extinction probability within 100 years of 64% when divided into 6 independent patches (17 ha each patch), increased the probability to 96%. On the other hand a 400 ha patch with an extinction probability of 36% when divided into 6 (67 ha each patch) reduced the probability of extinction to 6%.

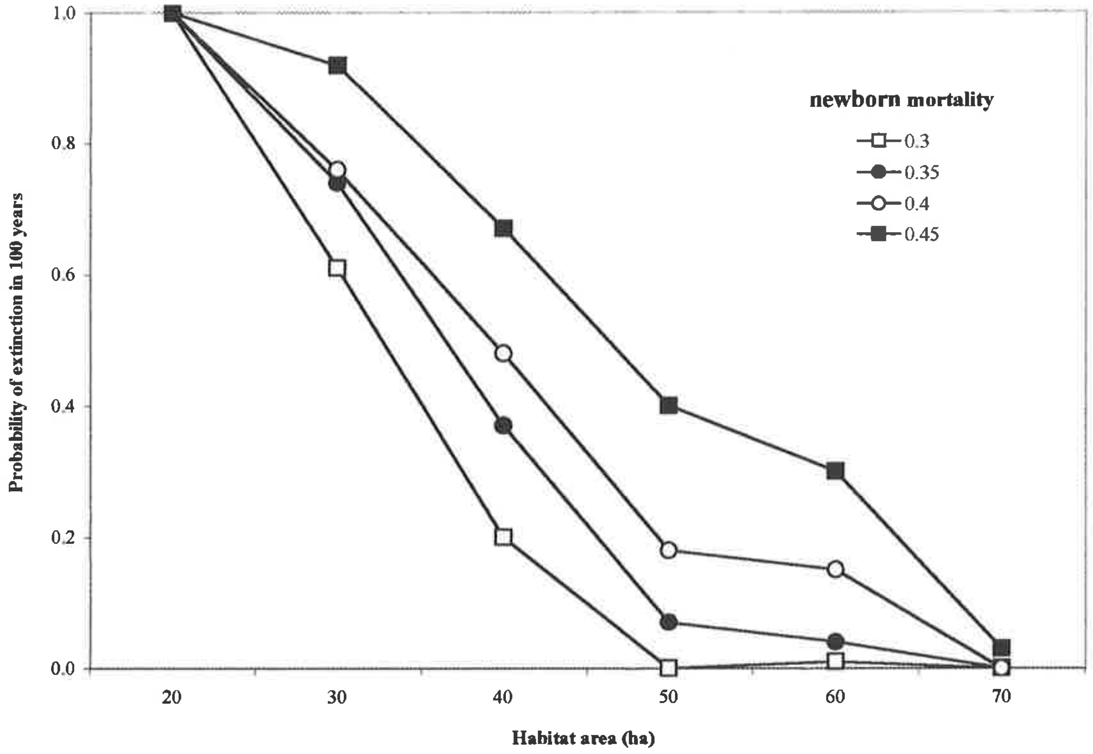


Fig. 7.2. Probability of extinction when the annual mortality of female newborn tarsiers is varied.

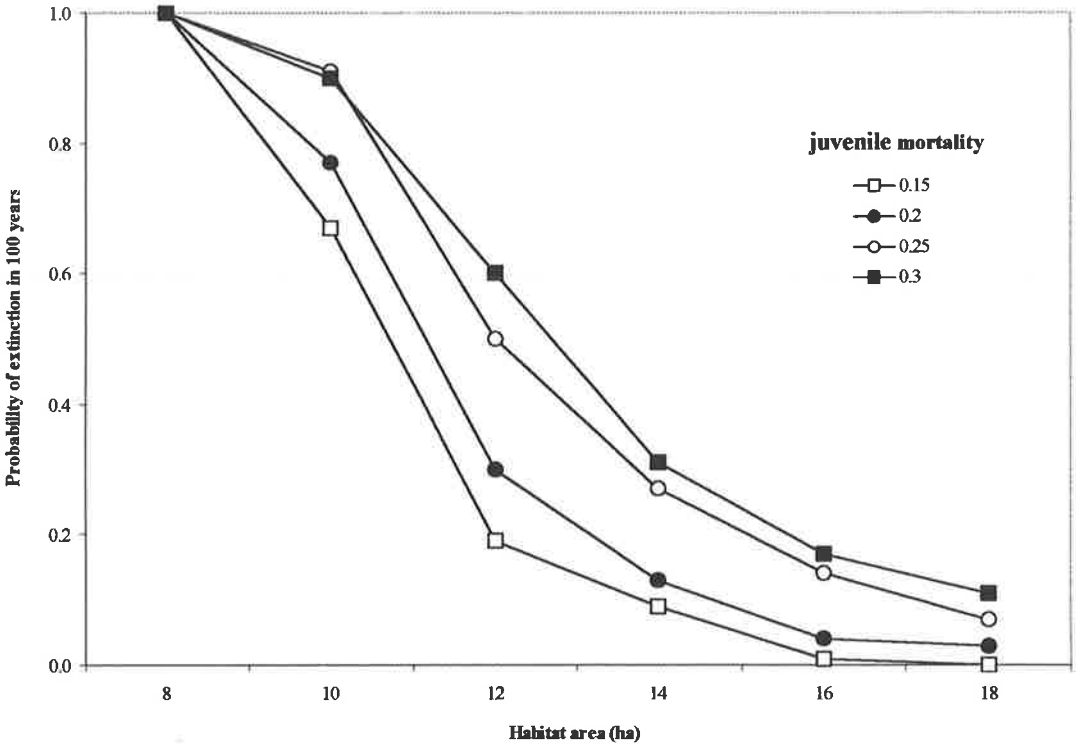


Fig. 7.3. Probability of extinction when the annual mortality of female juvenile tarsiers is varied.

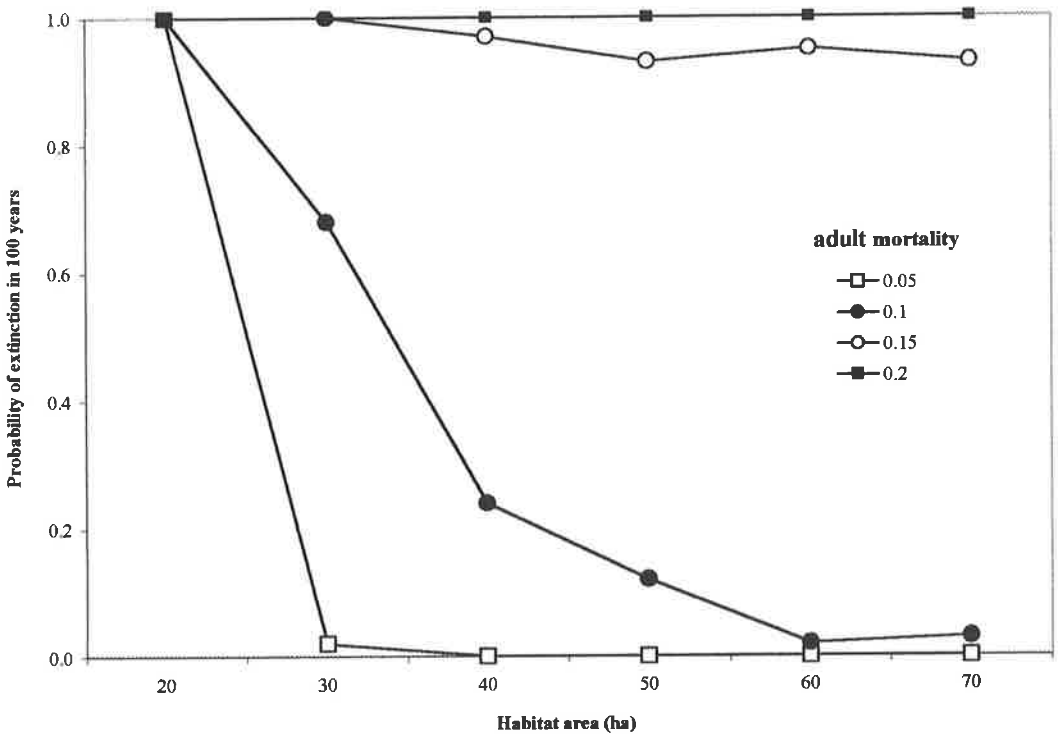


Fig. 7.4. Probability of extinction when the annual mortality of female adult tarsiers is varied.

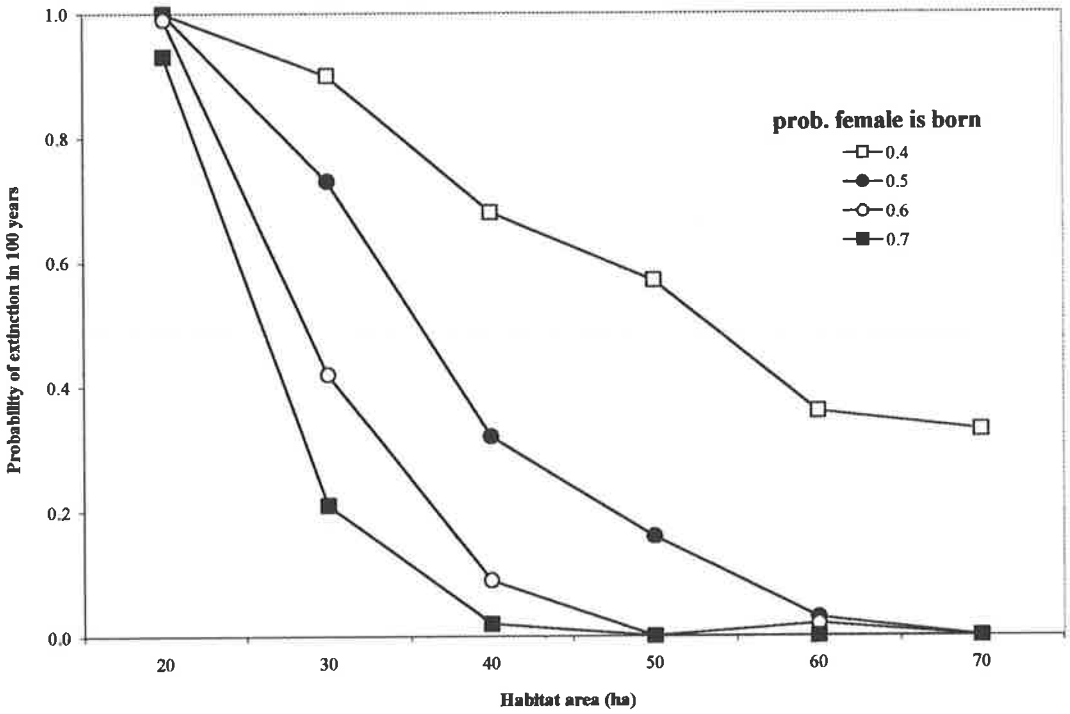


Fig. 7.5. Probability of extinction when the probability of female being born is varied.

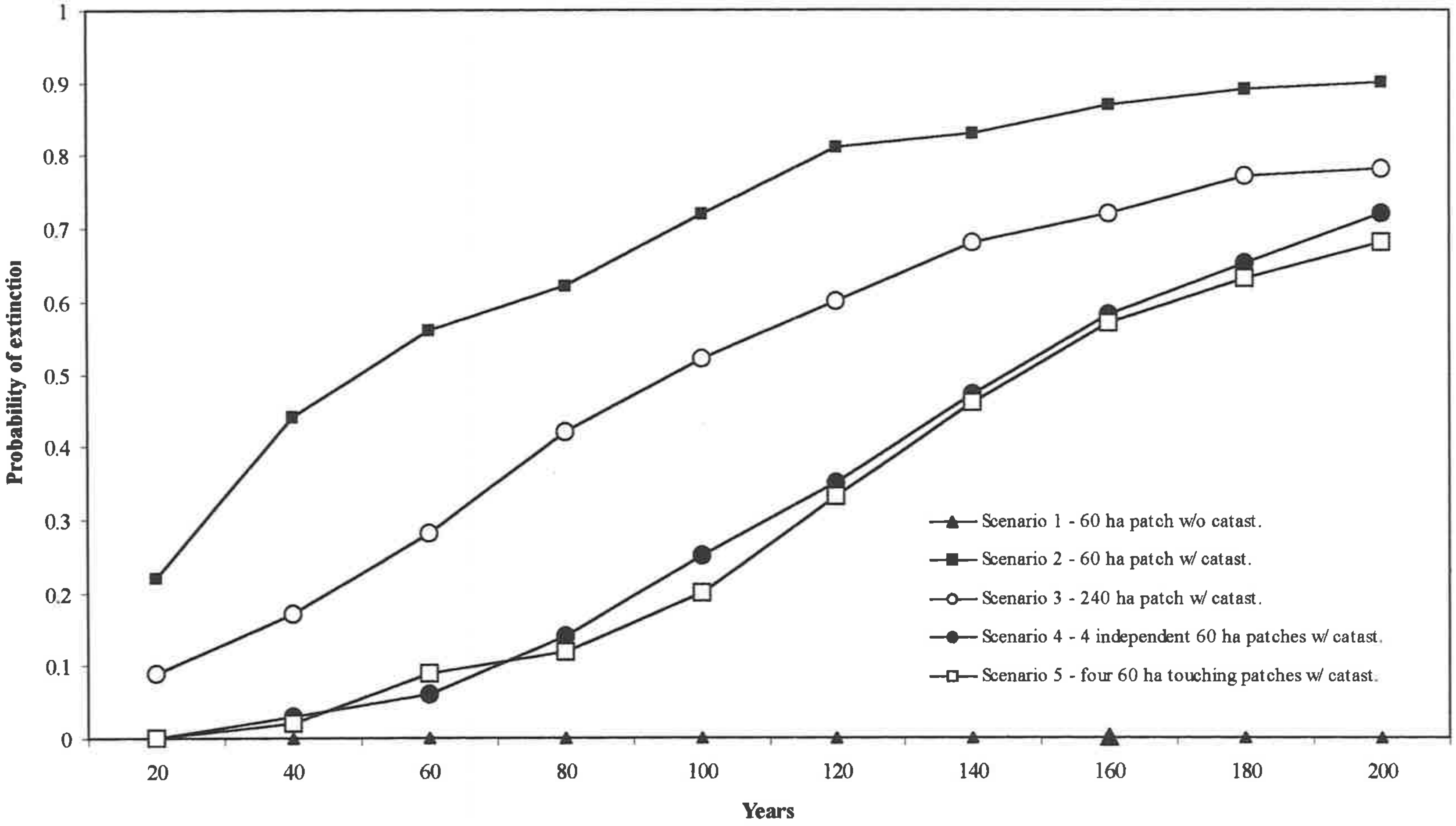


Figure 7.6. Probability of extinction in different scenarios.

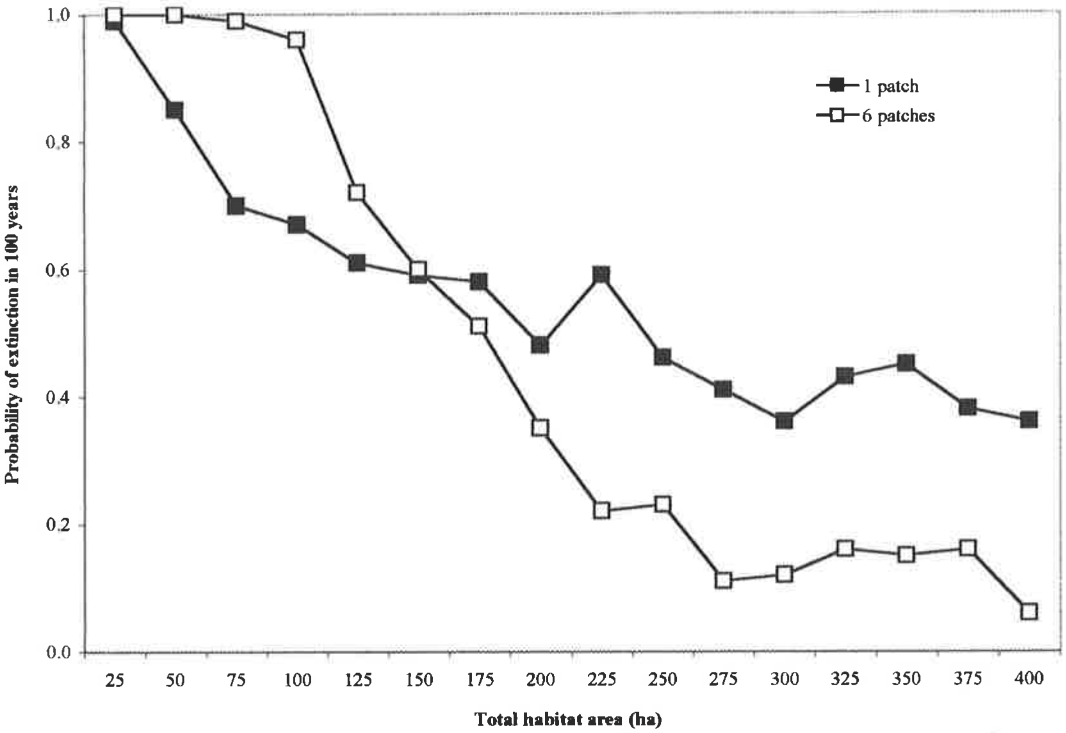


Figure 7.7. Probability of extinction when a patch area is subdivided into 6 equal patches.

7.4 DISCUSSION

The use of plausible assumptions in the simulation model indicated that, in the absence of any environmental catastrophe, a minimum viable habitat area (defined as having less than 5% probability of extinction within 100 years) of 60 ha can support a viable population of 24 female tarsiers. This estimate takes into consideration that the whole patch are fully occupied, which in the wild is most often not the case. It should also be noted that this estimate is based on life history parameters derived mainly from this study conducted in just one site in Corella, Bohol. The values should be handled with caution because of these limitations. Long-term field work in other areas of the tarsier's known distribution is warranted, to distinguish between baseline variations and extraordinary datasets, which can be confused by short-term observations (Trivelpiece *et al.*, 1990).

Sensitivity analysis showed that the model's output was influenced by the values used for newborn, juvenile and adult mortality but the effect of variation on adult mortality was more pronounced. The model showed that with regards to the newborn and juvenile mortality rate, if a sufficient high enough number (18 or more in a single patch) of female tarsiers are maintained the effect on probability of extinction by slight variation on their rates can be reduced to a nearly negligible value. In the case of variation in adult mortality, even the increase in number of female tarsiers was not able to considerably reduce the differences of the probability of extinction of the each variation. A slight increase in the adult mortality renders the population very unstable. The adult mortality rate used as baseline parameter (0.10) for the model was derived from a single captive individual that was reported to have survived for 12 years. This period largely exceeded the duration of this field study, hence this parameter is difficult to confirm. Further studies need to be done to determine actual mortality rates of adult females in the wild.

The model showed that adult mortality rate greatly influences the probability of extinction of the species. Measures should therefore be taken to reduce mortality in wild populations such as strict reinforcement on the ban for hunting, control of the predator (cat) population in the reserve site and maintaining a large enough area so that variations in mortality will have reduced impact on population stability.

The birth sex ratio also influences the viability of the population. Although it is difficult to determine the actual sex birth ratio of the species and there is not much that can be done to modify it, a more accurate value for this would improve PVA modelling of the species.

From the results of the introduction of catastrophe and variation in patch parameters in the model, it appears that the tarsier would have better viability in several smaller patches than in a few large patches or in just one big patch. Increasing the area of a single patch improved the viability of the population but subdividing the patch area into smaller patches further improved it. However, the smaller patches have a critical minimum size (*e.g.* >25 ha) (**Figure 7.7**) for which the population will still be viable; anything less will exhibit instability characterised by high rate of extinction. The addition of diffusion corridors and variation in diffusion parameters did not significantly change the probability of extinction. The model showed that in order for the species to remain viable, it is advantageous to have several suitable and sufficient habitats maintained across the range instead of just a single area.

It has already been suggested that an archipelago of refuges might actually be an optimal design for conservation (Boecklen, 1986). Recommendations have also been made regarding intentional and managed fragmentation of populations, with low migration among subpopulations being the best strategy to preserve genetic variation in threatened species (Boecklen, 1986; Goodman, 1987; Lacy, 1987). Small and fragmented reserves play a significant role in conserving local endemics (Terborgh and Winter, 1983), especially those with low area requirements (Burkey, 1989).

Based on the results of this model, the same strategy can be applied to *T. syrichta*. Subdividing population *per se* may not be the best option in Bohol. I would recommend that the 174 ha forest reserve be kept intact considering that its size is not far more than what is considered the minimum viable habitat area. The reserve is not also entirely comprised by suitable habitat areas. However, taking into consideration fire as a major catastrophe in this model, it would be better to create several new reserves across the known geographical distribution of *T. syrichta* rather than just a single one in Bohol. An approach involving reconstructing or rehabilitating several degraded habitats across the known geographical distribution of *T. syrichta* must also be considered. These management options are important criteria in setting up reserves (Soule and Simberloff, 1986) and will be a hedge not only against fire, but also against diseases, drought or predation. These recommendations of putting several sufficient habitats across the landscape parallel that for the northern spotted owl *Strix occidentalis caurina* (Murphy and Noon, 1992) and the yellow-bellied glider *Petaurus australis* (Goldingay and Possingham, 1995).

Chapter 8:

Conservation

CHAPTER 8: CONSERVATION

8.1 INTRODUCTION

Tarsius syrichta is the only species of the genus *Tarsius* found in the Philippines. It has previously been reported as rare and decreasing (Anon., 1979) and listed as endangered by the IUCN (1990). *T. syrichta* was also described as threatened due to heavy deforestation and increasing agriculture in its natural habitat (Wright, 1987). The IUCN/SSC Primate Specialist Group gave the species a Conservation Priority Rating 4, which defines the species as highly vulnerable, with the remaining population threatened by habitat destruction and hunting (Eudey, 1987). However, subsequent informal observations from the wild (Heaney and Utzurrum, 1992; Rickart *et al.*, 1993) have reported that *T. syrichta* is more widespread in distribution than previously thought, although no long-term study on its ecology has been conducted. It is currently listed as Data Deficient (IUCN, 1996). In this chapter, I consider the recent legislation protecting the animal and discuss possible management options for the conservation of the species. I then present conclusions, recommendations and directions for future research based on the results of this study.

8.2 LEGISLATION EFFORTS

Efforts to protect the Philippine tarsier by law started only recently. In 1991, the Department of Environment and Natural Resources (DENR)-Philippines specified the Philippine tarsier as among the country's protected wildlife species. The inclusion of *T. syrichta* in Appendix 2 of the Convention on the International Trade of Endangered Species (CITES), endorses restricted exportation of the species from the Philippines (Heaney *et al.*, 1998). The listing of the species under CITES Appendix 1 has been proposed by the DENR-Philippines. The first legal measure to protect the *Tarsius syrichta* began in 1997, in the form of Presidential Proclamation No. 1030, which declared the species as special protected faunal species of the Philippines. The proclamation prohibits the hunting of the species and directs efforts in establishing sanctuaries for conservation. These efforts are in their infancy and results cannot be assessed until the proposed rules are strongly implemented. It is important to note that the species have been hunted and sold domestically as pets. The 'pet-trade' is difficult to prohibit unless a widespread public awareness campaign is sustained. They must be made aware that tarsiers don't thrive well in captivity and despite their cute appearance, will not really make good pets. As long as mis-informed tourists buy tarsiers for pets, farmers will continue to catch them as an alternative source of income. Local DENR personnel should be strict in imposing fines for violators and confiscate animals which could be used for re-introduction programs.

8.3 MANAGEMENT OPTIONS

8.3.1 Captive Breeding

Tarsiers require a diet of live prey and are extremely difficult to maintain in captivity. Although there has been recent success in studying *T. bancanus* in captivity (Roberts and Cunningham, 1986; Roberts and Kohn, 1993; Roberts, 1994) the record of captive births of *T. syrichta* remains low (Wright *et al.*, 1987; 1989). Relatively few *T. syrichta* have been kept in international zoos, and in general these animals do not seem to thrive in artificial settings. Captive breeding does not appear to be a viable option for the species. *Ex-situ* conservation will therefore contribute little to the survival of the species.

8.3.2 Ecotourism

The proposed tarsier reserve in Corella, Bohol is being promoted as a major tourist attraction of the island province. Ecotourism can serve as a vehicle for promoting public awareness on conservation issues such as that of the Philippine tarsier. However, tourism can have long-term negative effects on reserves and communities if uncontrolled or improperly managed (Pleumarom, 1993). The potential negative impacts of tourism in the area must be taken into account by concerned government and private agencies. The 'tolerable-levels' of visitation must be observed and the 'recreational carrying capacity' (*i. e.* the number of user-unit use-periods that a recreation site can provide (each year) without permanent biological or physical deterioration of the site's ability to support recreation, Tivy, 1972) of the reserve site considered. It is important to implement regulations on human activities while inside the reserve because wildlife species that serve as main attractions in such recreation sites come in close proximity with humans and may suffer stress from disturbance that can predispose them to diseases. Preliminary observations on the effect of tourism on *T. spectrum* in Tangkoko Dua Saudara Nature Reserve, Sulawesi show that large tourist groups delay tarsiers from leaving their sleeping sites and therefore significantly reduce early evening foraging opportunities (Kinnaird and O'Brien, 1996). Similar studies to determine the impact of tourist groups on *T. syrichta* behaviour should be done to determine measures on how to manage the species within the reserve. A survey should also be conducted to determine the carrying capacacity of the reserve site and set up criteria such as vegetation and soil characteristics to serve as critical indices in order to gauge potential impact of visitors and site deterioration

8.3.3 Local Communities

There is a growing recognition that in order to successfully preserve biodiversity in protected areas such as national parks and wildlife reserves, there should be greater participation of local people in decision making. It is often the case that local residents perceive protected areas as restricting their ability to earn a living. Conflicts therefore occur between park managers and local communities (Wells and Brandon, 1993). It has also been further suggested that unless wildlife species are of some use to people, they will not be valued (Robinson and Redford, 1991; Heinen, 1995).

In the case of the tarsier sanctuary in Bohol, local communities around the reserve are comprised mainly of subsistence farmers who plant rice, coconuts and cocoa. They harvest timber for constructing houses although on a relatively smaller scale and for firewood to be sold in the market. These farmers can be encouraged to plant tree seedlings to replace trees that they cut thus helping in maintaining the cycle of regrowth in the rainforest. They can also be introduced to other alternative livelihood such as handicraft making, poultry and pig raising, aquaculture and planting of cash crops *i.e.* garlic, ginger and onions which can augment their incomes. A strong incentive program for reforestation should be organised because it is often difficult to motivate people to plant trees especially that monetary benefits can be achieved only after several years. A tree planting fund can be organized from local tax revenues and provide loans for farmers to plant trees (Gradwohl and Greenberg, 1988). In the absence of a buffer zone around the reserve, concerned government and private agencies should work with the local people to demarcate a forest boundary, within which tree-felling would be strictly regulated. These measures would alleviate unsustainable landuse practices and lessen the pressure on the remaining population of tarsiers in the area.

Most local people are familiar with tarsiers, and their skills can be utilised by employing them as park rangers or tour guides, giving them a stake in the survival of the tarsier population. A regular community outreach program can be conducted to increase the knowledge of local people on the importance of preserving natural resources. They can also be trained on the basic techniques of field observations and data collection to enhance their interest and appreciation in conducting research for conservation. This kind of program has successfully been conducted in communities surrounding protected areas in West Java, Indonesia (Kyes *et al.*, 1997). The same set-up can also be applied in Bohol.

A recent review of integrated conservation and development projects (ICDPs) in Indonesia (Wells *et al.*, 1999*)* showed that villagers around protected areas who cut trees and hunt wildlife are not strictly the main threat to the areas. The most serious direct threats were derived from well-financed outsiders who illegally log and mine the areas on a larger scale. Indirect threats were also caused by poor logging practices within adjacent areas, construction of badly sited roads that provide access to illegal activities and rapid urban encroachment. Although not all these factors may be applicable to the current Bohol set up (they can be in other protected areas in the Philippines), some may pose as potential threats. A strong community-based program, together with strict law enforcement and organised regional planning and development will help in the long-term viability of protected areas in the Philippines.

8.3.4 Protected Areas

In 1992, the National Integrated Protected Area Systems (NIPAS) Law was passed identifying 116 protected sites (**Figure 8.1**), ten of which were considered priority sites (Jimenez, 1995) (**Table 8.1**). The priority list shows four protected areas: Siargao Island and Agusan Marsh, categorised as wildlife sanctuaries and Mt. Kitanglad and Mt. Apo as natural parks (**Figure 8.2**), that coincide with the known distribution of *T. syrichta*. Although previous reports indicate that *T. syrichta* is not found in any protected areas (Wolfheim, 1983; Burton and Pearson, 1987), it is possible that the species is found in any one or two of these protected sites. Siargao Island protected area would most likely include *T.* syrichta. A survey to confirm this possibility would be useful, as there is no current information of the species' location falling within the confines of a protected area. *In-situ* propagation would probably be the best option for *T. syrichta*.

Table 8.1. The ten priority sites under the National Integrated Protected Area System (NIPAS).

Protected Area	**Location**	**Category**
Batanes Islands	north of Luzon	protected seascape and landscape
Northern Sierra Madre	northeast Luzon	natural park
Mangyan Heritage	Mindoro	natural park
Apo Reef	Mindoro	marine natural park
Mt. Canlaon National Park	Negros	natural Park
Siargao Island	northeast Mindanao	wildlife sanctuary
Agusan Marsh	eastern Mindanao	wildlife sanctuary
Mt. Kitanglad	central Mindanao	natural park
Mt. Apo National Park	southern Mindanao	natural park
Turtle Islands	Sulu Sea	marine natural park

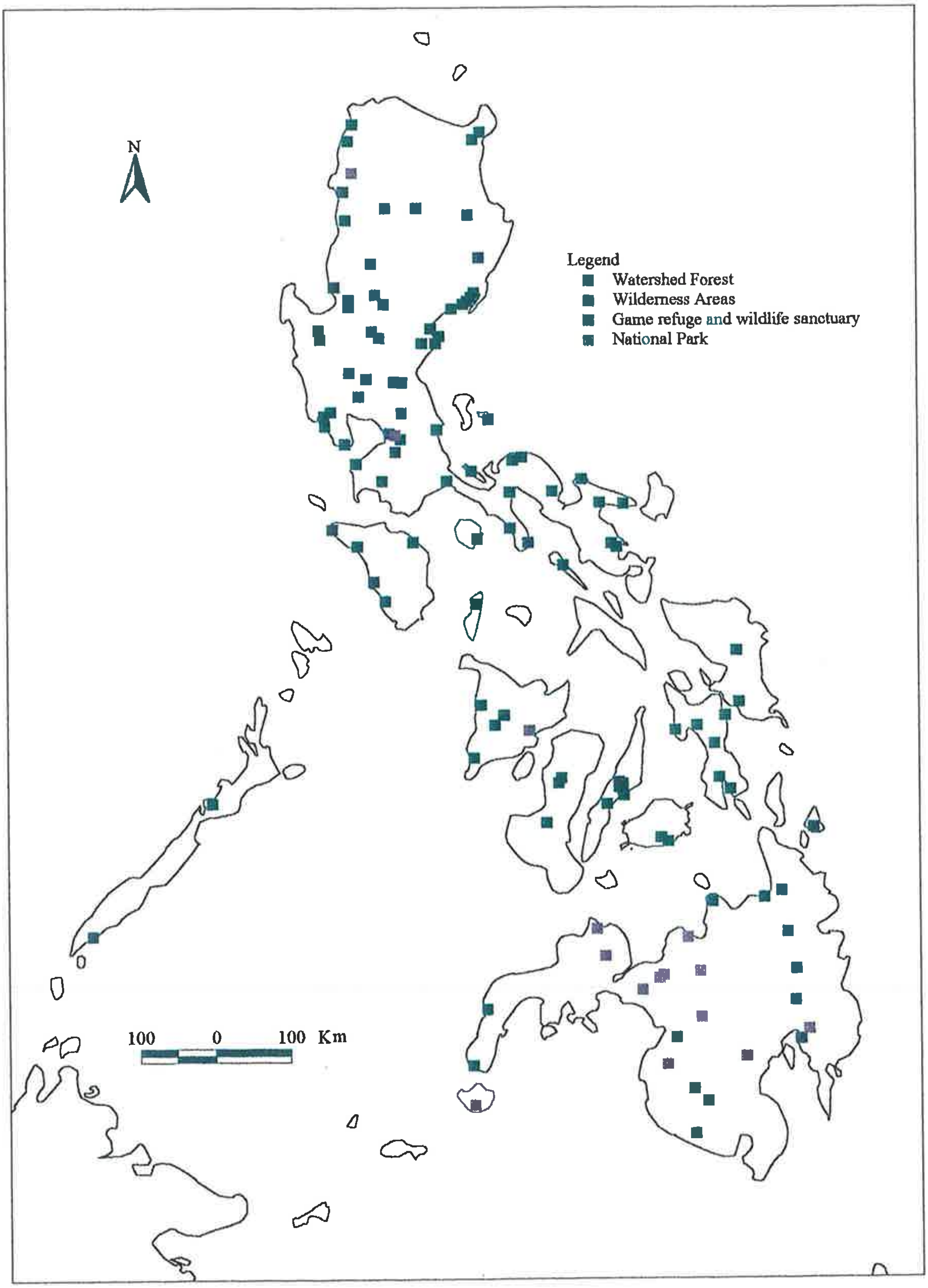


Figure 8.1. The location and distribution of protected areas in the Philippines (DENR/UNEP, 1997; Bagarinao, 1998)

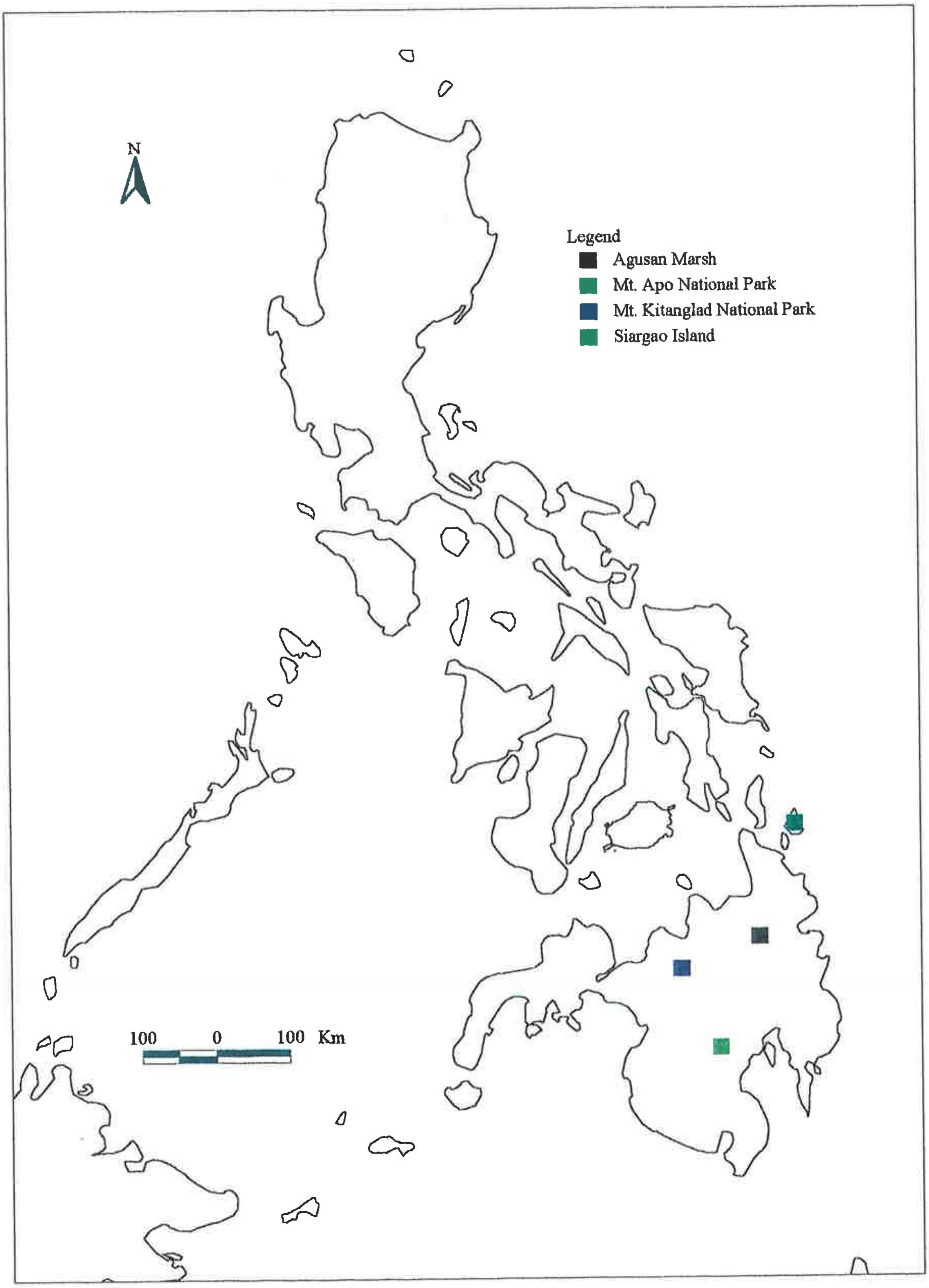


Figure 8.2. The location of four protected areas that coincide with the distribution of the Philippine tarsier.

8.4 CONCLUSIONS and RECOMMENDATIONS

There are varying implications to be drawn for the conservation of *T. syrichta* across a number of areas:

The results of this study show that *T. syrichta* maintain a medium-high density (males: 16 individuals/ sq km and females: 41 individuals/ sq km) using relatively small individual home-range areas in a mosaic of forest fragments. However, the absence of any designated protected area in forests where it is known to exist would still make habitat destruction a major threat to its survival. Although *T. syrichta* is mainly a rainforest inhabitant, several types of rainforest in different stages of succession are found in the Greater Mindanao faunal region. The preference of *T. syrichta* for regrowth forest in early to mid succession stage indicates the importance of maintaining the cycle of regrowth of tropical rainforest in areas where tarsiers are known to occur to provide adequate habitat for the species. This habitat preference further suggests that tarsier conservation is not incompatible with regulated exploitation of the forest's resources.

Before any further management decisions are made for this species based on these results of home range and habitat utilisation, it would be beneficial to conduct similar studies in more contiguous forest with different floristic characteristics. In order to compare population structure between habitats with varying level of disturbance or non-disturbance, and determine which habitat type supports the most number of individuals indicating optimum level of reproductive success for the species. Other potential avenues for research are:

i) to examine edge effects on the population structure of the animals in varying proportions of forest fragments and

ii) in conjunction with the study on edge effects, to investigate the extent of usage of habitat corridors and relate corridor structure *i.e.* length and width, to the dispersal rate of the animal

iii) to conduct a longer field study covering both breeding and non-breeding seasons and examine variations of home range size and configurations

iv) to set up a GIS database on the tarsier's density and distribution and map remaining available forest habitat in other regions in the Philippines where tarsiers are known to exist. The survey will show areas that could possibly be set up as a regional network of reserves, instead of just one reserve as currently proposed in Corella, Bohol. This will be in line with the results and recommendations generated from the PVA in Chapter 7.

v) The data from such studies would provide a better insight into how *T. syrichta* utilises different components of their habitat, and consequently generate sound management decisions for the species. Based on the gap of information on the ecology of the species that needs to be filled, the current conservation status of the Philippine tarsier (Data deficient) should remain until further survey and studies are done and policies implemented to protect its habitat.

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Appendices

Appendix 1. Taxonomic list of trees identified in four vegetation survey sites in Corella, Bohol.

Family	Genus	Species	Local Name
Acanthaceae	*Hemigraphis*	*primulaefolia (Nees) F.Vill.*	pilamoras
Agavaceae	*Cordyline*	*fruticosa (L.) Chev.*	uway sa Kastila
Anacardiaceae	*Buchanania*	*arborescens Blm.*	an-an; anugas
	Semecarpus	*philippinensis Engl.*	dungas
	Swintonia	*acuminata Merr.*	maksa
Annonaceae	*Polyalthia sp.*		anonang
Apocynaceae	*Alstonia*	*scholaris (L.) R.Br.*	dita; tanitan
	Alstonia	*macrophylla Wall.*	ninog; linog
	Alyxia	*concatenata (Blco.) Merr.*	balagit-dalagon
	Tabernaemotana	*pandacaqui Poir.*	pandakaki
Araceae	*Amorphophallus*	*rivieri Durand*	
	Arisaema	*polyphyllum (Blco.) Merr.*	
Araliaceae	*Polyscias*	*nodosa (Blm.) Seem.*	binliw; malapapaya
	Schefflera	*actinophylla (Endl.) Harms.*	
Bignoniaceae	*Radermachera*	*pinnata (Blco.) Seem.**	kamjan
Burseraceae	*Garuga*	*floribunda F.-Vill.*	banban; bugo
Compositae	*Blumea*	*spectabilis DC*	
	Elephantopus	*mollis HBK*	dila-dila
	Eupatorium	*odoratum L.*	hagonoy
Cyperaceae	*Cyperus*	*brevifolius (Rottb.) Hassk.*	pugo-pugo
	Scleria	*scrobiculata Nees*	
Dioscoreaceae	*Dioscorea*	*hispida Dennst.*	gayos
Ebenaceae	*Diospyros*	*maritima Blm.*	kanumay; kalumai
Euphorbiaceae	*Agrostistachys*	*leptostachya Pax & Hoffm.*	ulam
	Antidesma	*bunius (L.) Sprengel*	bugnay
	Breynia	*cernua (Poir.) Muell.-Arg.*	tug-tug
	Flueggea	*virosa (Roxb.) Baill.*	magaspang
	Homalanthus	*populneus Merr.*	
	Macaranga	*bicolor Muell. & Arg.*	hamindan
	Macaranga	*tanarius (L.) Muell.-Arg.*	binunga; minungaw

*endemic species

Family	**Genus**	**Species**	**Local Name**
Euphorbiaceae	*Mallotus*	*philippinensis (Lam.) Muell.-Arg.*	sala
Flacourtiaceae	*Flacourtia sp.*		
Flagellariaceae	*Flagellaria*	*indica Linn.*	huag
Gesneriaceae	*Agalmyla sp.*		
Gnetaceae	*Gnetum*	*gnemon L.*	bago
Gramineae	*Dinochloa*	*luconiae (Munro.) Merr.*	butong; bolokaui
	Miscanthus	*floridulus (Labill.) Warb.*	tapak
Guttiferae	*Garcinia*	*binucao (Blco.) Choisy**	batwan; bilar
	Garcinia sp.		bilar
Lauraceae	*Cassytha sp.*		
Leguminosae	*Albizzia*	*procera (Roxb.) Benth.*	bansilay; payhot
	Albizzia	*falcata sensu Backer*	
	Caesalpinia	*bonduc (L.) Roxb.*	
	Leucaena	*leucocephala (Lamk.) de Wit.*	
Liliaceae	*Dracaena*	*angustifolia (Roxb.) P.E.Br.*	
Malvaceae	*Hibiscus sp.*		
Meliaceae	*Aglaia sp.*		
	Melia	*azedarach L.*	bagawnga
	Swietenia	*macrophylla King.*	mahogany
Moraceae	*Artocarpus*	*blancoi (Elm.) Merr.**	tipolo; kolo
	Artocarpus	*heterophyllus Lamk.*	nangka
	Ficus	*balete Merr.**	balite
	Ficus	*benjamina L.*	sagosahis
	Ficus	*chrysolepis Miq.*	gakit
	Ficus	*cumingii Miq.*	labnog
	Ficus	*gigantifolia Merr.*	kayot
	Ficus	*nota (Blco.) Merr.**	tuyokai
	Ficus	*pseudopalma Blco.**	hamumuaya
	Ficus	*pubinervis Bl. var. pubinervis*	dungo
	Ficus sp.		
	Ficus	*ulmifolia Lamk.**	labnog (puti); agusabis

*endemic species

Family	*Genus*	Species	Local Name
Myrsinaceae	*Myrsine*	*philippinensis A.DC.**	bato-bato; hanigad
	Ardisia	*squamulosa Presl*	tagpod; babagiyon
Myrtaceae	*Syzygium*	*alcinae (Merr.) Merr. & Perry*	hambibinlod
Nyctaginaceae	*Pisonia*	*umbellifera (Forst.) Seem.*	bududub; malasaging
Ochnaceae	*Brackenridgea sp.*		
	Gomphia	*angustifolia (Vahl) Baill.*	sugkad
Palmae	*Arenga*	*pinnata (Wurmb.) Merr.*	sagisi; bagatbat
	Caryota	*cumingii Lodd.**	patikan; batikan
	Cocos	*nucifera L.*	lubi
	Daemonorops sp.		
Pandanaceae	*Pandanus sp.*		
Piperaceae	*Piper*	*celtidiforme Opiz.*	saog
Pittosporaceae	*Pittosporum*	*pentandrum (Blco.) Merr.*	hagbuyo; antoan
	Pittosporum sp.		bayog
Rhamnaceae	*Zizyphus*	*cumingiana Merr.*	
Rubiaceae	*Guettarda sp.*		
	Ixora	*longistipula Merr.**	
	Nauclea	*orientalis Linn.*	melo-melo
	Morinda	*bracteata Roxb.*	apatot
	Psychotria	*luzoniensis (Cham. & Schult.)*	tongog-tongog;
	*F. Vill.**		malaigang
	Psychotria sp.		
	Timonius	*arboreus Elm.*	
Rutaceae	*Evodia*	*ternata (Blco.) Merr.**	bahay
	Lunasia	*amara Blco.*	labau
Sapindaceae	*Guioa*	*koelreuteria (Blco.) Merr.**	sagasa; uyos
	Harpullia	*arborea (Blco.) Radlk.*	
Sapotaceae	*Planchonella sp.*		
Smilacaceae	*Smilax*	*bracteata Presl**	
Sterculiaceae	*Pterospermum*	*niveum Vidal*	kolitingan
Tiliaceae	*Colona*	*serratifolia Cav.*	anilaw
Thymeliaceae	*Wikstroemia*	*polyantha Merr.**	siyapo

*endemic species

Family	***Genus***	**Species**	Local Namc
Ulmaceae	*Trema*	*orientalis (Linn.) Blm.*	anislag; hanadgong
Urticaceae	*Leucosyke cap*	*itellata (Poir.) Wedd.*	
	Pipturus	*arborescens (Link.) C.B. Rob.*	dalonotan
Verbenaceae	*Clerodendron*	*intermedium Cham.*	aloksok
	Vitex	*parviflora Juss.*	adgaunon
Vitaceae	*Leea*	*manillensis Walp.*	mamali
Zingiberaceae	*Alpinia*	*brevilabris Presl*	tugis
	Globba	*marantina Linn.*	

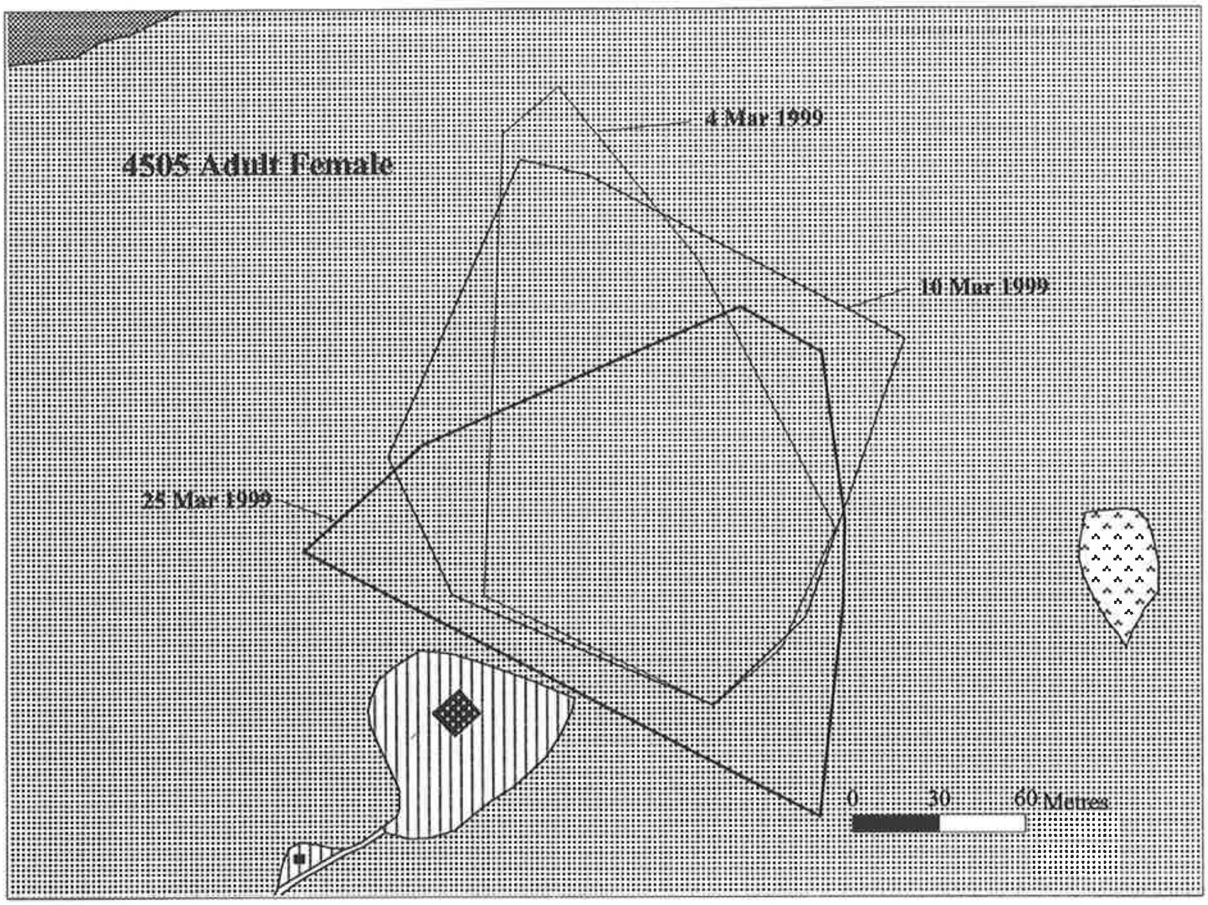
*endemic species

Appendix 2. Importance value of tree species identified in the four vegetation survey sites in Corella, Bohol.

Species	RelDom	RelDen	RelFreq	IV
Aglaia sp.	0.24	0.28	0.20	0.72
Agrostistachys leptostachya	0.10	0.28	0.39	0.78
Albizzia procera	0.12	0.43	0.59	1.14
Alstonia macrophylla	4.25	10.68	10.76	25.69
Alstonia scholaris	0.08	0.14	0.20	0.43
Antidesma bunius	0.04	0.14	0.20	0.38
Ardisia squamulosa	1.02	1.99	2.15	5.16
Arenga pinnata	4.08	4.27	4.89	13.24
Artocarpus blancoi	0.19	0.14	0.20	0.53
Artocarpus heterophyllus	2.21	0.57	0.39	3.17
Buchanania arborescens	2.63	5.13	6.26	14.02
Caryota cumingii	0.14	0.43	0.39	0.96
Cocos nucifera	12.52	3.85	3.72	20.08
Dinochloa luconiae	0.06	0.14	0.20	0.40
Diospyros maritima	0.22	0.43	0.59	1.24
Dracaena angustifolia	0.13	0.28	0.20	0.62
Evodia ternatea	0.36	0.28	0.39	1.04
Ficus balete	0.02	0.14	0.20	0.36
Ficus benjamina	0.20	0.28	0.39	0.88
Ficus chrysolepis	3.19	1.28	1.57	6.04
Ficus cumingii	0.80	1.57	1.76	4.13
Ficus gigantifolia	2.78	1.28	1.76	5.82
Ficus nota	0.30	0.71	0.78	1.80
Ficus sp.	0.76	0.85	1.17	2.78
Ficus ulmifolia	0.09	0.28	0.39	0.77
Flacourtia sp.	0.02	0.14	0.20	0.36
Garcinia binucao	0.69	0.85	0.78	2.33
Garuga floribunda	11.16	15.53	13.50	40.19
Gnetum gnemon	1.71	1.85	1.96	5.52
Gomphia angustifolia	3.05	8.97	6.85	18.87
Guettarda sp.	0.02	0.14	0.20	0.36
Guioa koelreuteria	1.00	2.28	2.94	6.22

Species	RelDom	RelDen	RelFreq	IV
Leucaena leucocephala	0.89	0.85	1.17	2.92
Leucaena leucocephala				
Leucosyke capitata				
Lunasia amara				
Mallotus philippinensis				
Meliaceae	0.56	0.28	0.39	1.23
Meliaceae				
Morinda bracteata				
Myrsine philippinensis				
Nauclea orientalis				
Pittosporum pentandrum				
Planchonella sp.	0.33	0.14	0.20	0.67
Polyalthia sp.	0.02	0.14	0.20	0.36
Polyscias nodosa	0.30	0.43	0.39	1.12
Polyscias nodosa				
Psychotria luzoniensis				
Pterospermum niverum				
Radermachera pinnata				
Semecarpus philippinensis	1.31	0.57	0.78	2.67
Semecarpus philippinensis				
Swietenia macrophylla	14.07	9.40	6.46	29.93
Swietenia macrophylla				
Swintonia acuminata				
Syzygium sp.				
Unknown	0.26	0.28	0.39	0.94
Unknown				
Unknown	0.16	0.14	0.20	0.49
Unknown	0.22	0.28	0.39	0.90
Unknown				
Unknown				
Vitex parviflora	7.99	3.85	4.50	16.34
Vitex parviflora				
	100	100	100	300

Appendix 3. Minimum convex polygons of areas covered by tarsiers during 12-hour (18h00 – 06h00) continuous tracking sessions.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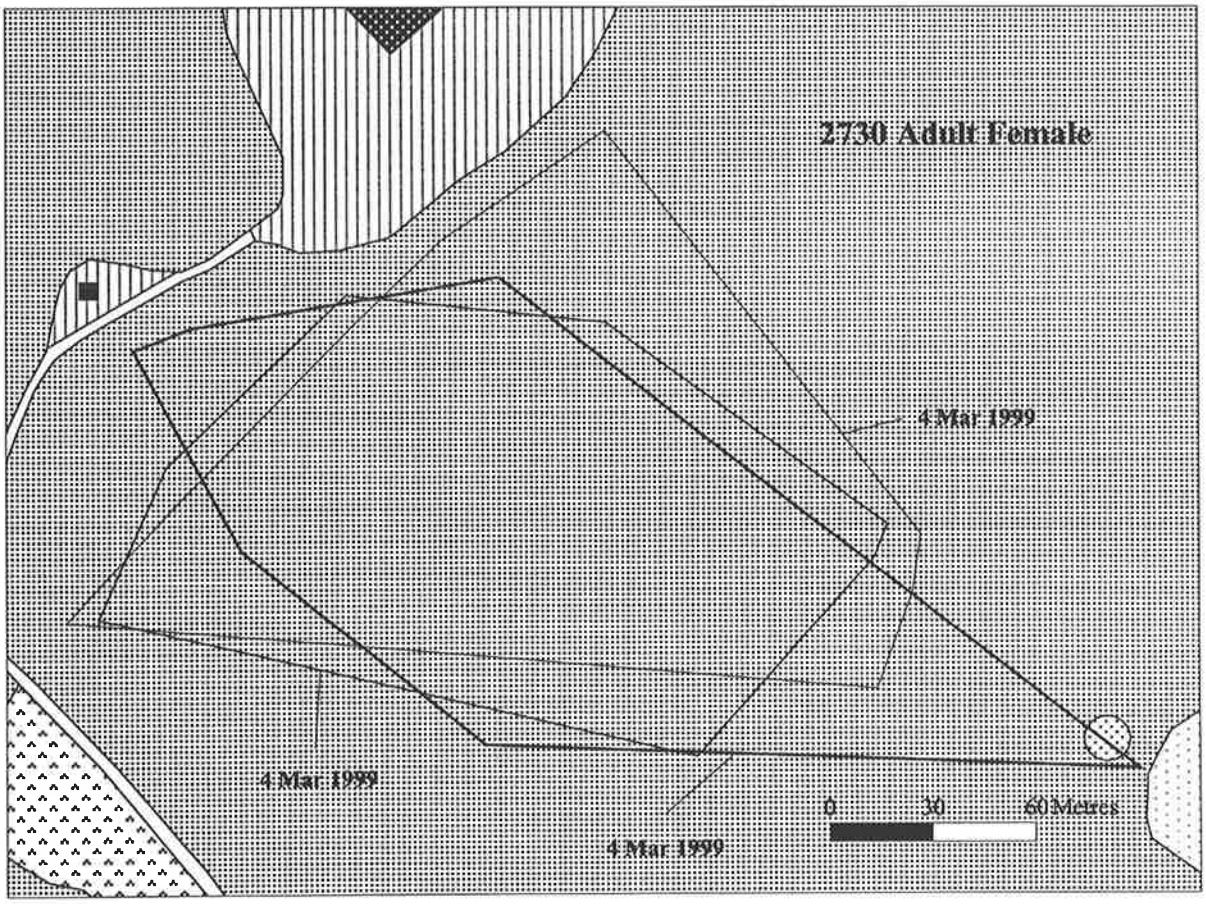
4 Mar 1999
10 Mar 1999
25 Mar 1999
0
30
60 Metres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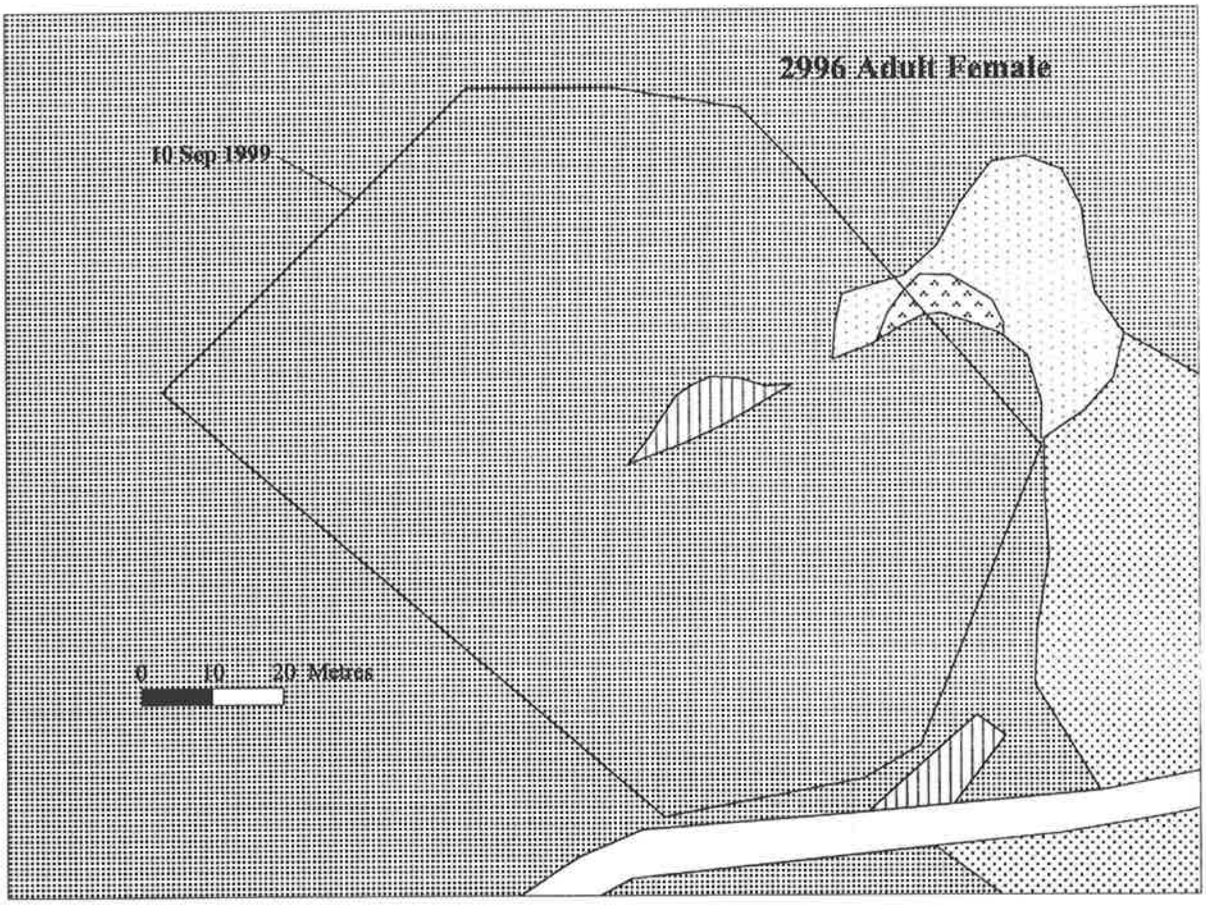
4 Mar 1999
4 Mar 1999
4 Mar 1999
0
30
60 Metres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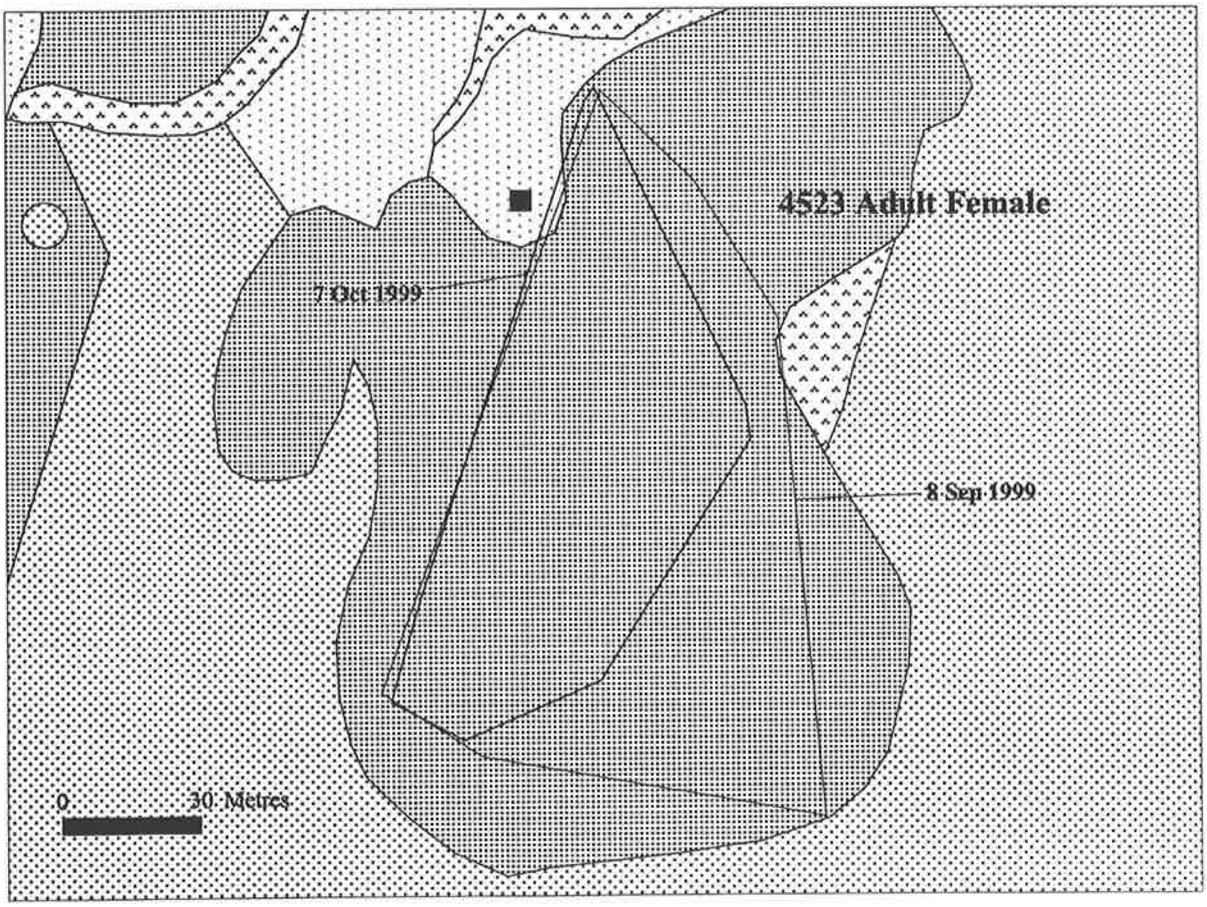
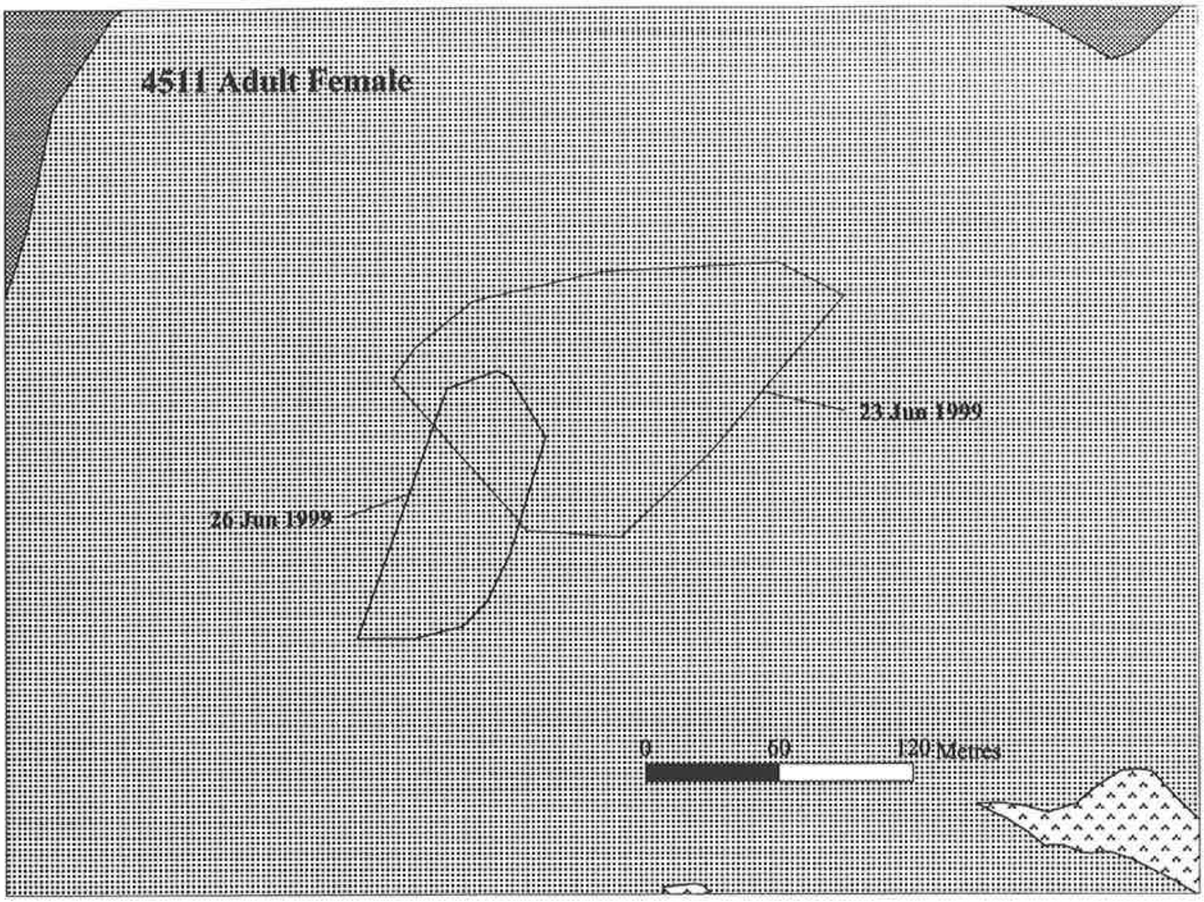
10 Sep 1999
0
10
20 Metres


4523 Adult Female
7 Oct 1999
8 Sep 1999
0
30 Metres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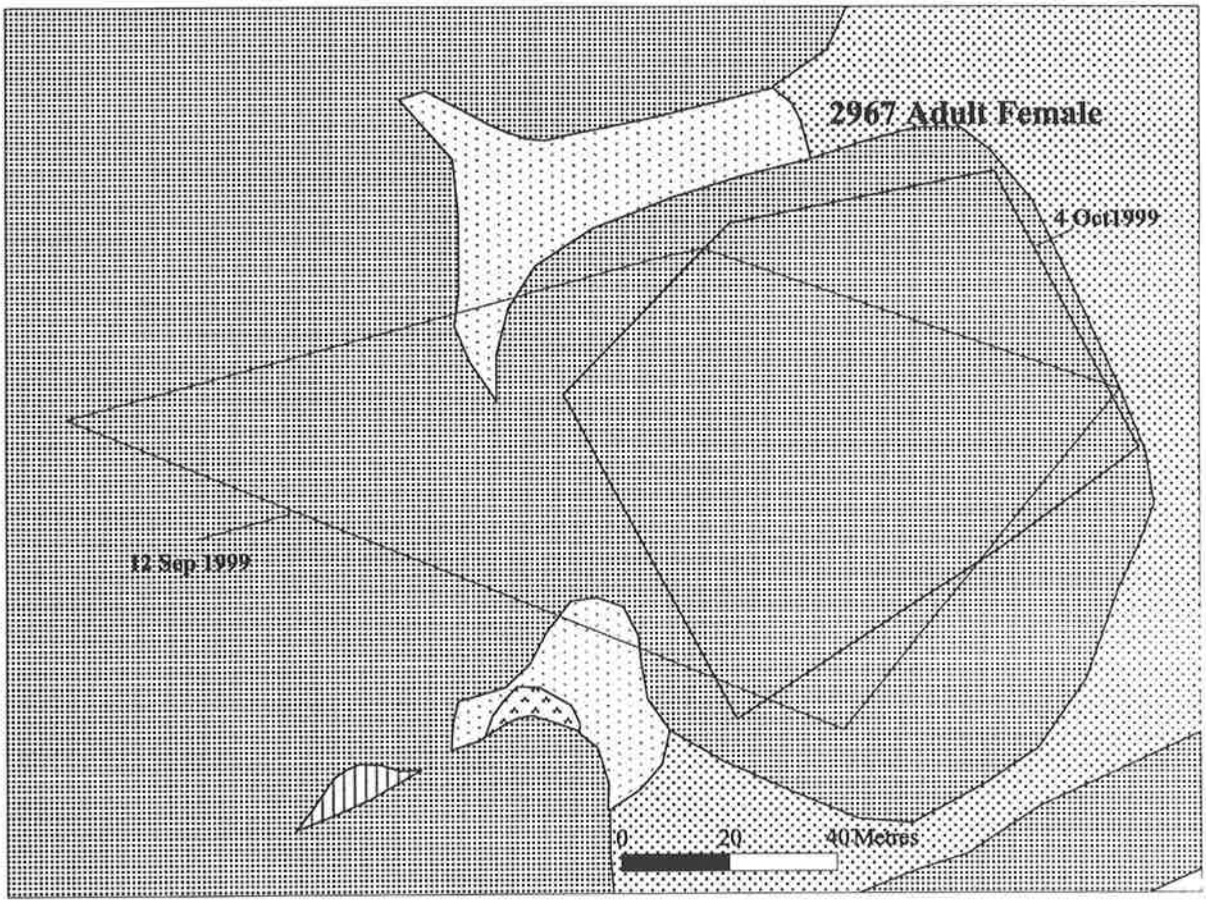
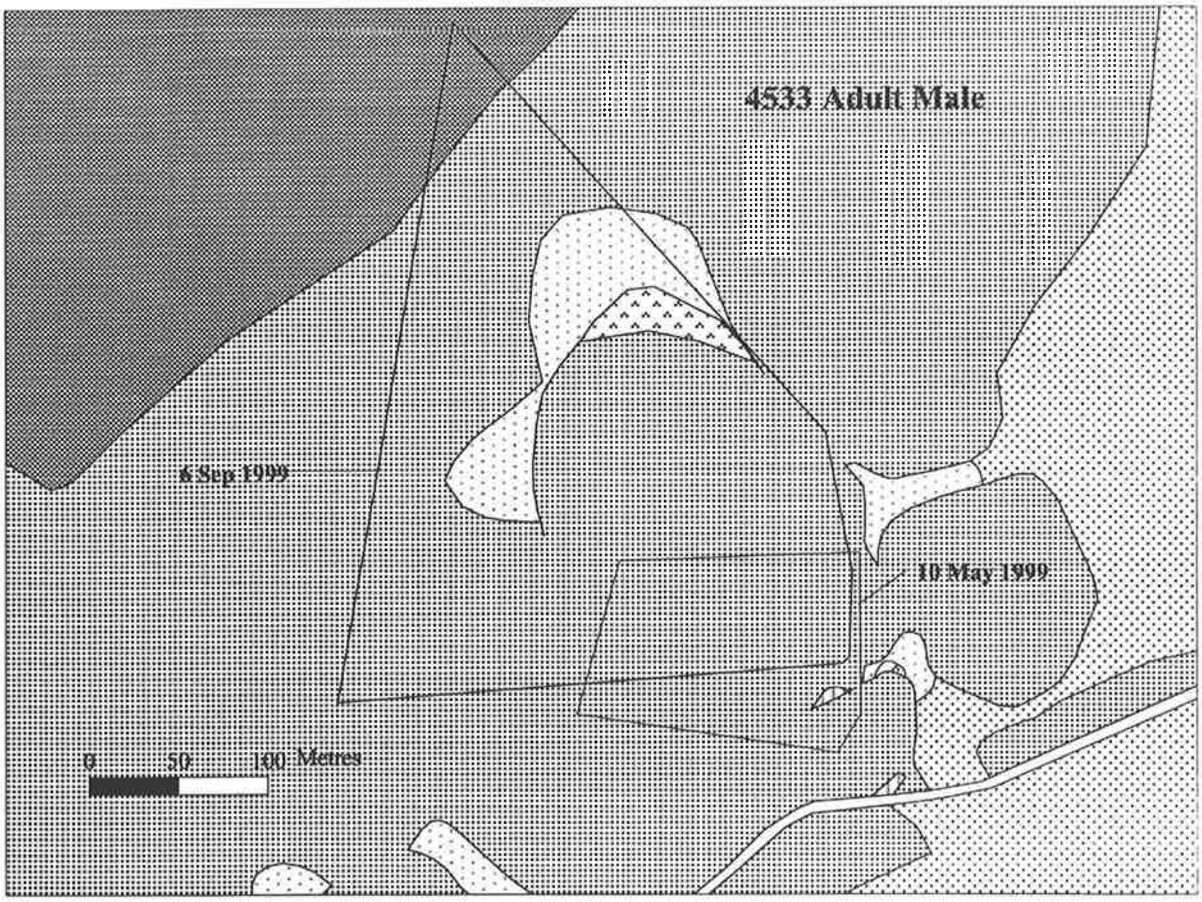
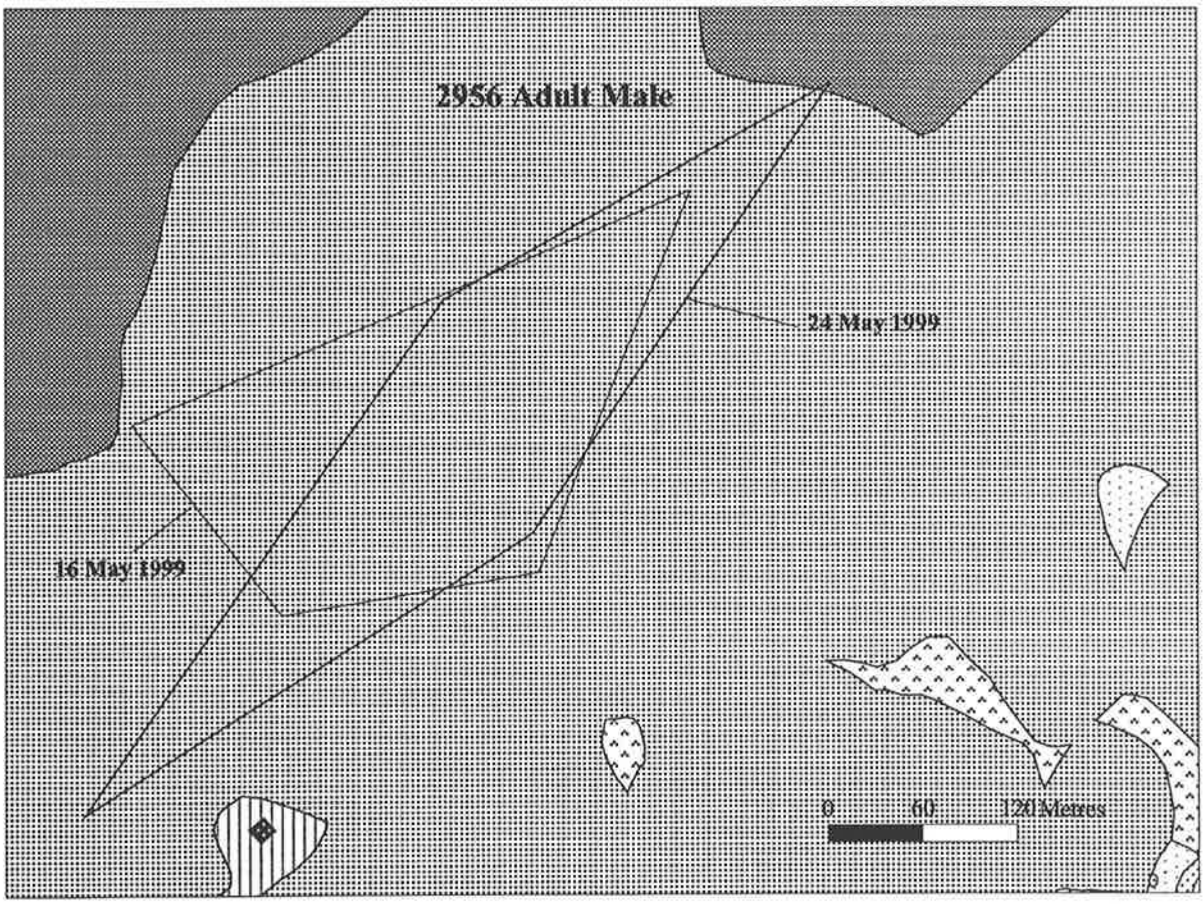
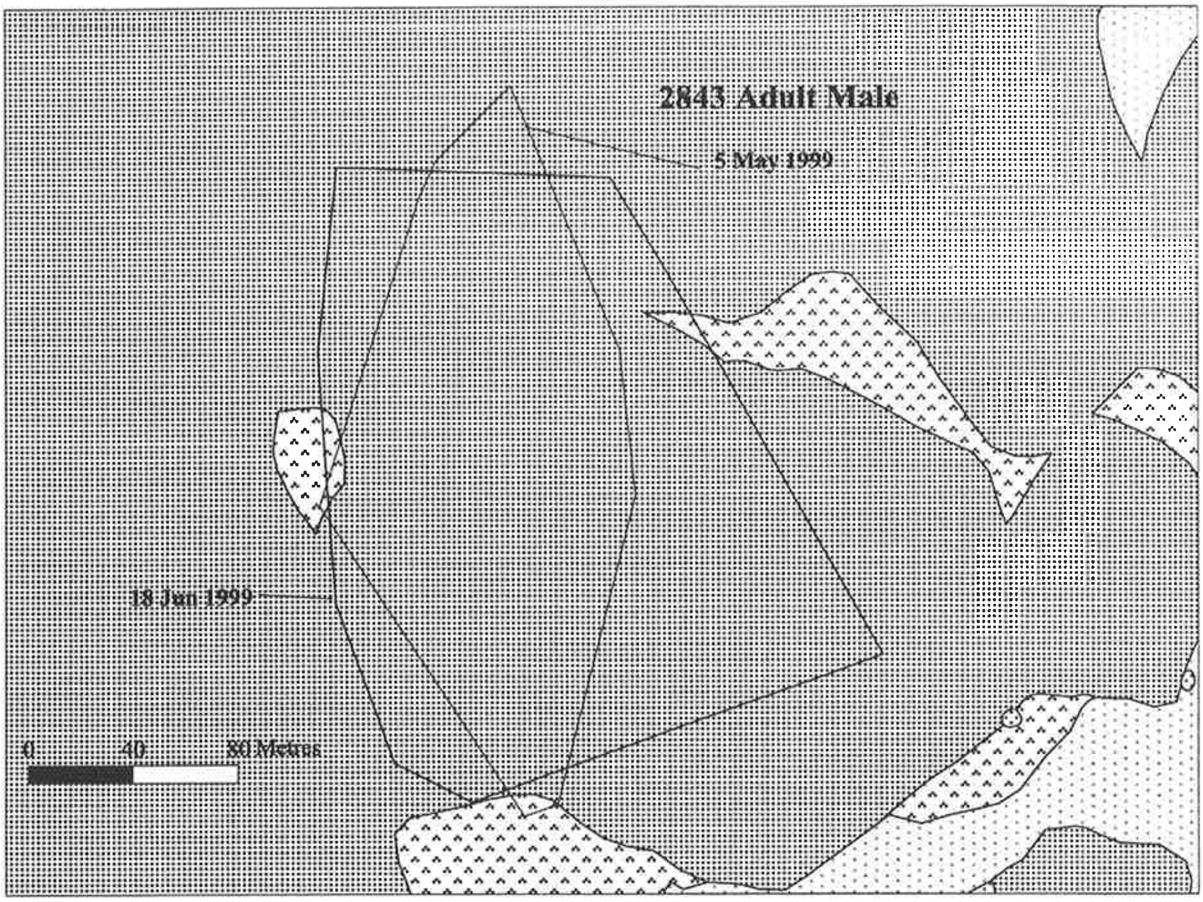
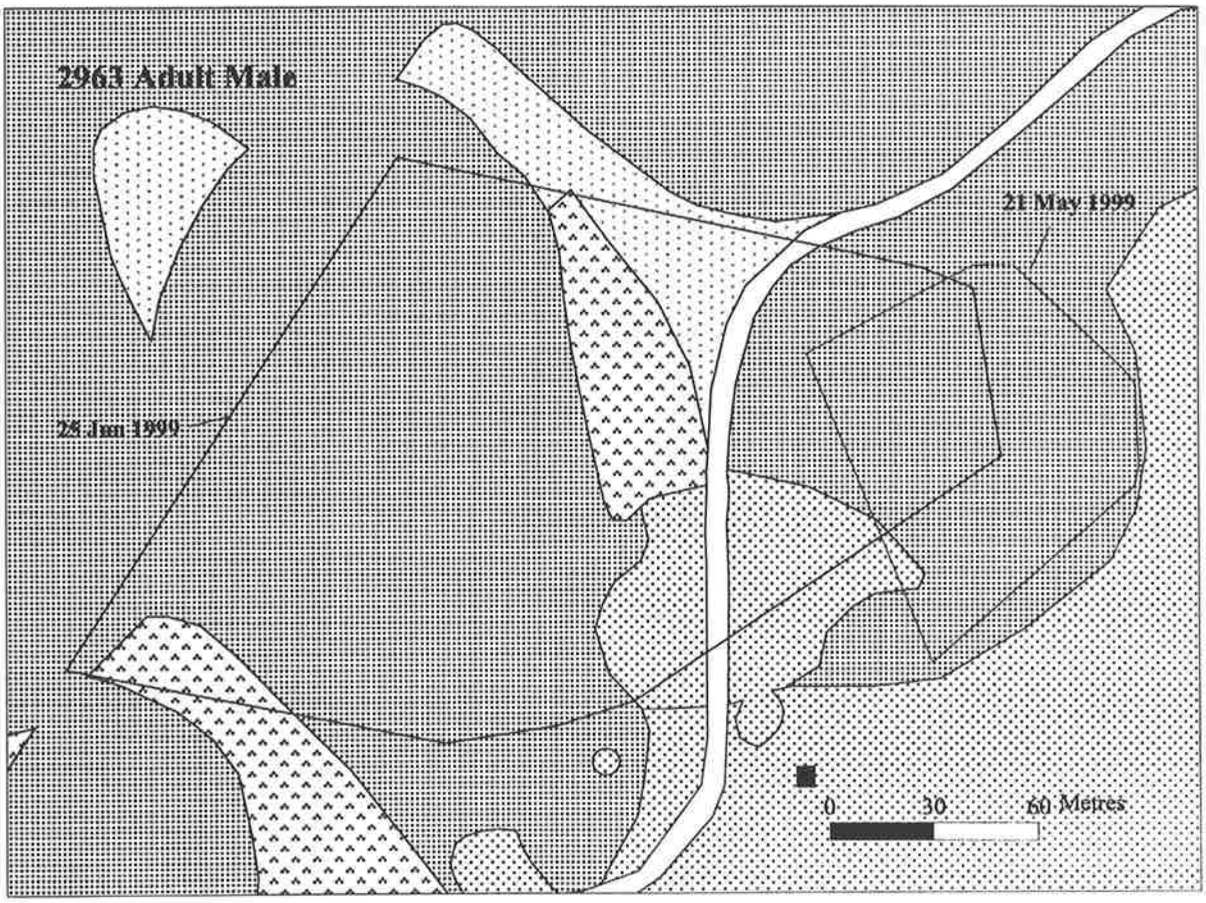
23 Jun 1999
26 Jun 1999
0
60
120 Metres

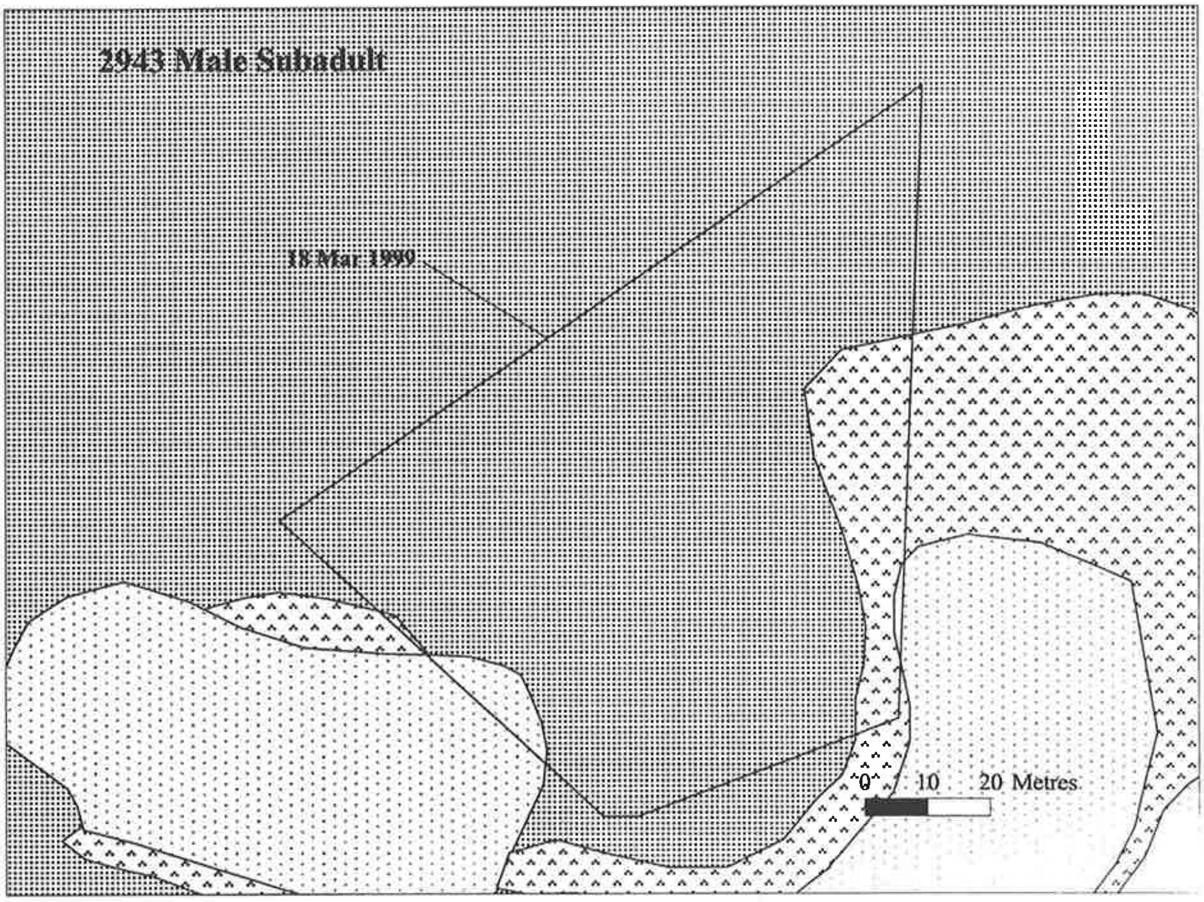

2967 Adult Female
4 Oct1999
12 Sep 1999
0
20
40 Metres


4533 Adult Male
6 Sep 1999
10 May 1999
0
50
100 Metres

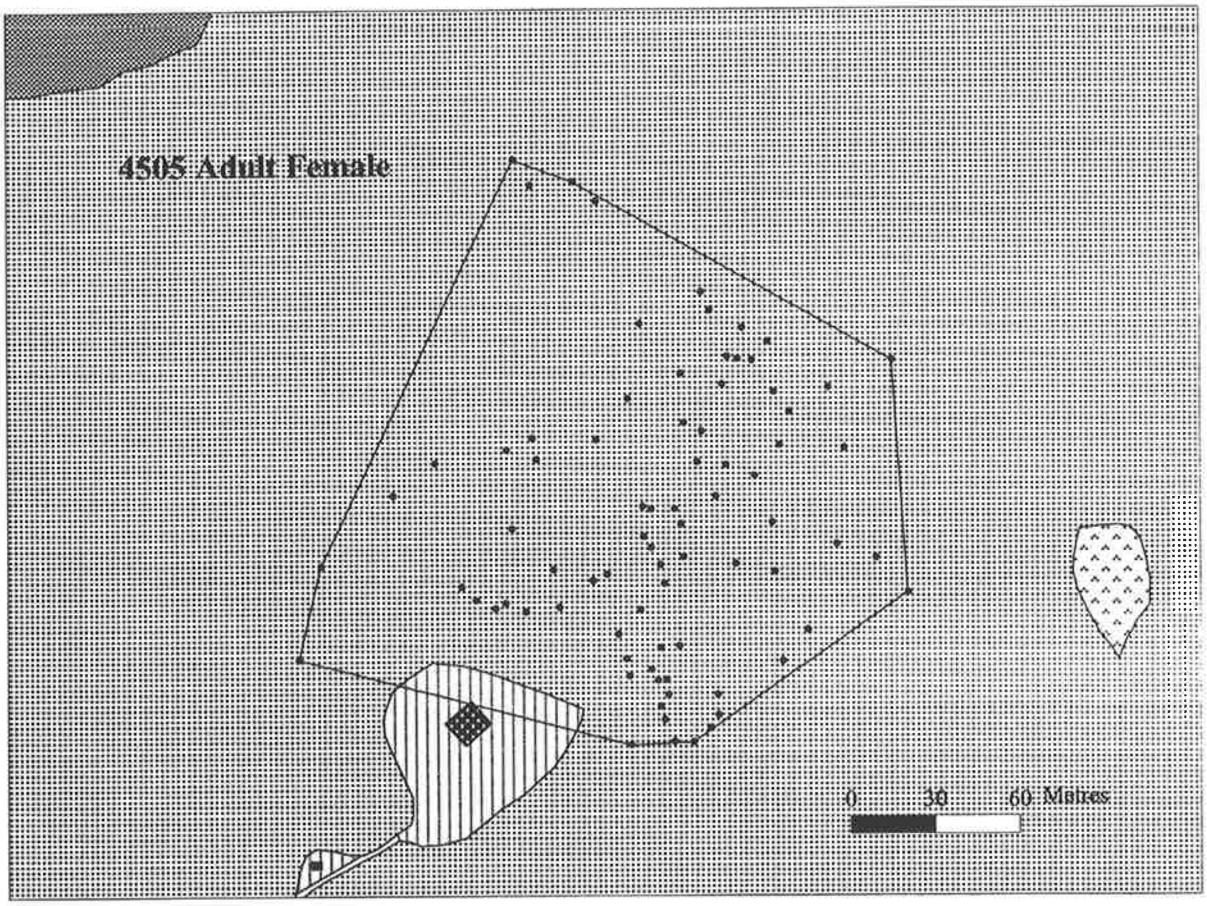

2956 Adult Male
24 May 1999
16 May 1999
0
60
120 Metres

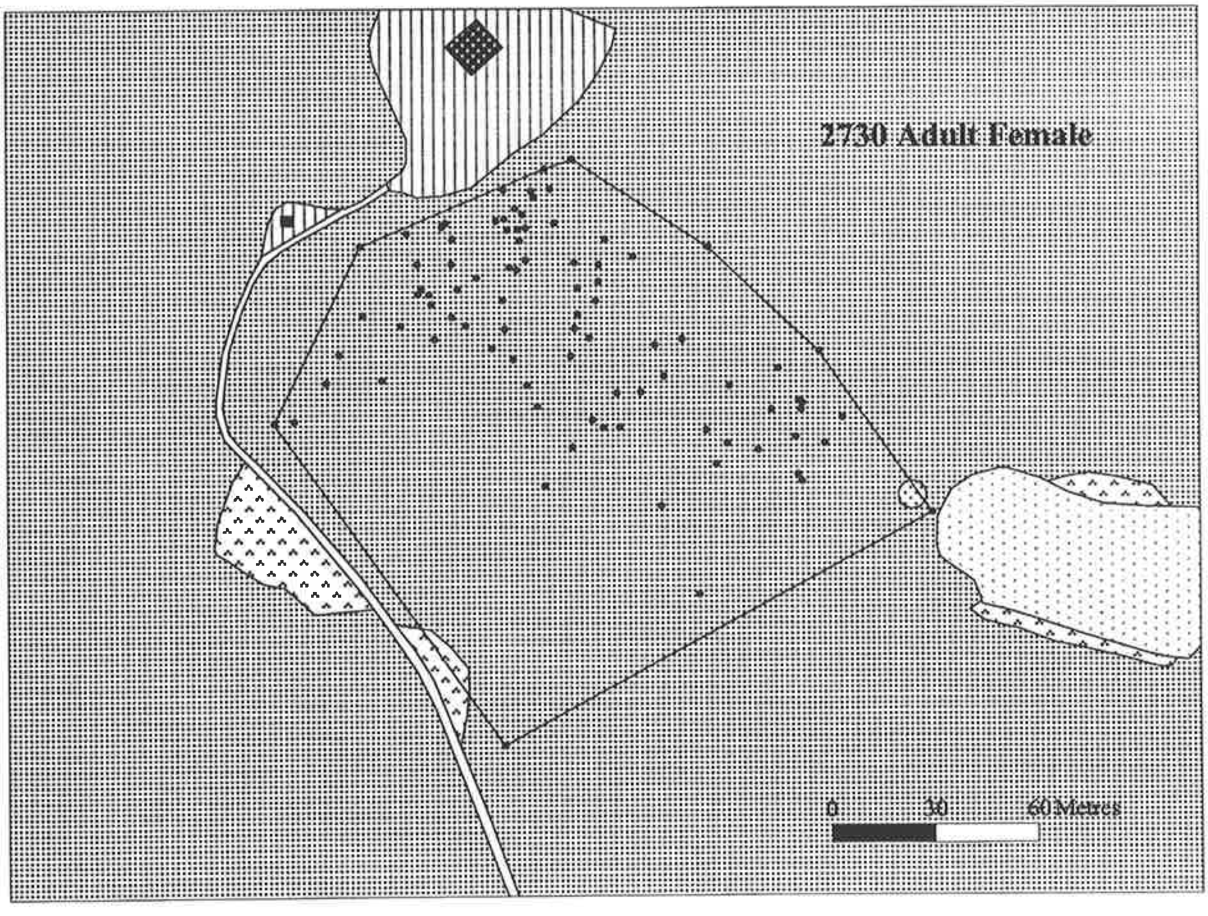

2843 Adult Male
5 May 1999
18 Jun 1999
0
40
80 Metres

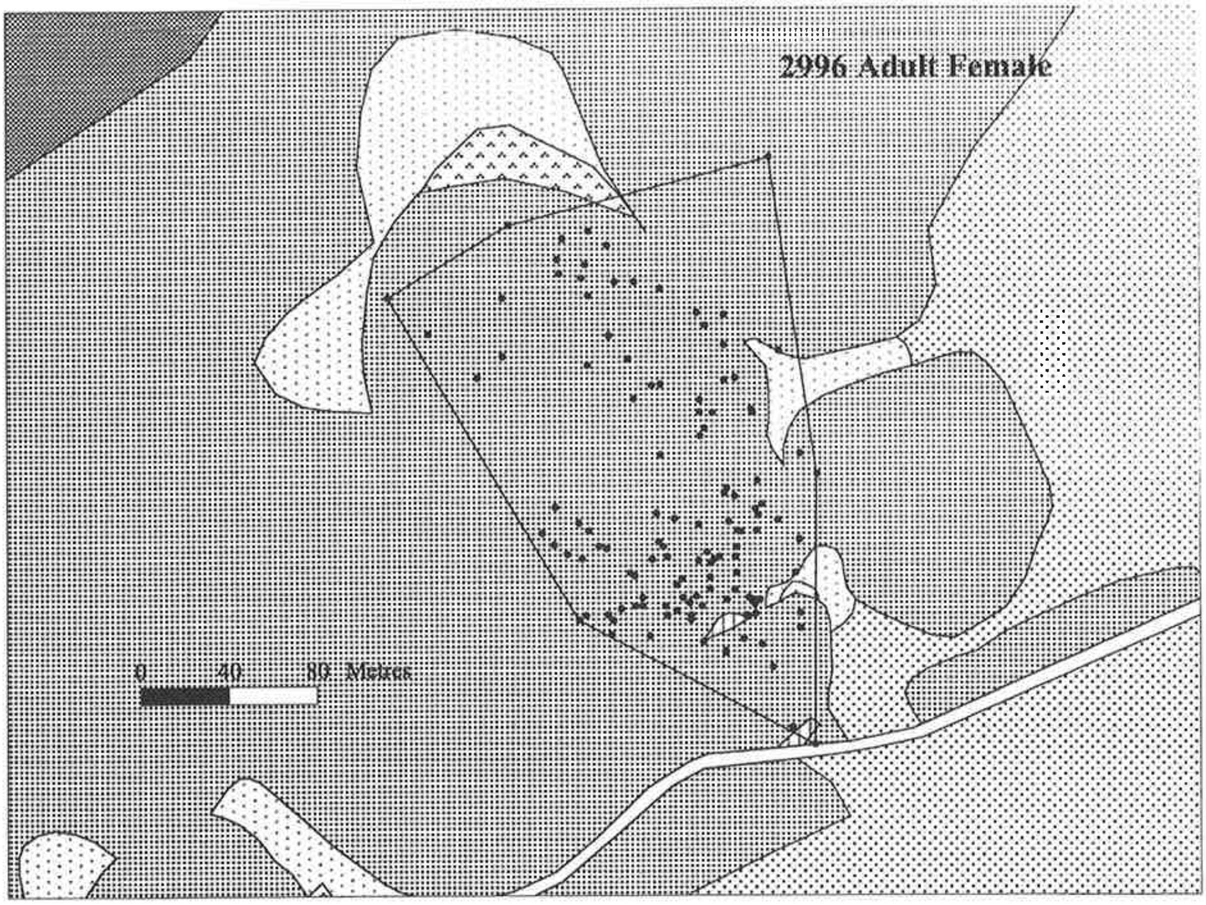

2963 Adult Male
21 May 1999
28 Jun 1999
0
30
60 Metres

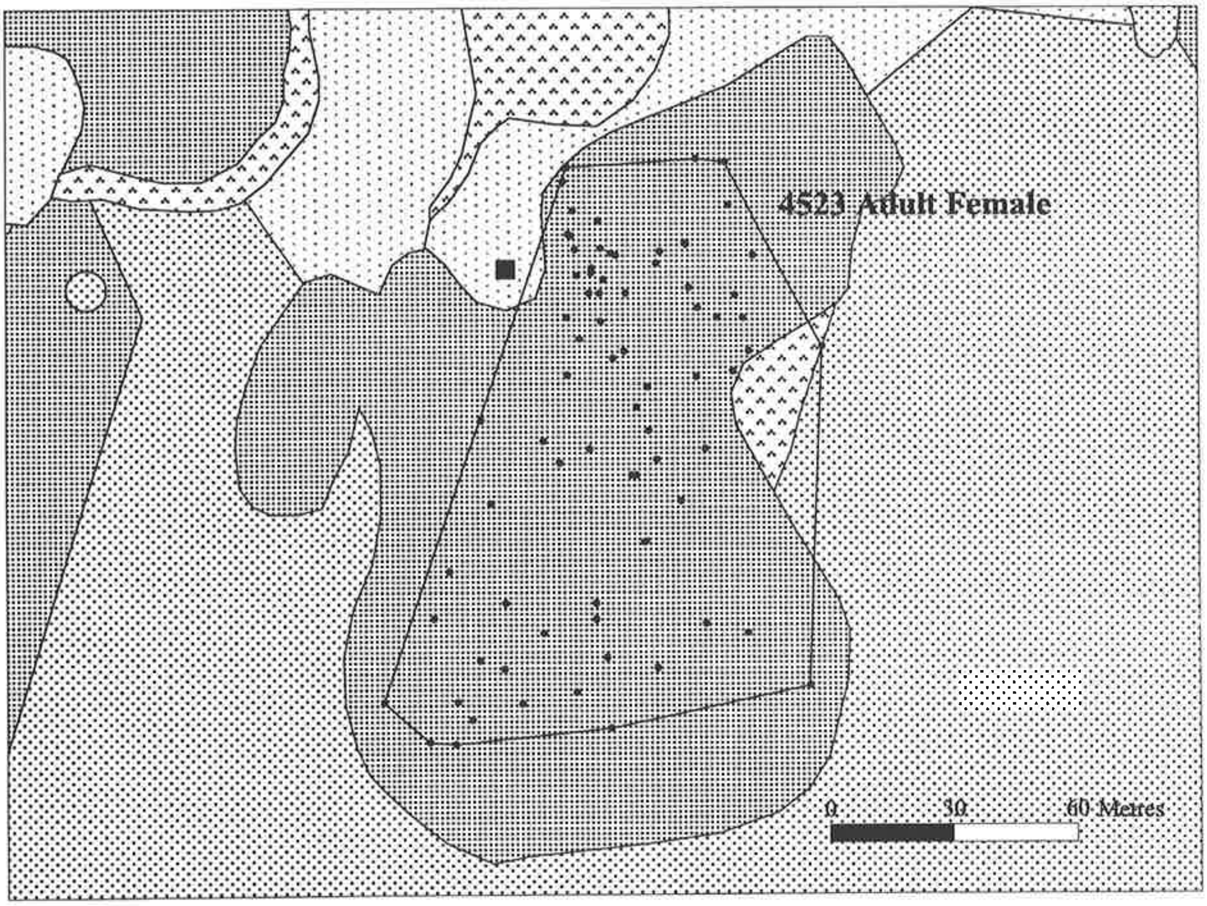

2943 Male Subadult
18 Mar 1999
0
10
20 Metres

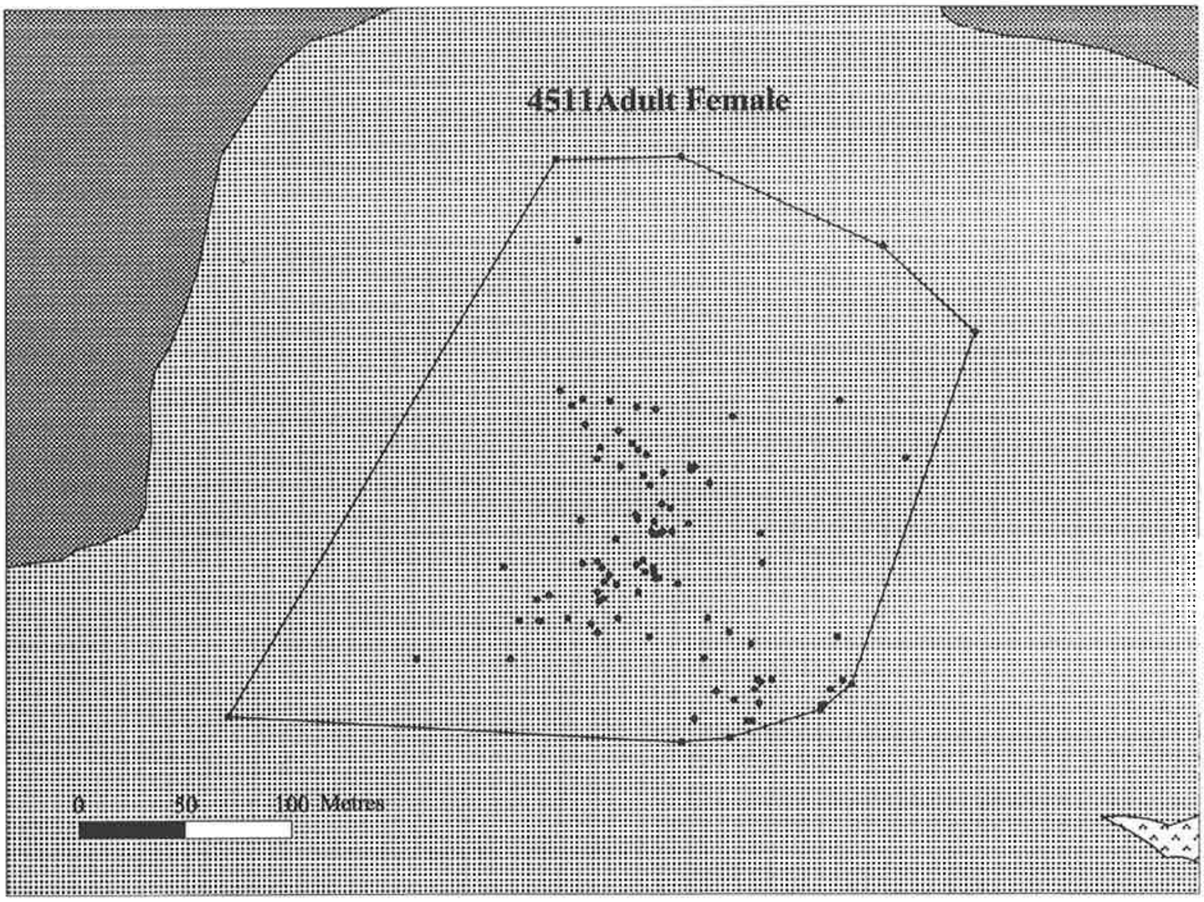
Appendix 4. Minimum convex polygon home ranges estimated from discontinuous point data.

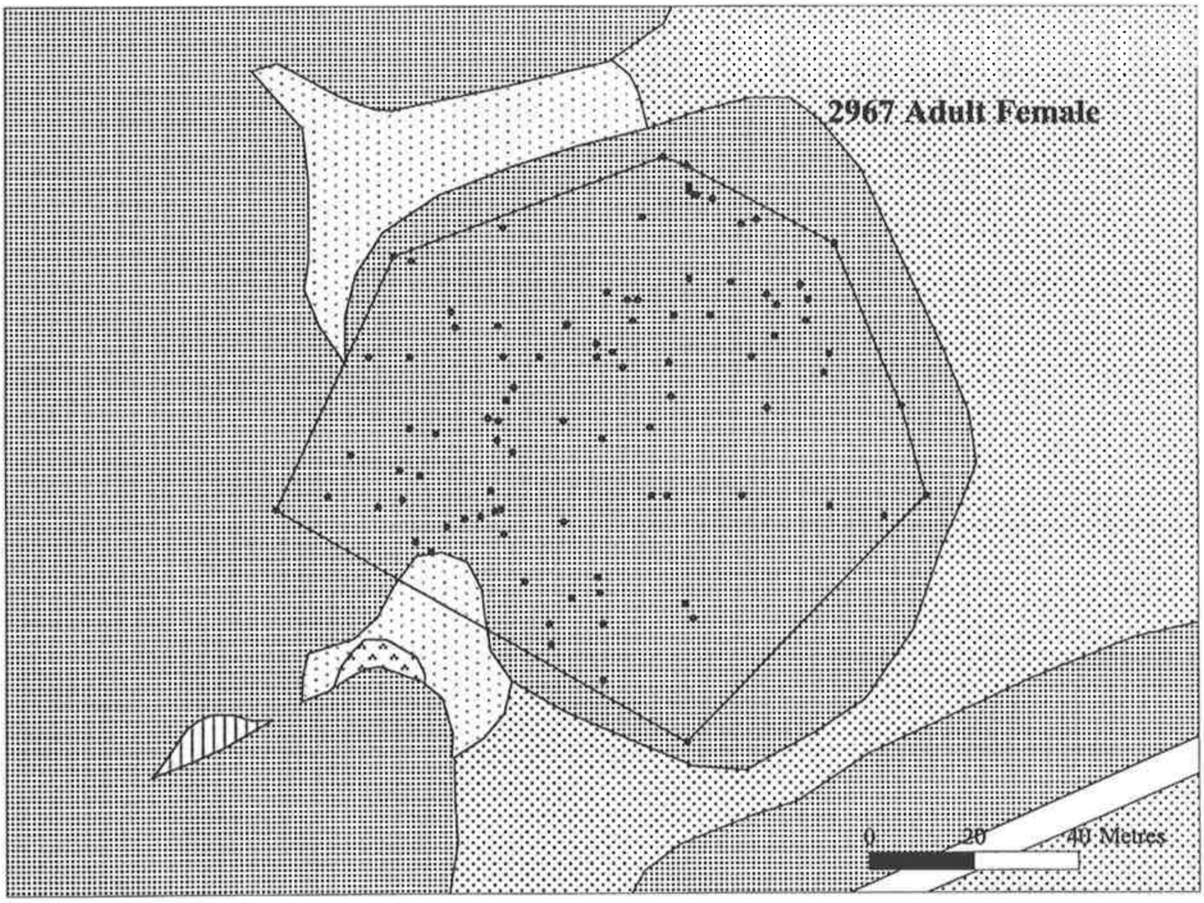

4505 Adult Female
0
30
60 Metres

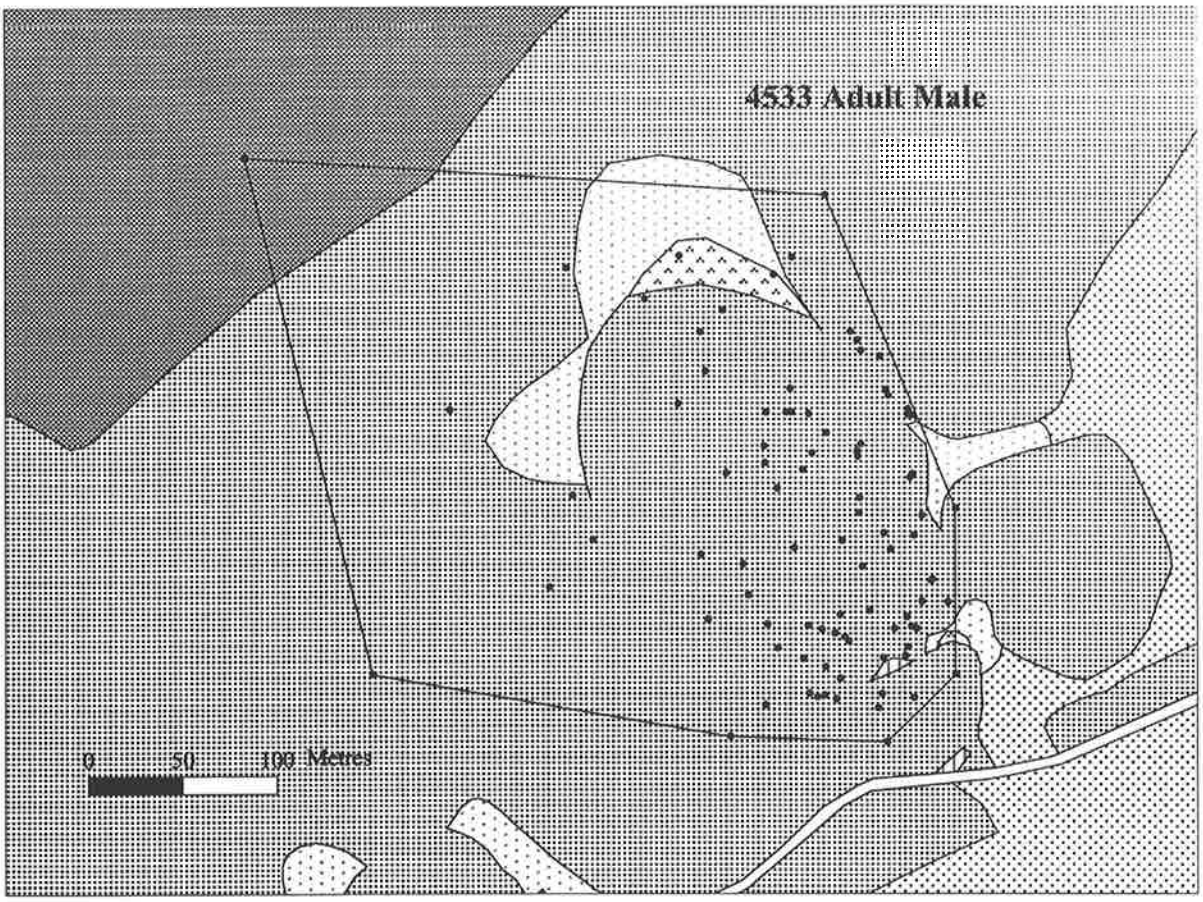

2730 Adult Female
0
30
60 Metres

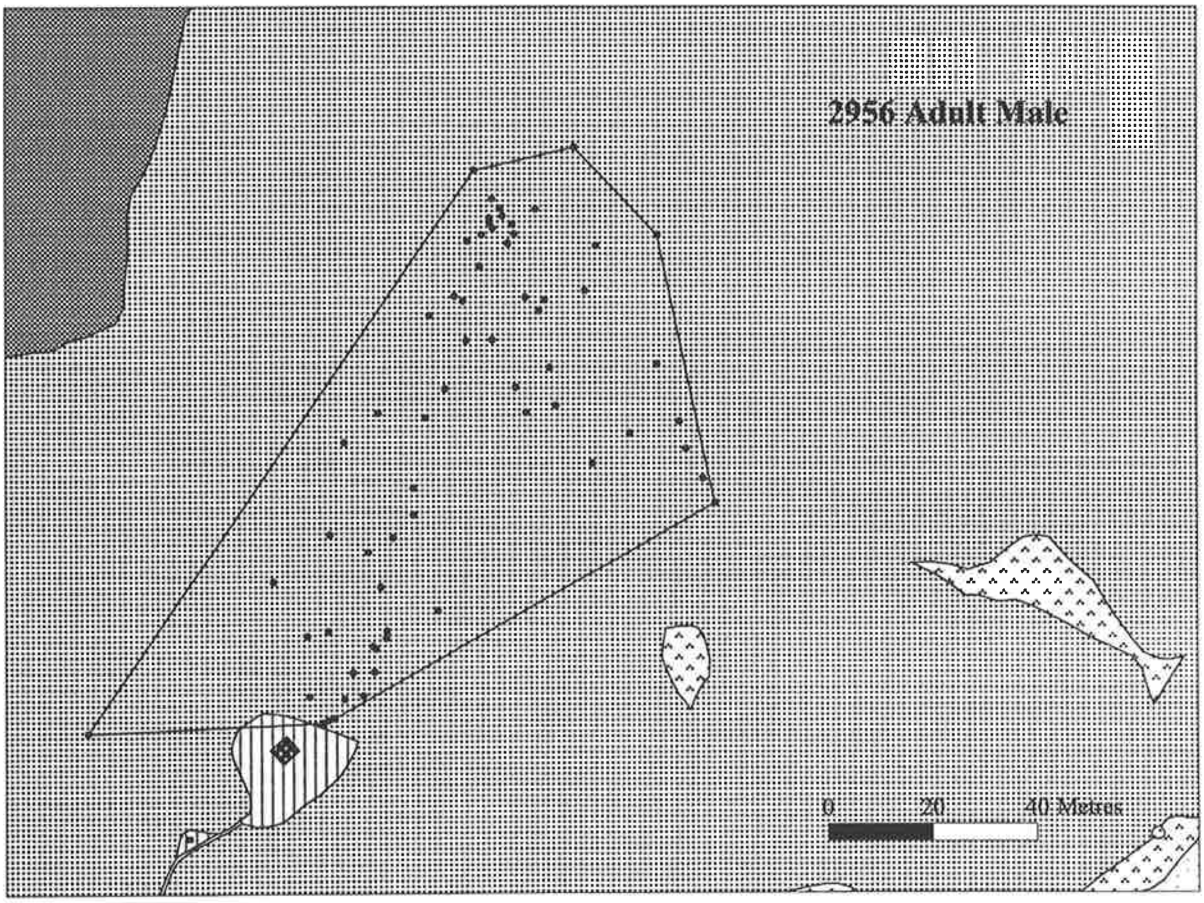

2996 Adult Female
0
40
80 Metres

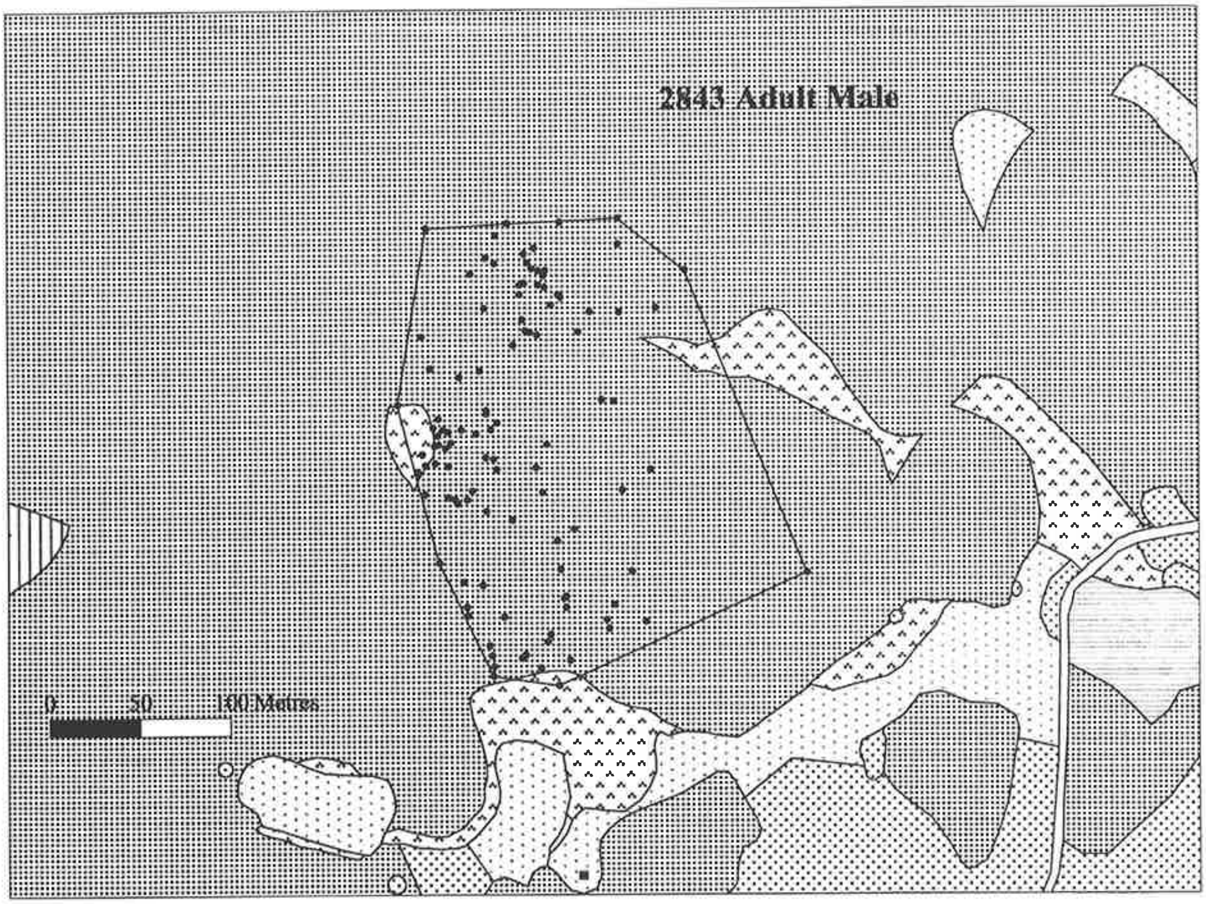

4523 Adult Female
0
30
60 Metres

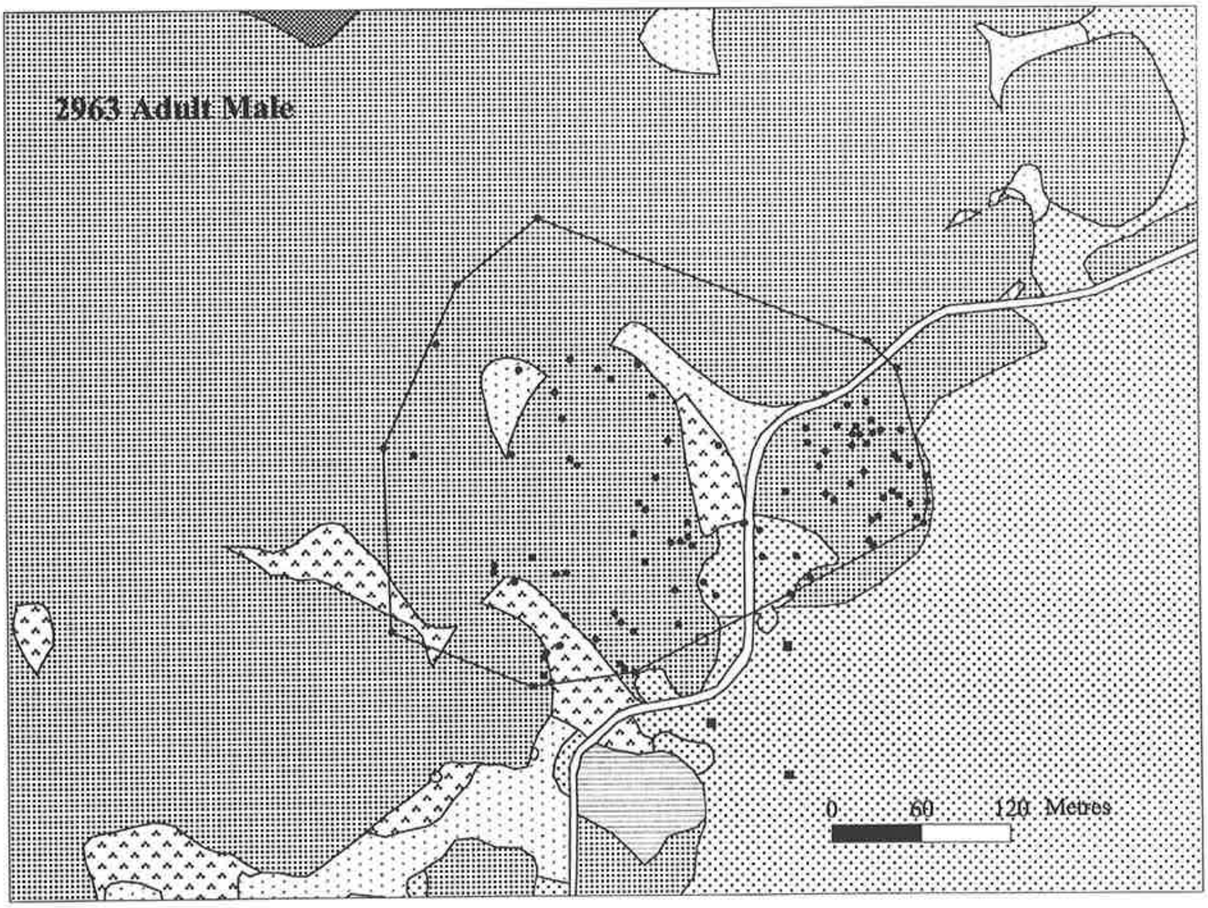

4511Adult Female
0
50
100 Metres

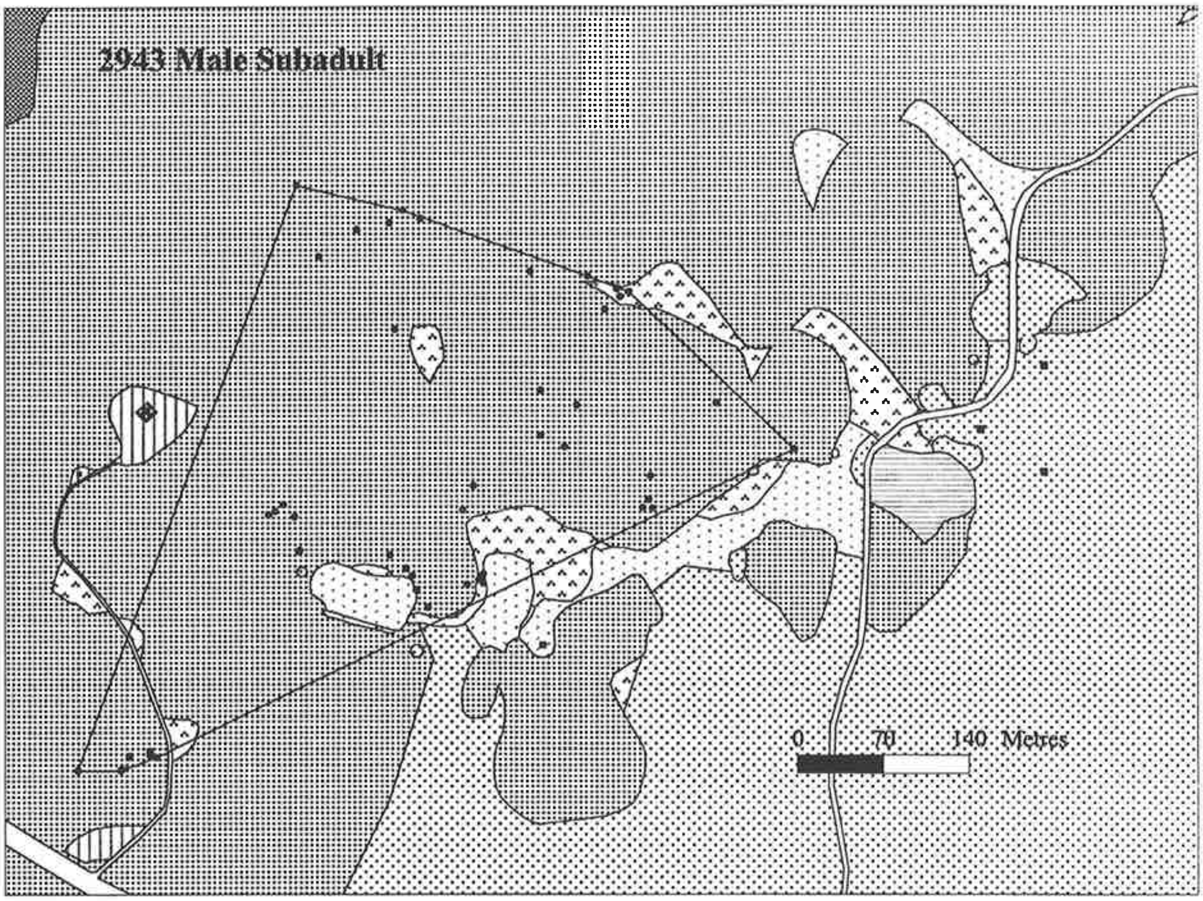

2967 Adult Female
0
20
40 Metres


4533 Adult Male
0
50
100 Metres

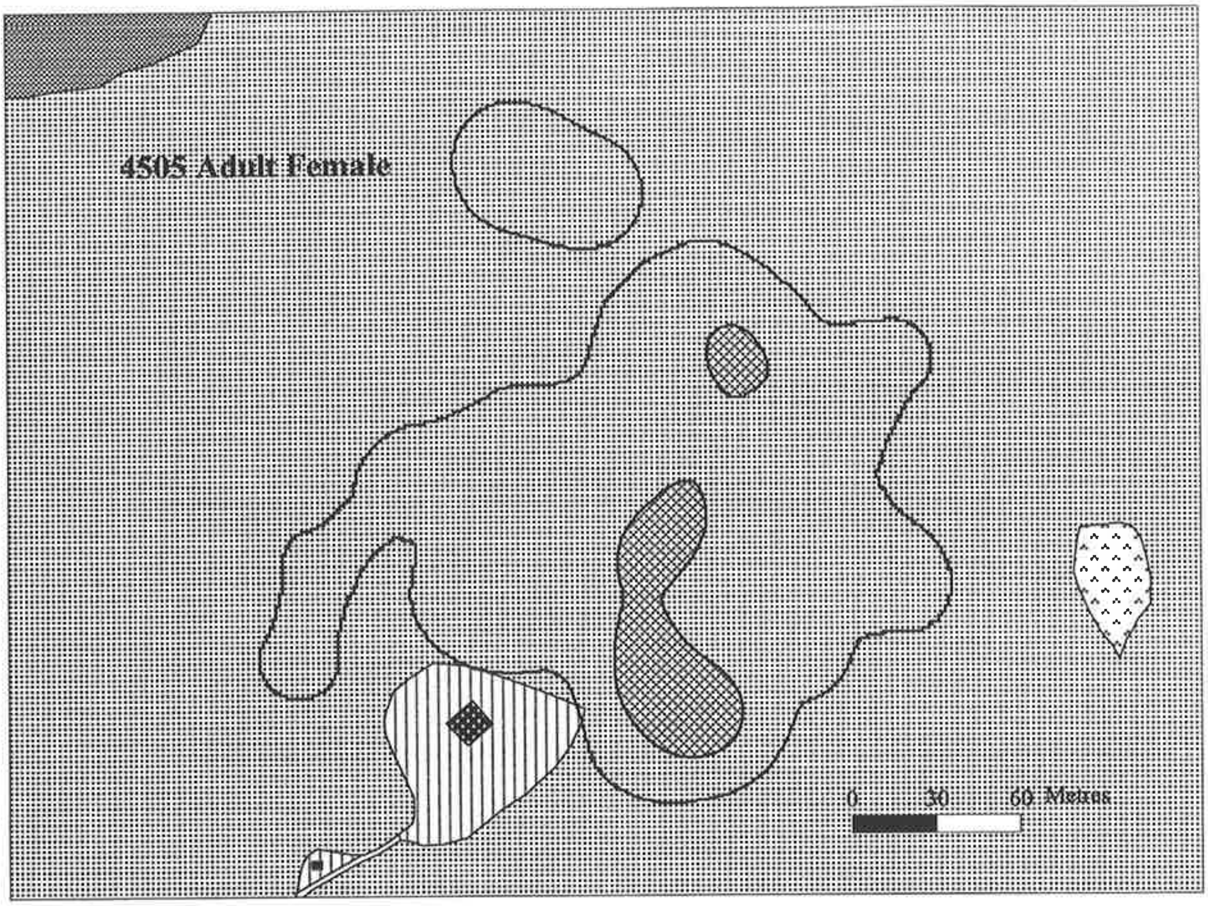

2956 Adult Male
0
20
40 Metres

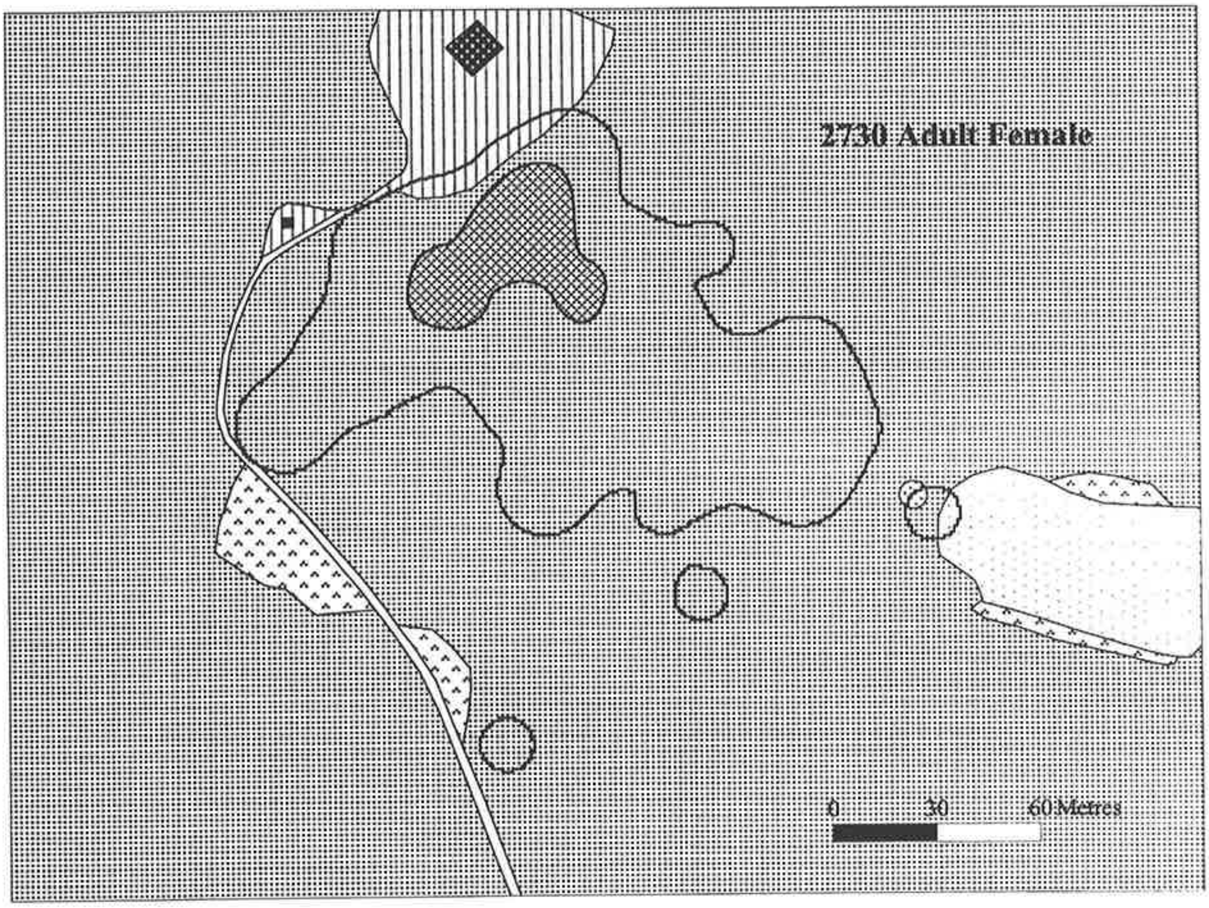

2843 Adult Male
0 50 100 Metres

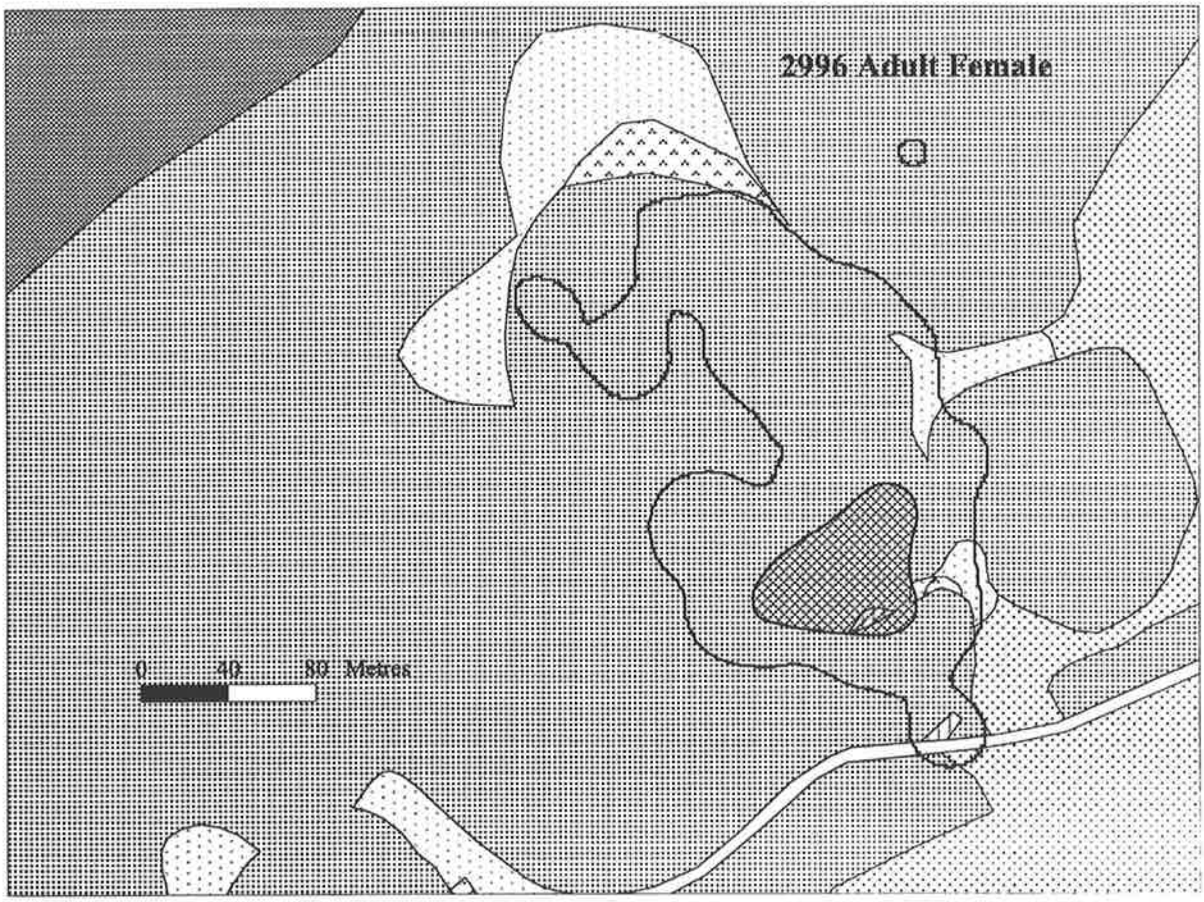

2963 Adult Male
0 60 120 Metres

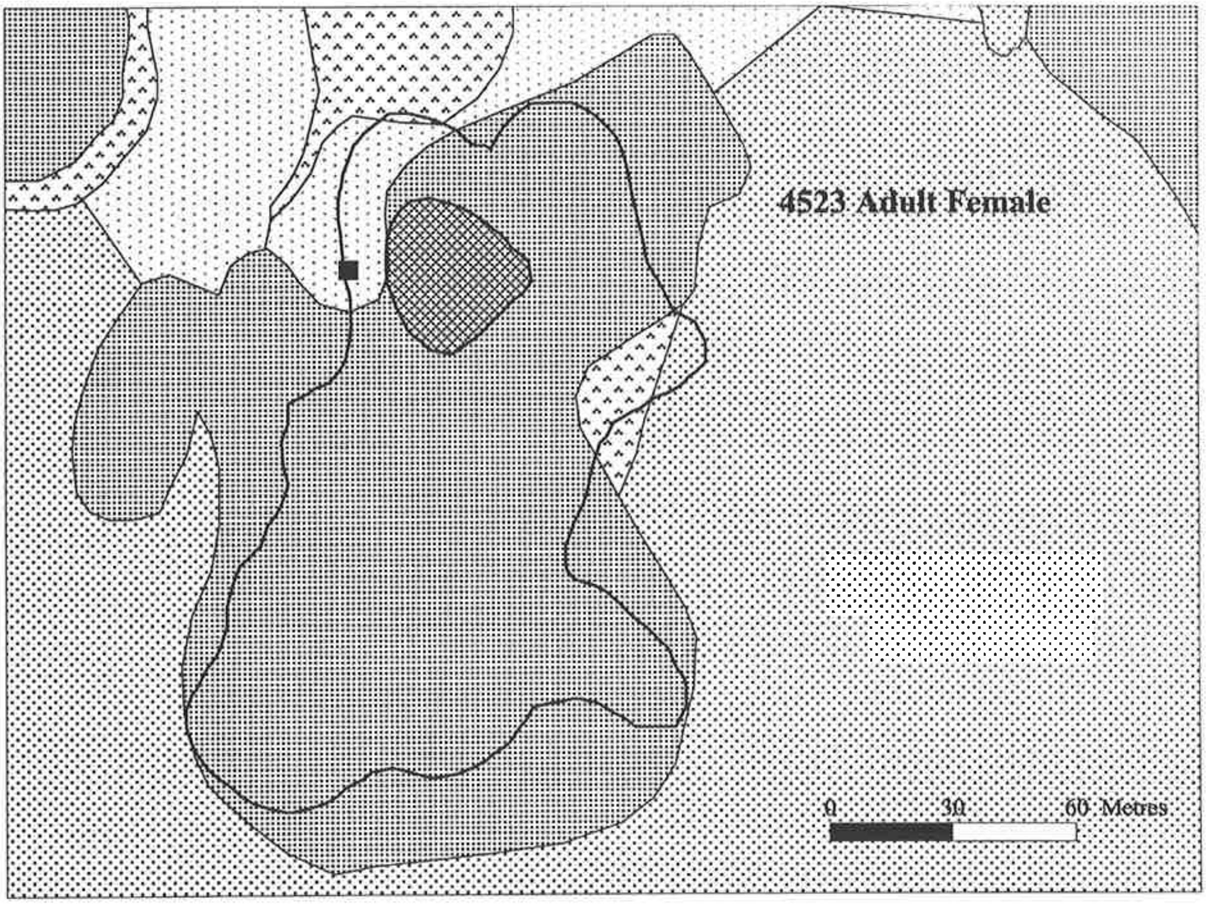

2943 Male Subadult
0
70
140 Metres

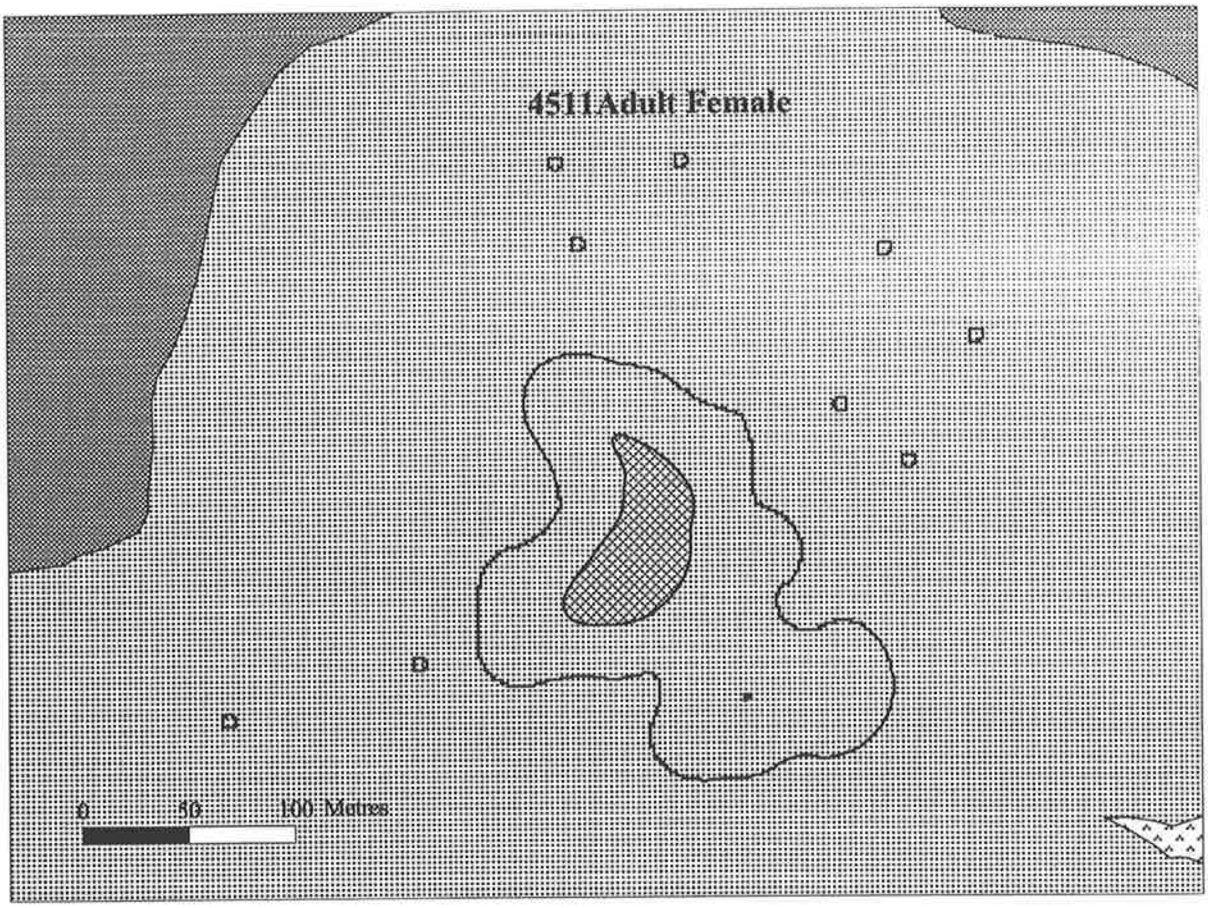
Appendix 5. Kernel 95% and 50% probability polygons.

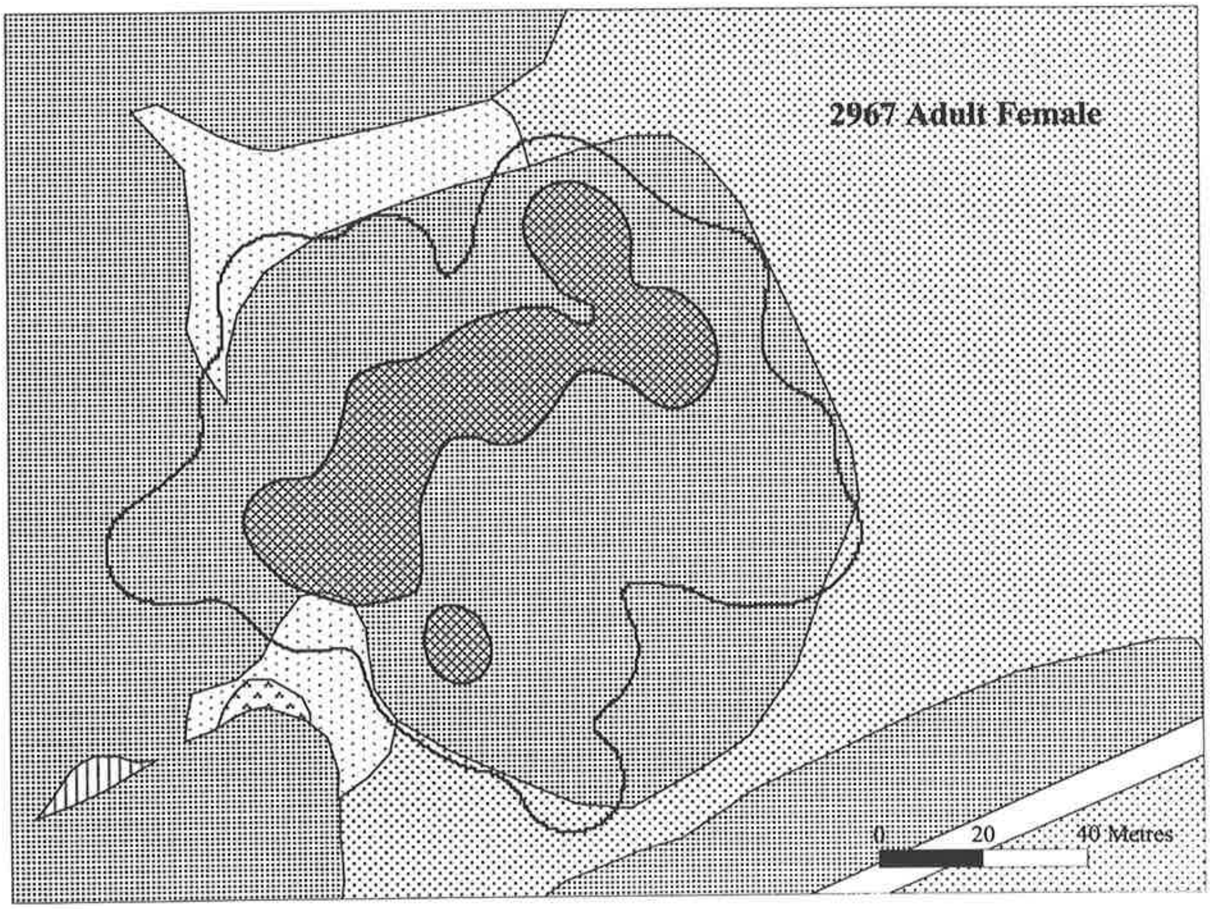

4505 Adult Female
0
30
60 Metres

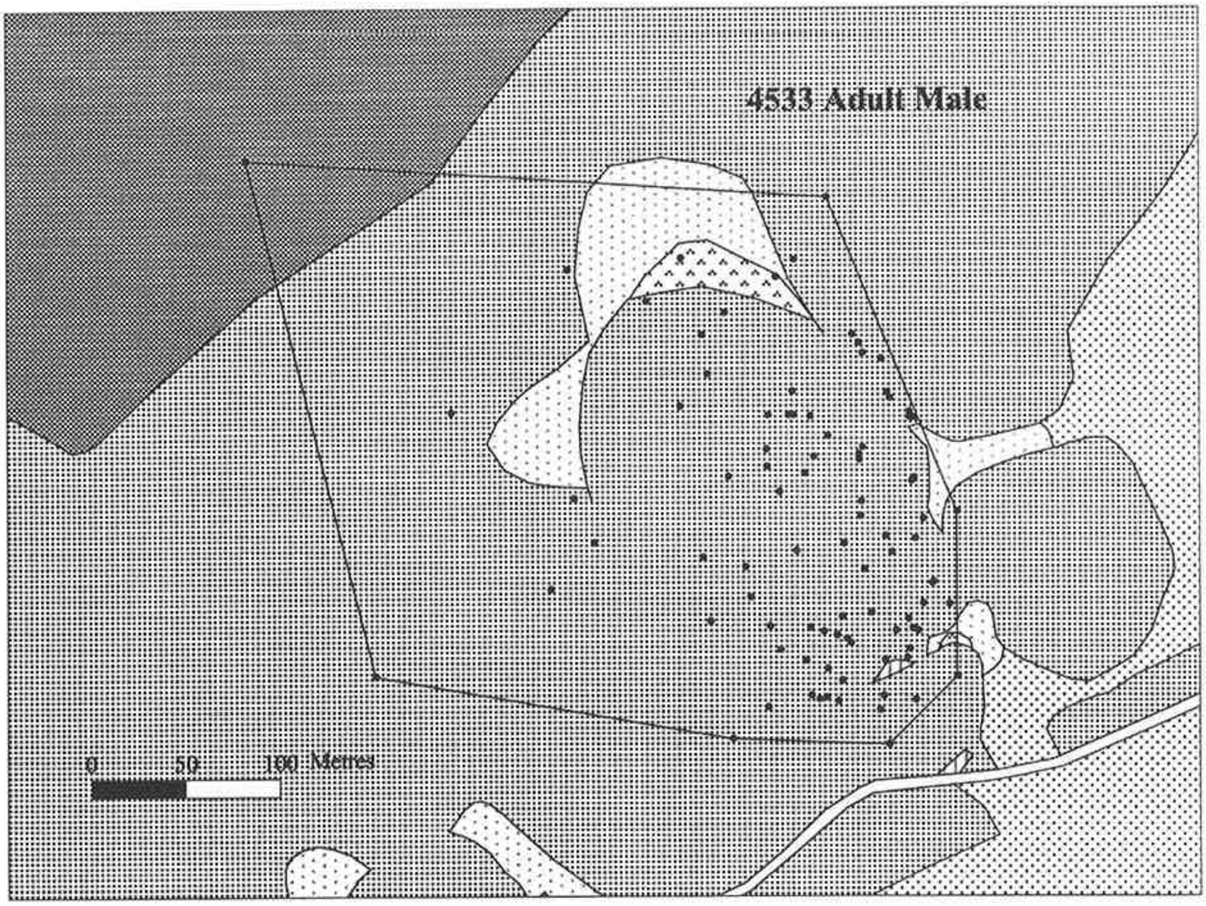

2730 Adult Female
0
30
60 Metres

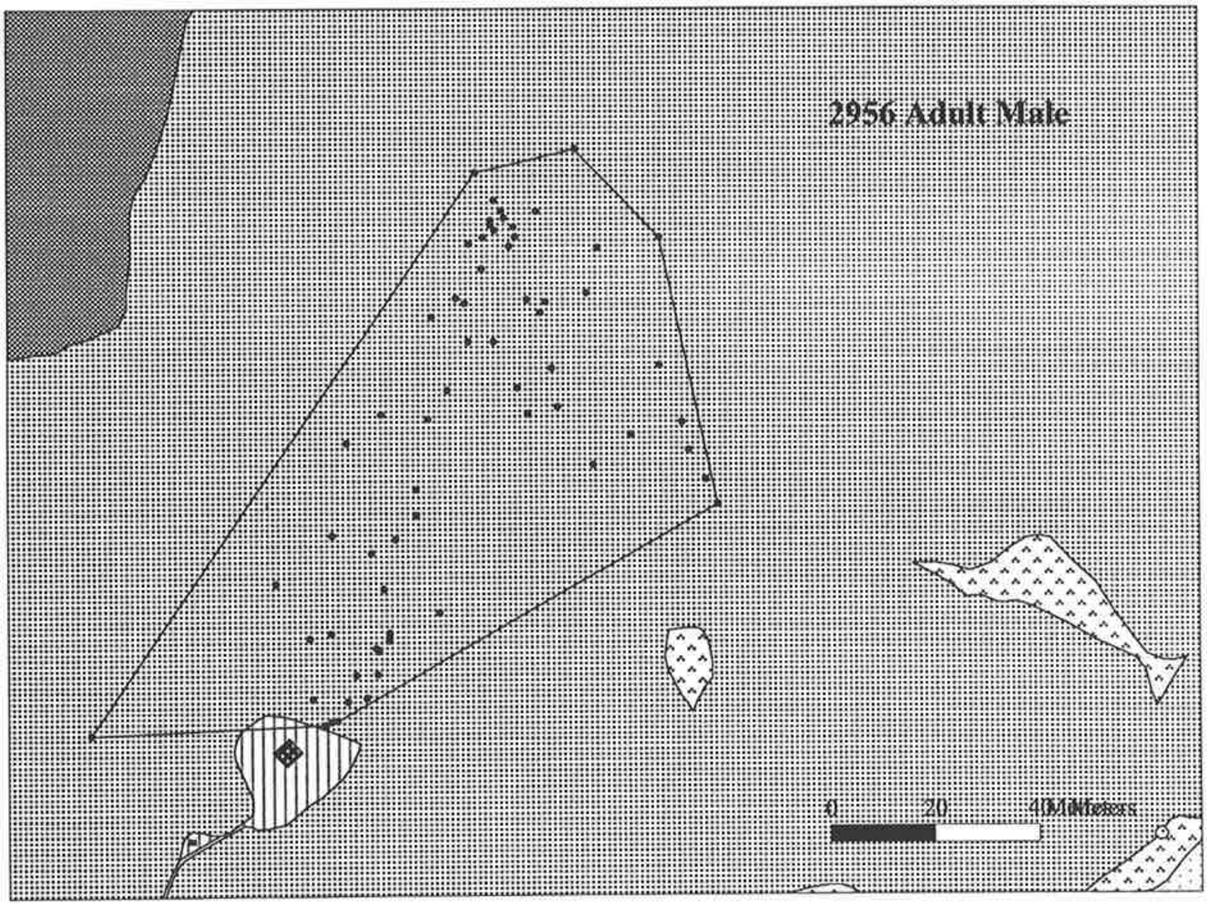

2996 Adult Female
0
40
80 Metres

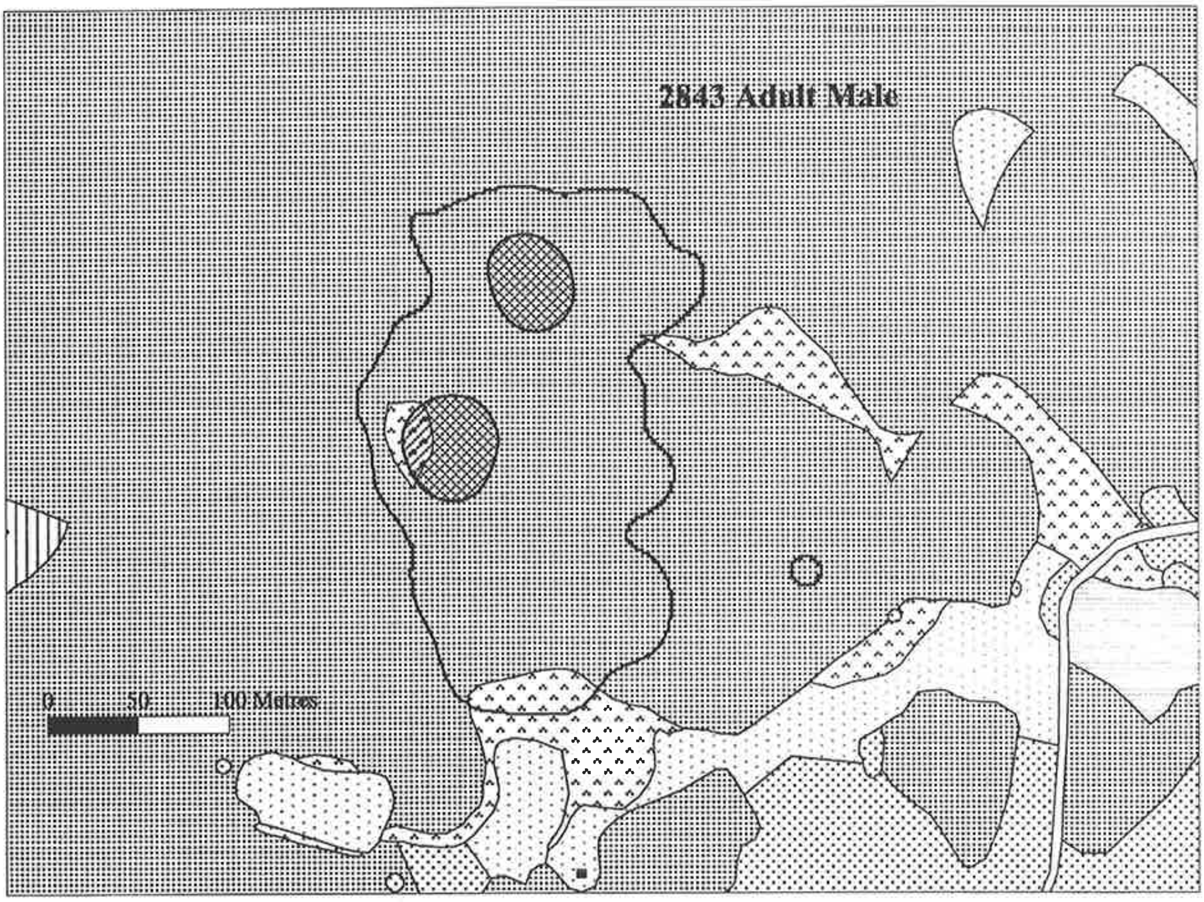

4523 Adult Female
0
30
60 Metres

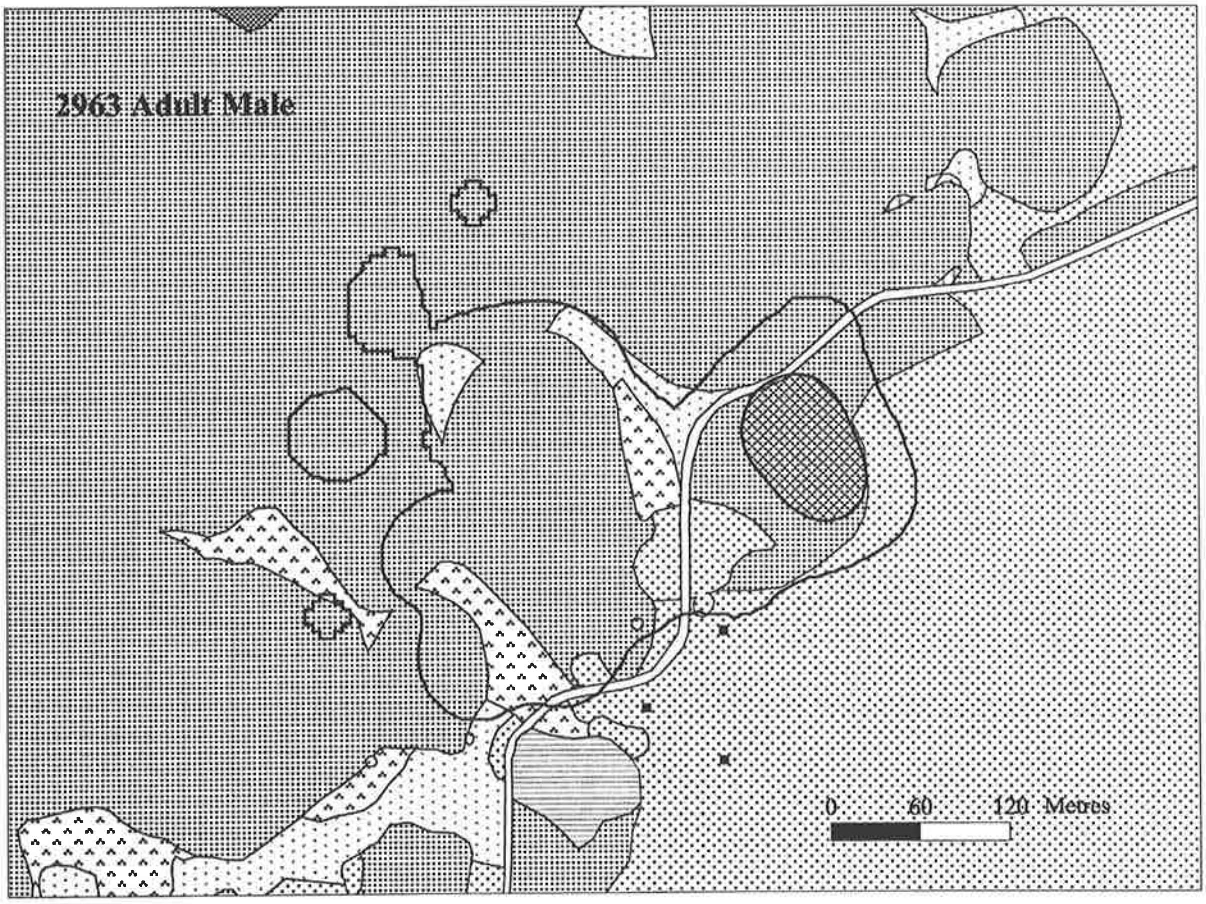

4511Adult Female
0
50
100 Metres

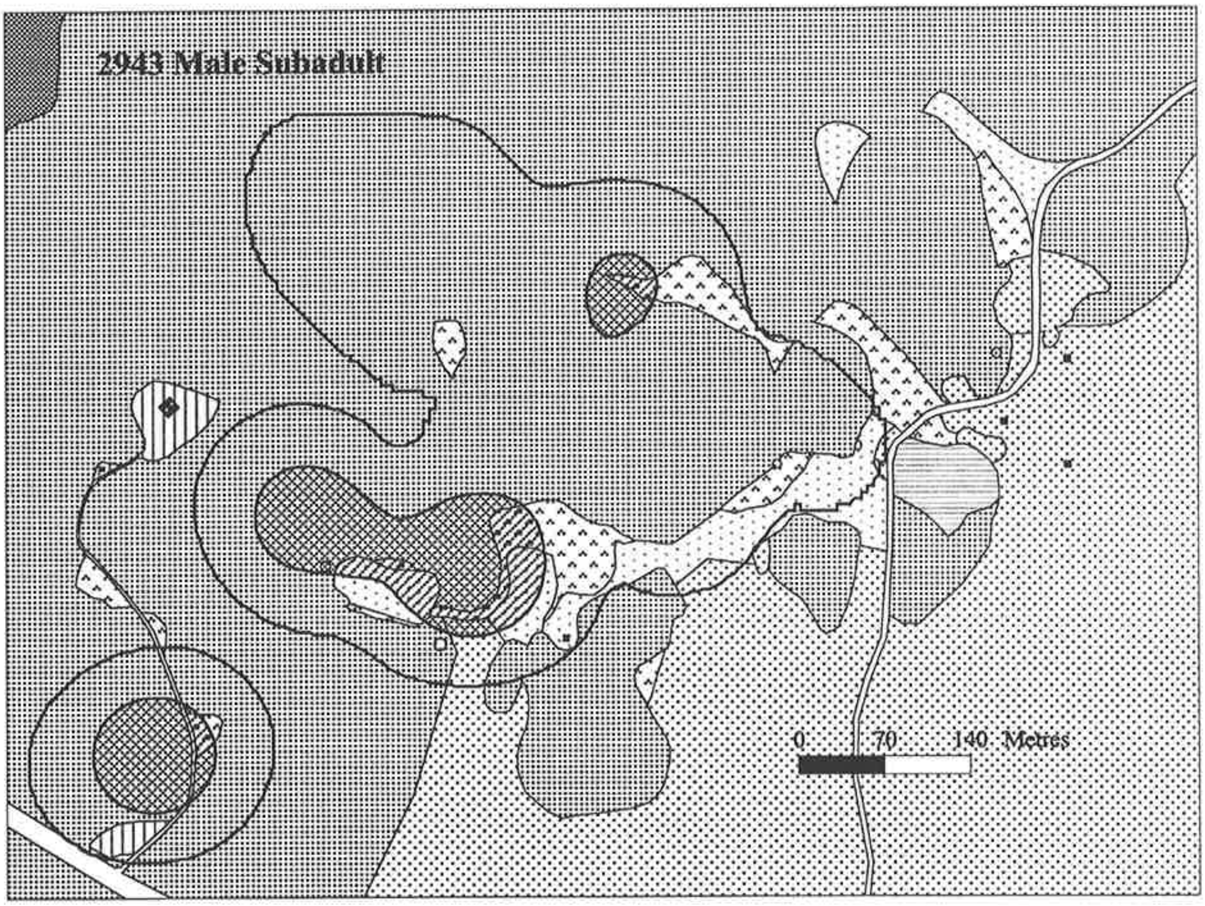

2967 Adult Female
0
20
40 Metres


4533 Adult Male
0
50
100 Metres


2956 Adult Male
0
20
40 Metres


2843 Adult Male
0
50
100 Metres


2963 Adult Male
0
60
120 Metres


2943 Male Subadult
0
70
140
Metres

Appendix 6. Morphological measurement of *Tarsius syrichta.*

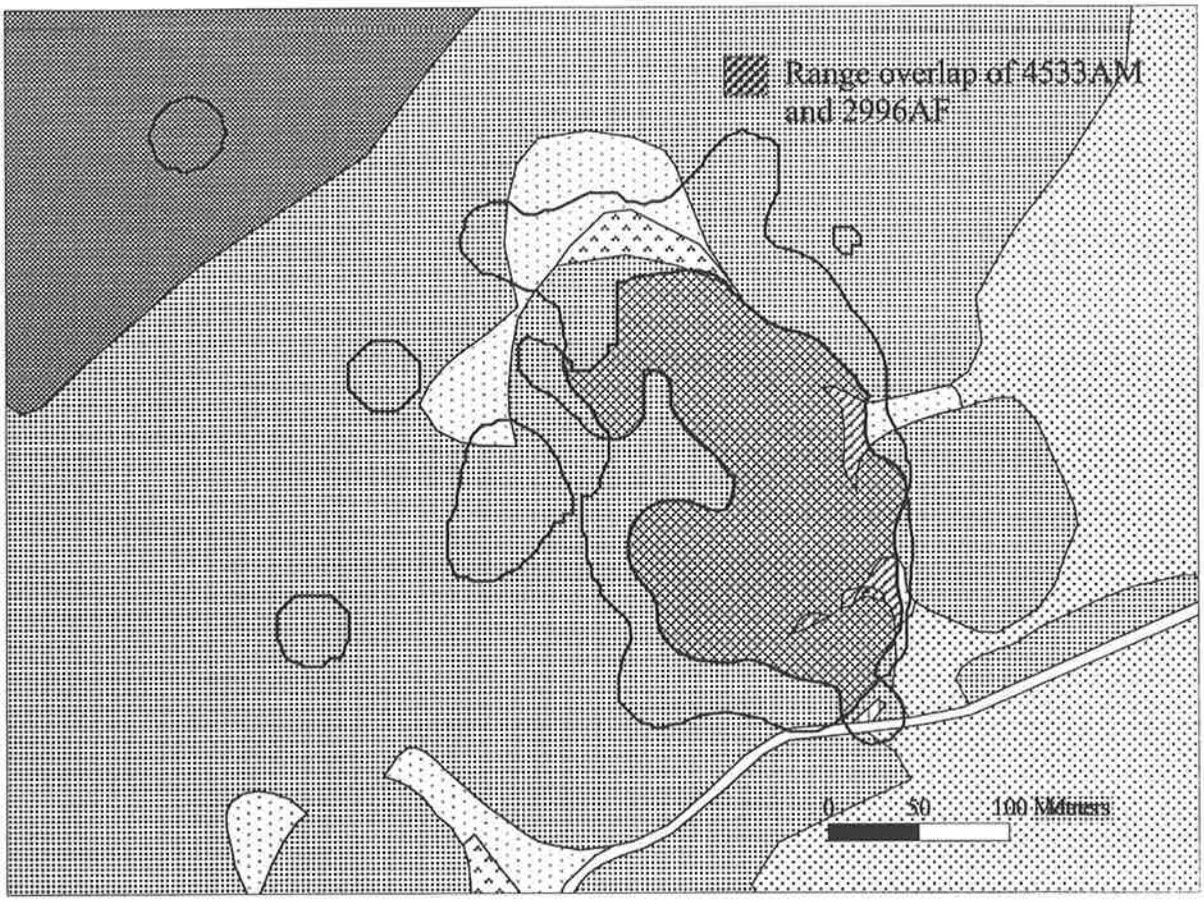
Animal ID	Sex	Age	Body weight (gm)	Total length (mm)	Body length (mm)	Tail length (mm)	Hindlimb length (mm)	Thigh length (mm)	Leg length (mm)	Foot length (mm)
4505	F	A	132	350	120	230	170	60	55	55
4505infant	M	I	34	200	80	120	105	30	40	35
2730	F	A	125	340	115	225	170	60	60	50
2943	M	A	105	360	125	235	190	60	70	60
4511	F	A	125	300	110	190	175	65	50	60
4511infant	F	I	29	170	70	100	90	25	30	35
2956	M	A	128	350	130	220	185	50	70	65
2843	M	A	143	360	130	230	185	60	55	70
2963	M	A	133	355	115	240	190	60	65	65
4523	F	A	112	340	120	220	160	45	50	65
4523infant	F	I	45	220	55	140	130	35	45	50
2996	F	A	107	350	125	220	185	60	60	65
2996infant	F	I	39	240	90	150	120	30	40	50
4533	M	A	138	350	110	240	180	55	60	65
2967	F	A	116	340	110	230	175	50	60	65

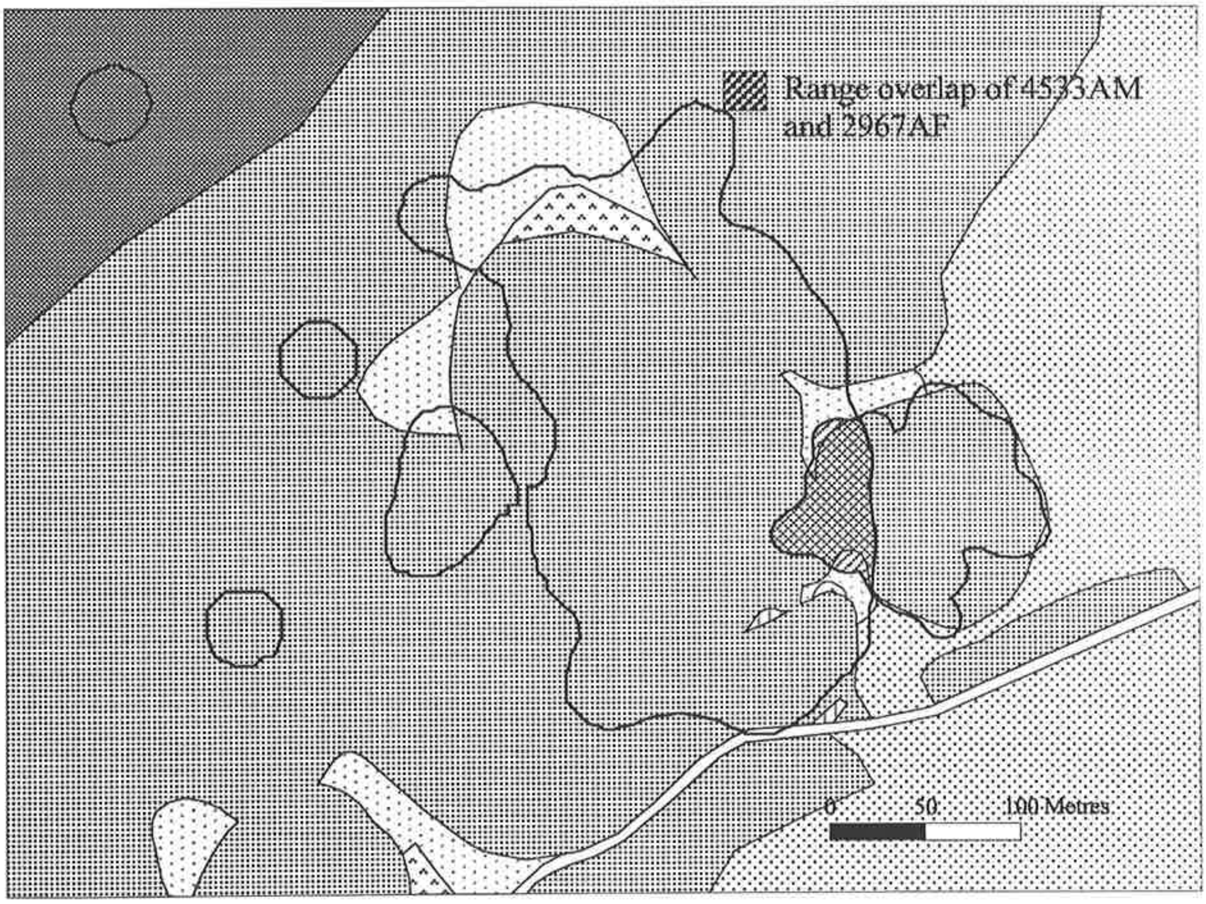
Appendix 6 continued…..

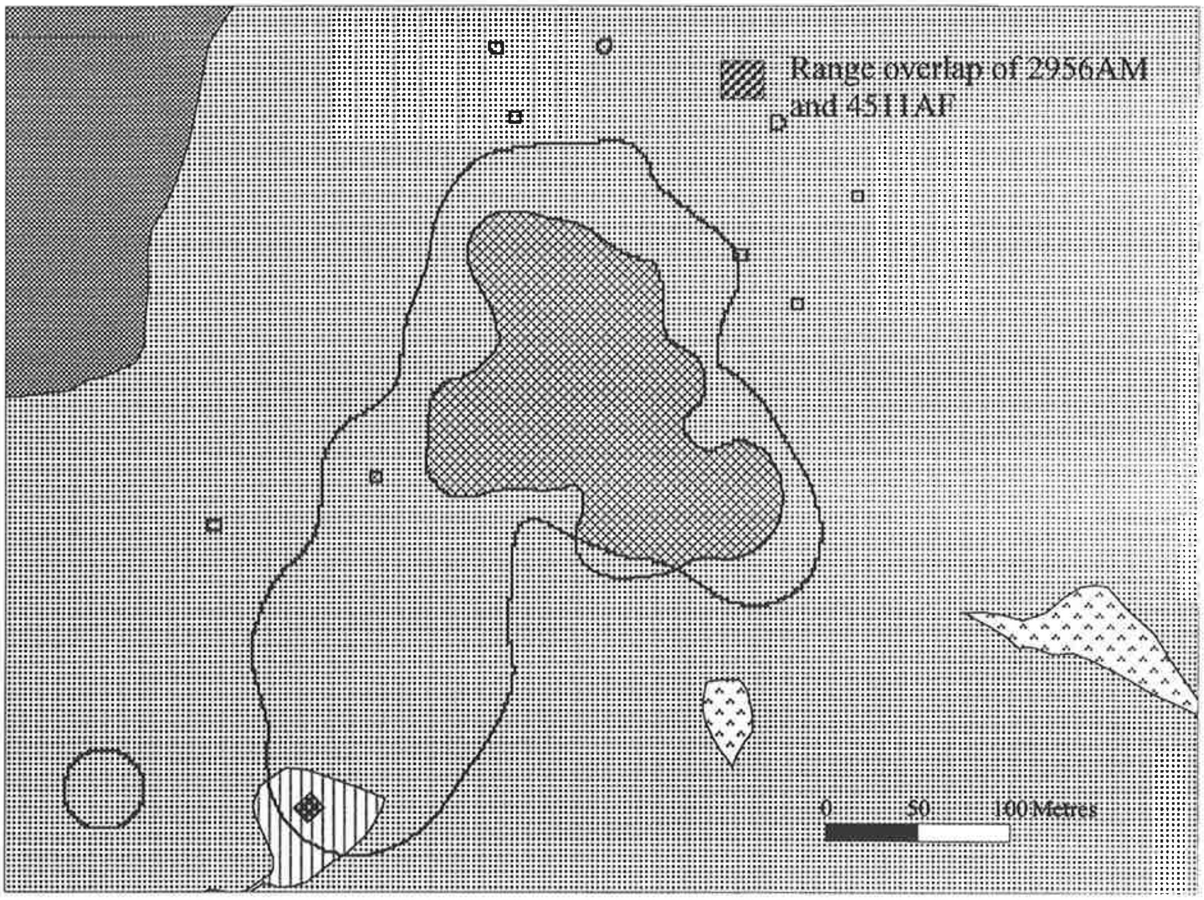
Appendix 6. Morphological Measurement of *Tarsius syrichta*

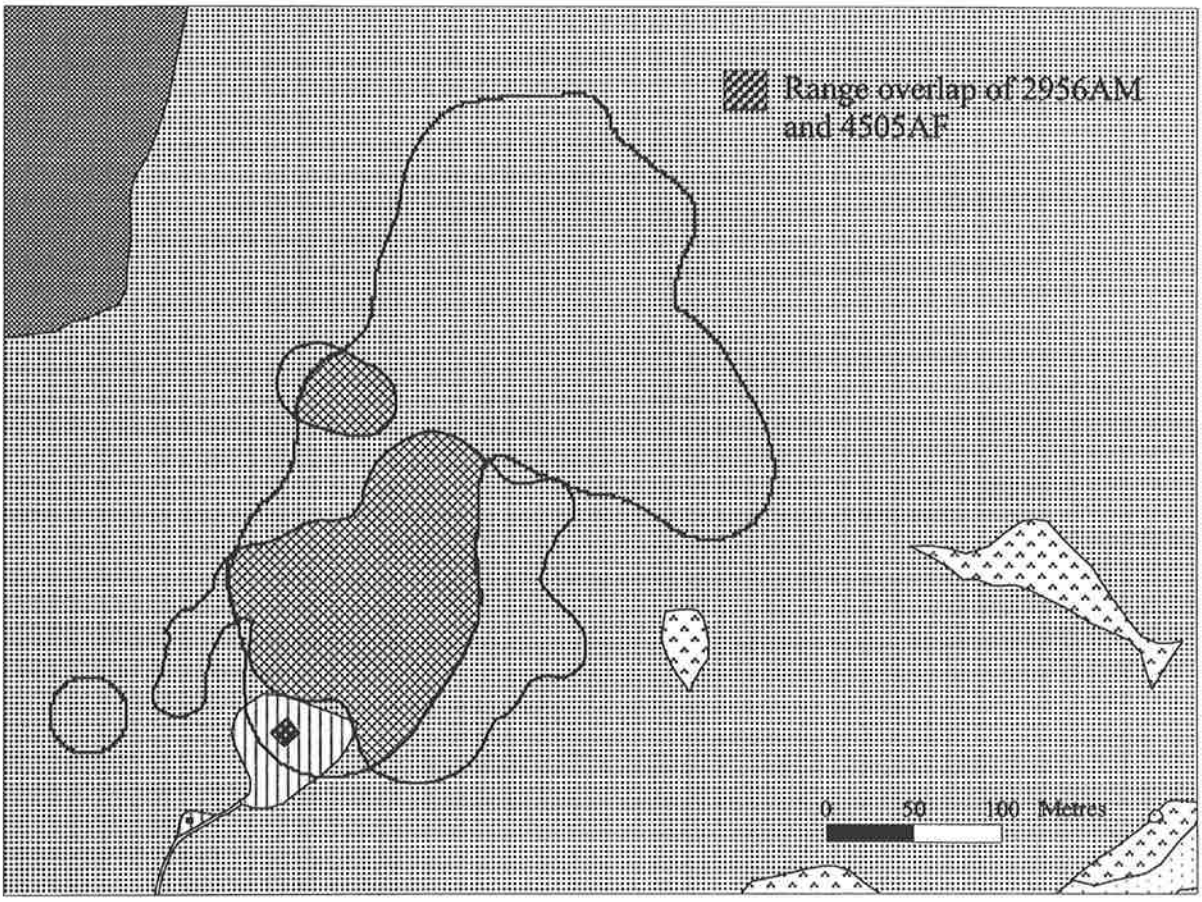
Animal ID	**Big toe length (mm)**	**Forelimb length (mm)**	**Arm length (mm)**	**Forearm length (mm)**	**Hand length (mm)**	**Thumb length (mm)**	**Testes length (mm)**	**Testes width (mm)**	**Ear length (mm)**
4505	20	105	35	35	35	13			21
4505infant	17	70	20	25	25				
2730	21	105	30	40	35	12			31
2943	22	120	40	40	40	10	15	18	25
4511	21	100	40	35	40	12			21
4511infant	18	70	20	25	25				
2956	21	110	30	45	40	11	18	21	26
2843	23	110	30	35	40	11	20	20	26
2963	24	115	30	35	45	14	14	15	26
4523	22	90	25	35	35	13			19
4523infant	17	70	15	25	30	12			18
2996	22	105	30	35	40	11			21
2996infant	22	75	15	30	30	9			18
4533	23	110	30	35	45	11	19	24	21
2967	23	125	30	40	45	11			20

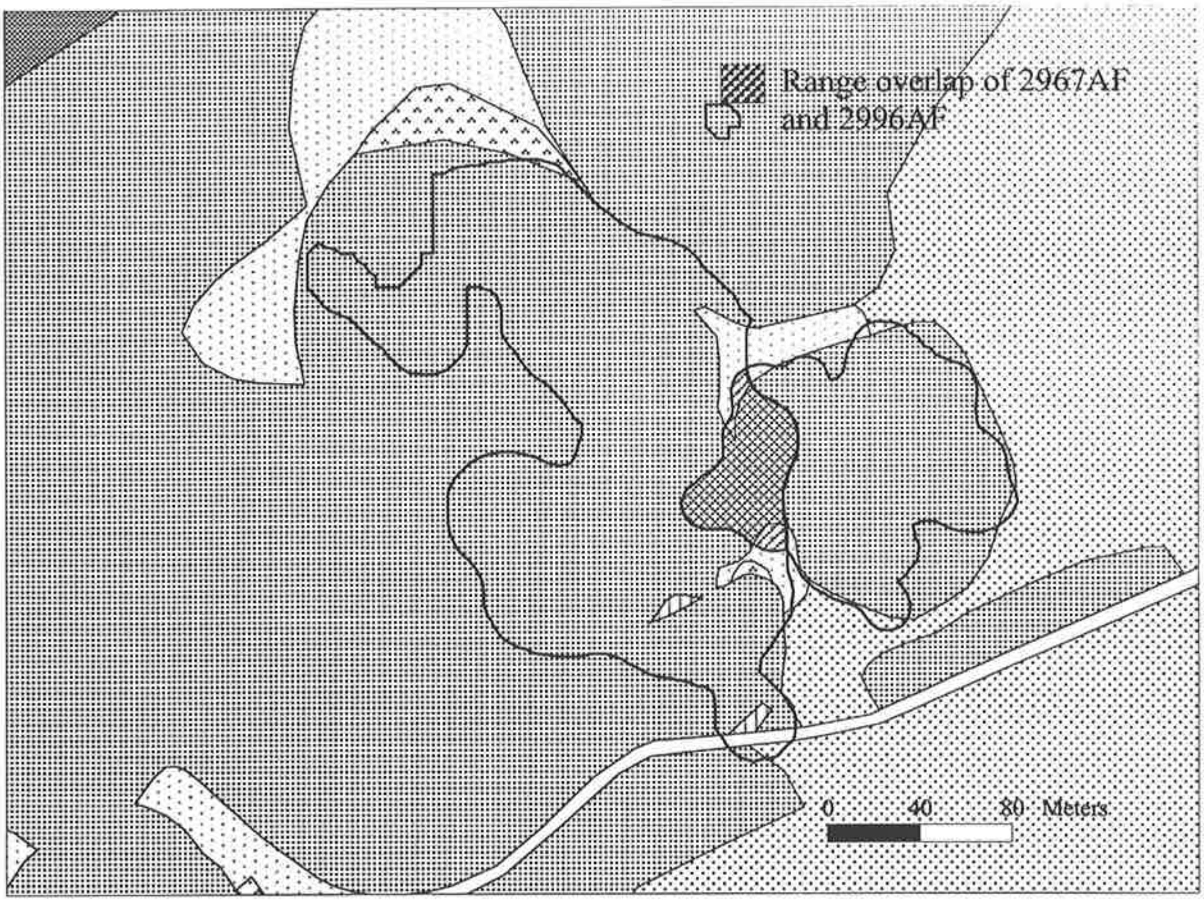
Appendix 7. Home range overlap of adjacent males and females using Kernel home range 95%.

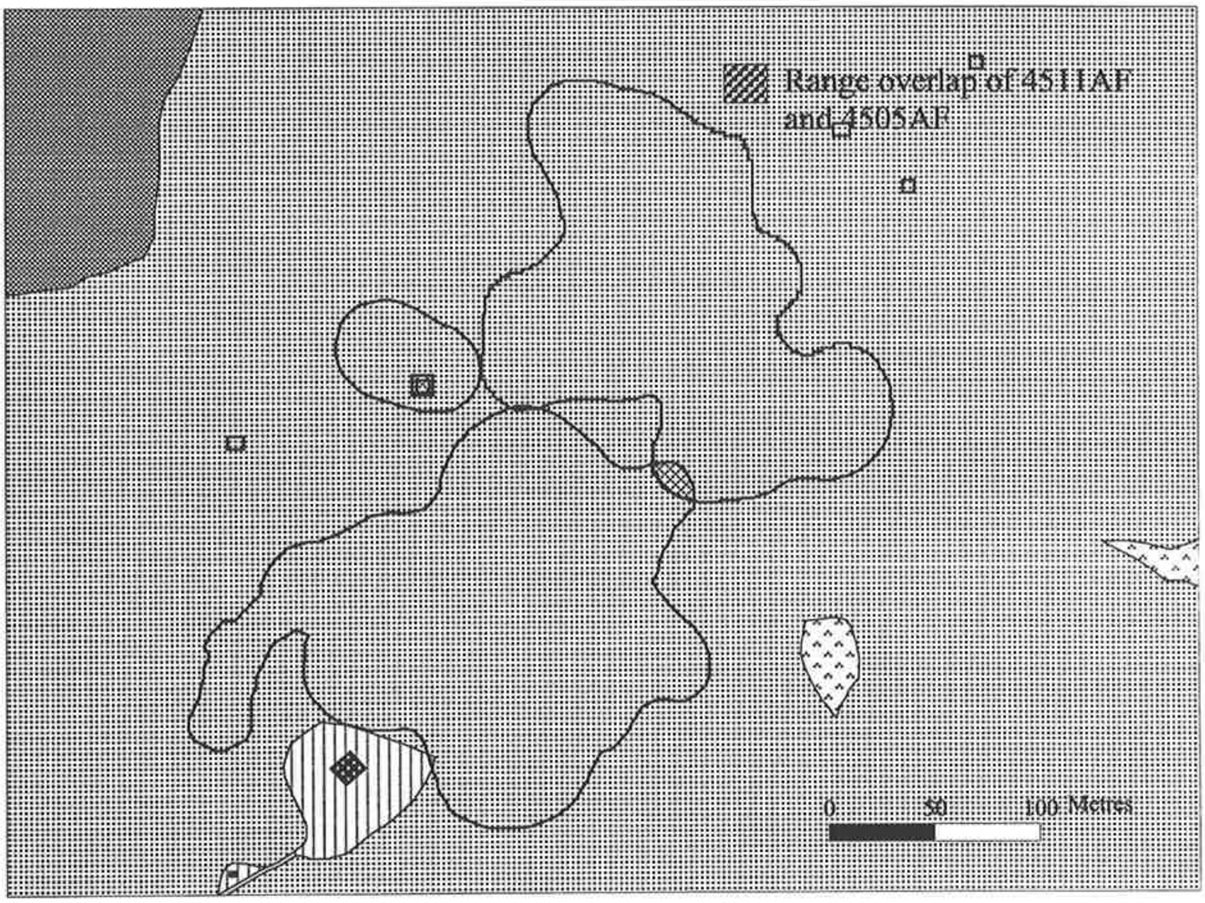

Range overlap of 4533AM and 2996AF
0
50
100 Metres

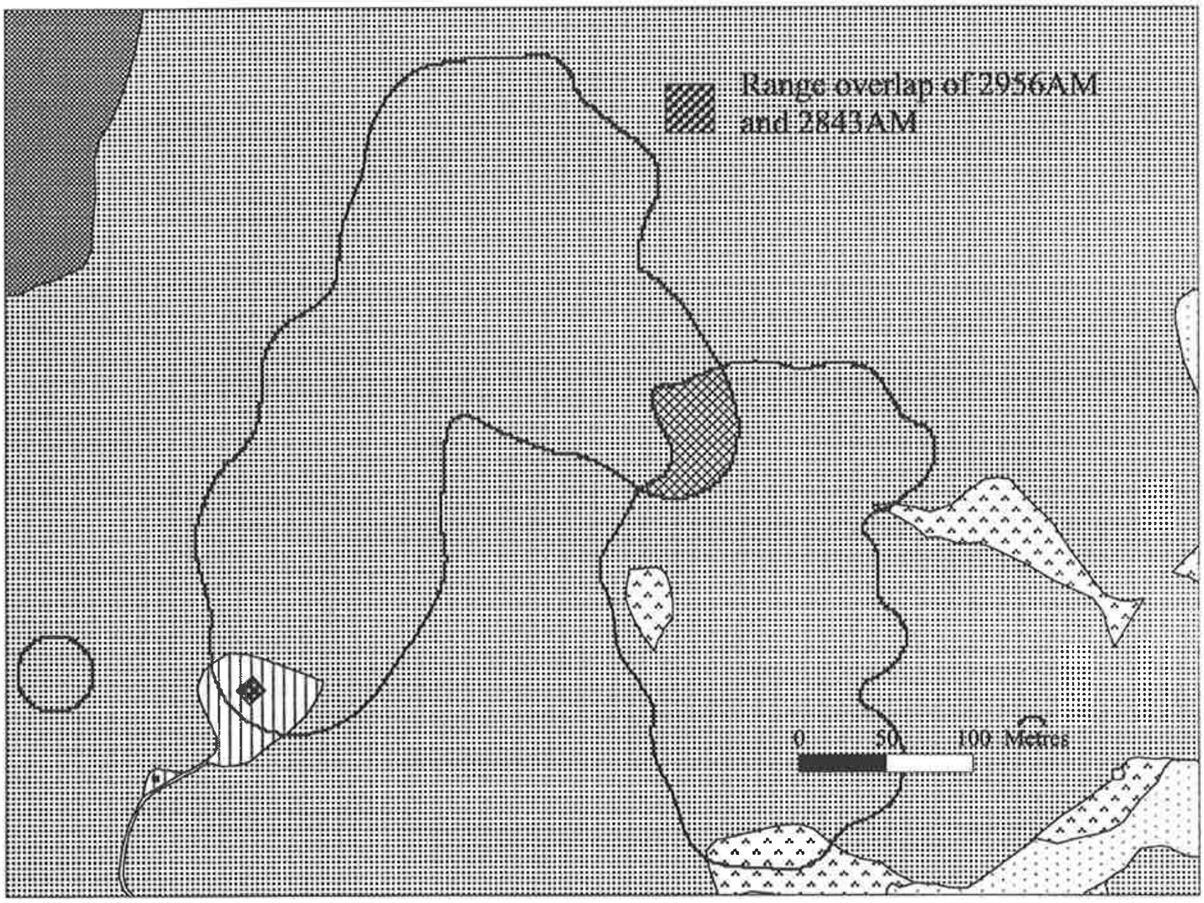

Range overlap of 4533AM and 2967AF
0
50
100 Metres


▨ Range overlap of 2956AM and 4511AF
0 50 100 Metres


▨ Range overlap of 2956AM and 4505AF
0 50 100 Metres


▨ Range overlap of 2967AF and 2996AF
0 40 80 Meters


▨ Range overlap of 4511AF and 4505AF
0 50 100 Metres


Range overlap of 2956AM and 2843AM
0
50
100 Metres

Appendix 8. Foraging and travelling data.

Foraging data

Individual	Substrate	Locomotor Type	Count
2947	Other	Other	7
2947	Ground	Other	15
2947	Ground	Climb	1
2947	Ground	Other	9
2947	St	CL	15
2947	St	Climb	1
2947	St	Climb	2
2947	St	VCL	13
2947	Tr	CL	4
2947	Tr	Climb	2
2947	Tr	Climb	1
2947	Tr	VCL	15
4505	Other	CL	3
4505	Ground	Other	6
4505	St	CL	20
4505	St	Climb	1
4505	St	VCL	2
4505	Tr	CL	19
4505	Tr	VCL	15
2996	Tr	CL	45
2843	Ground	Other	5
2843	Ground	Other	8
2843	St	CL	75
2843	Other	CL	33
2843	Tr	CL	60
2963	Other	Other	5
2963	St	CL	20
2963	Tr	CL	145
2956	Other	Other	17
2956	St	CL	15
4523	Other	CL	6
4523	Tr	CL	2
2730	St	CL	16
2730	St	Climb	1
2730	St	Climb	2
2730	St	VCL	4
2730	Tr	CL	86
2730	Tr	VCL	4

Individual	Substrate	Locomotor	Count
4511	Ground	Other	6
4511	St	CL	12
4511	St	Climb	1
4511	St	Climb	1
4511	St	VCL	9
4511	Tr	CL	32
4511	Tr	VCL	4

Travelling data

Individual	**Substrate**	**Locomotor**	**Count**
4505	Tr	VCL	3
4505	Tr	Climb	2
4505	Tr	Other	1
4505	St	VCL	15
4505	Gr	VCL	1
4505	Gr	Other	1
2947	Tr	VCL	6
2947	Tr	Climb	1
2947	St	VCL	4
2947	St	Climb	1
4511	Tr	VCL	27
4511	Tr	Climb	5
4511	St	VCL	21
2956	Tr	VCL	3
2956	Tr	Climb	5
2956	St	VCL	9
2956	Br	VCL	1
2956	Br	Other	5
2956	Other	VCL	3
2843	Tr	VCL	33
2843	Tr	Climb	29
2843	St	VCL	28
2843	St	Climb	16
2843	Gr	VCL	1
2843	Br	VCL	1
2843	Other	VCL	1
2963	Tr	VCL	29
2963	Tr	Climb	24
2963	St	VCL	19
2963	St	Climb	4
2963	Gr	Other	11
2963	Br	VCL	1
2730	Tr	VCL	4
2730	Tr	Climb	13
2730	St	VCL	15
2730	Br	VCL	1
2730	Br	Climb	5
Uncollared		VCL	7
Uncollared		VCL	7

Individual	**Substrate**	**Locomotor**	**Count**
2996	Tr	VCL	12
2996	Tr	Climb	30
2996	St	VCL	16
2996	Br	VCL	1
2996	Br	Other	7

Appendix 9. Foraging and travelling fitted model.

Foraging - Models fitted

```
> summary(for.glm, corr=F)

Call: glm(formula = Count ~ Individual + Substrate * Locomotion, family = poisson, data = forage, link = log)
Deviance Residuals:
          Min          1Q           Median          3Q        Max
    -6.469735   -1.781312   -3.972055e-015    1.241601   5.444135

Coefficients: (6 not defined because of singularities)
                            Value   Std. Error       t value
        (Intercept)   1.862386082   0.19377495   9.611077377
        Individual1  -0.103968180   0.08412330  -1.235902294
        Individual2   0.133823355   0.05901996   2.267425543
        Individual3   0.226696329   0.02745708   8.256389407
        Individual4   0.181994400   0.02029577   8.967110891
        Individual5   0.009241150   0.03318192   0.278499559
        Individual6  -0.311608856   0.05128700  -6.075786106
        Individual7   0.052193284   0.01496346   3.488048906
        Individual8  -0.029951735   0.01554949  -1.926219650
         Substrate1  -0.055975956   0.12536478  -0.446504628
         Substrate2   0.182072334   0.25675424   0.709130779
         Substrate3   0.167381645   0.11228158   1.490731170
        Locomotion1  -1.356549720   0.27852689  -4.870444420
        Locomotion2   0.271066995   0.27223984   0.995691855
        Locomotion3  -0.022268582   0.13692194  -0.162637062
Substrate1Locomotion1          NA           NA            NA
Substrate2Locomotion1 0.001251974   0.18468095   0.006779117
Substrate3Locomotion1 -0.065099343  0.11435128  -0.569292646
Substrate1Locomotion2          NA           NA            NA
Substrate2Locomotion2 0.131012454   0.21085853   0.621328688
Substrate3Locomotion2          NA           NA            NA
Substrate1Locomotion3          NA           NA            NA
Substrate2Locomotion3          NA           NA            NA
Substrate3Locomotion3          NA           NA            NA

 (Dispersion Parameter for Poisson family taken to be 1 )

      Null Deviance: 1178.96 on 44 degrees of freedom

      Residual Deviance: 237.1976 on 27 degrees of freedom

      Number of Fisher Scoring Iterations: 4
```

```
> summary (for.glm1, corr=F)

Call:  glm(formula = Count ~ Individual + Substrate + Locomotion, family = poisson, data = forage, link = log)
Deviance Residuals:
            Min            1Q             Median          3Q          Max
     -6.3175515      -1.79701          0.0926488      1.356352     5.09981

Coefficients:
                                 Value         Std. Error           t value
               (Intercept)   1.779474278     0.10284518
               Individual1  -0.098377705     0.08369785        -1.17539107
               Individual2   0.143199605     0.05890003         2.43123134
               Individual3   0.225229228     0.02741078         8.21681133
               Individual4   0.181290466     0.02026066         8.94790701
               Individual5   0.002210521     0.03281382         0.06736554
               Individual6  -0.308635277     0.05128978        -6.01748131
               Individual7   0.052904993     0.01492422         3.54490823
               Individual8  -0.029484917     0.01552781        -1.89884635
                Substrate1  -0.055076812     0.12201660        -0.45138787
                Substrate2   0.065728340     0.07437624         0.88372770
                Substrate3   0.221987719     0.03718863         5.96923613
               Locomotion1  -1.372753282     0.14451918        -9.49876193
               Locomotion2   0.168075806     0.09500425         1.76913981
               Locomotion3   0.006336617     0.04642594         0.13648871

(Dispersion Parameter for Poisson family taken to be 1

Null Deviance: 1178.96 on 44 degrees of freedom

Residual Deviance: 241.474 on 30 degrees of freedom

Number of Fisher Scoring Iterations: 4
```

```
> summary(for.glm2a, corr=F)

Call:  glm(formula = Count ~ Individual + Locomotion, family poisson, data = forage, link = log)
Deviance Residuals:
              Min          1Q         Median          3Q         Max
        -7.615599   -1.853799     -.00457064   0.9303662    7.077257

Coefficients:
                    Value   Std. Error      t value
 (Intercept)   1.89426733   0.09430158   20.0873340
 Individual1  -0.16634488   0.08293742   -2.0056675
 Individual2   0.27387813   0.05779631    4.7386789
 Individual3   0.17185583   0.02661630    6.4567880
 Individual4   0.17891421   0.01946575    9.1912321
 Individual5  -0.06104168   0.03068204   -1.9894923
 Individual6  -0.30890575   0.05108502   -6.0468944
 Individual7   0.05994898   0.01484624    4.0379907
 Individual8  -0.02447966   0.01545654   -1.5837738
Locomotion1   -1.49701367   0.14318568  -10.4550518
Locomotion2    0.03551460   0.06106339    0.5816022
Locomotion3    0.08056824   0.04091402    1.9692084

(Dispersion Parameter for Poisson family taken to be 1

    Null Deviance: 1178.96 on 44 degrees of freedom

Residual Deviance: 338.6865 on 33 degrees of freedom

Number of Fisher Scoring Iterations: 4
```

```
> summary(for.glm2b, corr=F)

Call:  glm(formula = Count ~ Individual + Locomotion, family poisson, data = forage, link = log)
Deviance Residuals:
              Min              1Q              Median             3Q           Max
        -6.281623       -2.849872          -0.8127977       1.857153      7.865082

Coefficients:
                          Value      Std. Error           t value

(Intercept)  2.4019697636   0.06706820   35.81384087

Individual1        0.1596002198      0.08196882      1.94708459
Individual2        0.3518132796      0.05766398      6.10109214
Individual3        0.3473538657      0.02704503     12.84353597
Individual4        0.2389811068      0.01960808     12.18788696
Individual5        0.0389045036      0.03224466      1.20654091
Individual6       -0.2676108079      0.05088886     -5.25873031
Individual7        0.0008442472      0.01462043      0.05774435
Individual8       -0.0668258769      0.01540240     -4.33866684
 Substrate1        0.1239923542      0.09636856      1.28664739
 Substrate2        0.1799184137      0.04037519      4.45616289
 Substrate3        0.3309044018      0.02159167     15.32555853

(Dispersion Parameter for Poisson family taken to be 1)

    Null Deviance: 1178.96 on 44 degrees of freedom

Residual Deviance: 467.9995 on 33 degrees of freedom

Number of Fisher Scoring Iterations: 4
```

Travelling - Models fitted

```
> summary(trav.glm, corr=F)

Call:  glm(formula = Count ~ Individual + Substrate * Locomotion, family = poisson, data = travel1, link =
log)
Deviance Residuals:
          Min          1Q           Median          3Q         Max
    -3.297505    -1.01214   1.053671e-008   0.8135828    2.741542

Coefficients: (4 not defined because of singularities)
                              Value    Std. Error       t value
            (Intercept)   0.180660812  0.39850087    0.4533511
            Individual1   0.289171028  0.18072191    1.6000884
            Individual2   0.457406678  0.07422930    6.1620774
            Individual3   0.349403972  0.04032468    8.6647674
            Individual4   0.153430710  0.02950874    5.1995010
            Individual5  -0.091564783  0.03597408   -2.5452985
            Individual6  -0.006940796  0.02727848   -0.2544422
            Individual7   0.056308898  0.01938192    2.9052286
            Individual8  -0.063085830  0.03082235   -2.0467558
             Substrate1  -2.063326003  0.54046509   -3.8176860
             Substrate2   0.220430683  0.21686062    1.0164625
             Substrate3   0.688740934  0.08486723    8.1155108
             Substrate4   0.397732914  0.05259452    7.5622502
            Locomotion1  -0.886067906  0.51311631   -1.7268364
            Locomotion2   0.319736741  0.17370929    1.8406428
Substrate1Locomotion1     3.028941821  0.72554651    4.1747039
Substrate2Locomotion1    -4.247482957  1.12912723   -3.7617399
Substrate3Locomotion1     0.332702970  0.09141501    3.6394785
Substrate4Locomotion1              NA          NA           NA
Substrate1Locomotion2     1.026730471  0.24716576    4.1540159
Substrate2Locomotion2              NA          NA           NA
Substrate3Locomotion2              NA          NA           NA
Substrate4Locomotion2              NA          NA           NA

(Dispersion Parameter for Poisson family taken to be 1)

  Null Deviance: 410.4206 on 43 degrees of freedom

Residual Deviance: 74.09246 on 25 degrees of freedom

Number of Fisher Scoring Iterations: 4
```

```
> summary(trav.glm1, corr=F)

Call:    glm(formula = Count ~ Individual + Substrate + Locomotion, family = poisson, data = travel1, link =
log)
Deviance Residuals:
              Min            1Q          Median          3Q        Max
        -3.595199     -1.243748      -0.1275064    0.9901271   4.153725
Coefficients:
         Value       Std. Error         t value
  (Intercept)    1.34711081    0.13869035     9.7130821
  Individual1    0.12171596    0.18643408     0.6528633
  Individual2    0.55848752    0.07408151     7.5388249
  Individual3    0.35306445    0.04166273     8.4743466
  Individual4    0.16692458    0.02935105     5.6871756
  Individual5   -0.06152024    0.03569098    -1.7236917
  Individual6    0.02260064    0.02591364     0.8721522
  Individual7    0.06935868    0.01941665     3.5721247
  Individual8   -0.05589325    0.03084630    -1.8119923
   Substrate1    0.08781235    0.17818504     0.4928155
   Substrate2   -0.10690017    0.18128747    -0.5896721
   Substrate3    0.47569413    0.05898117     8.0651864
   Substrate4    0.30769533    0.03642959     8.4463018
  Locomotion1    0.45174779    0.14457383     3.1246858
  Locomotion2   -0.06534455    0.05031971    -1.2985876

(Dispersion Parameter for Poisson family taken to be 1)

    Null Deviance: 410.4206 on 43 degrees of freedom

Residual Deviance: 122.8979 on 29 degrees of freedom

Number of Fisher Scoring Iterations: 4
```