THESIS

ECOLOGY OF THE LEOPARDS (PANTHERA PARDUS LINN.)
IN HUAI KHA KHAENG WILDLIFE SANCTUARY

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GRADUATE SCHOOL, KASETSART UNIVERSITY
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THESIS

ECOLOGY OF THE LEOPARD (PANTHERA PARDUS LINN.) IN HUAI KHA KHAENG WILDLIFE SANCTUARY

SAKSIT SIMCHAROEN

A Thesis Submitted in Partial Fulfillment of
the Requirements for the Degree of
Doctor of Philosophy (Forestry)
Graduate School, Kasesart University
2008

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Saksit Simcharoen 2008: Ecology of The Leopard (*Panthera pardus* Linn.) in Huai Kha Khaeng Wildlife Sanctuary. Doctor of Philosophy (Forestry), Major Field: Forestry, Interdisciplinary Graduate Program. Thesis Advisor: Associate Professor Utis Kutintara, Ph.D. 114 pages.

The ecology of leopards was researched in Huai Kha Khaeng Wildlife Sanctuary, west-central Thailand from 1994 to 1999. Sixteen leopards were captured in order to weigh and measure body size and fit them with radio collars to study their ecology and behavior. Data indicated that adult male leopards were significantly longer ($t=4.799$, $DF=6.404$, $p=0.003$) and heavier ($t=5.316$, $DF=9$, $p<0.001$) than adult female leopards. Eleven leopards were collared comprising four males and seven females. Radio telemetry data showed that home range size differed among sexes. However, home range size was found to be similar among leopards of the same sex. The average minimum convex polygon annual home range sizes (95%) were 45.3±6.0 km^2, 22.3±5.1 km^2 and 26.9 km^2 for adult males, adult females and sub-adult males respectively. Seasonal home range size of leopards was not found to be significantly different. Home range overlap was found between sexes (54.2%) and among females (38.6%), but overlap was not found among males. The average daily distances traveled were 2.30 km, 1.67 km and 1.71 km for adult males, adult females and sub-adult females respectively. Adult male daily movement was significantly different from that of adult female ($p<0.001$) or sub-adult female ($p<0.001$). The density estimate from radio telemetry was 6.1±2.4 leopards/100 km^2. Using camera traps the density estimate from 1996 to 1999 based on capture-recapture statistical was 6.0 leopards/100 km^2 (range 9 to 29 leopards). Leopard densities decreased yearly over the study period from 7.9 to 5.2 and 4.9 leopards/100 km^2. A probable cause of density decrease was an increase in tiger density in the same area.

Leopards target a wide variety of prey including insects, reptiles and mammals. At least 22 species of mammals were found in leopard scats; the most common were ungulate (72.0%) and primate (16.3%). A comparison between tiger and leopard prey found that tiger selected larger mammals than leopard. Habitat selection varied to some degree between second and third order analysis. In general, leopards tended to select mixed deciduous forest types, low to medium slope types and areas close to stream channels. These results will help prioritize areas in Thailand for future leopard conservation efforts.

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INTRODUCTION

Leopards *(Panthera pardus)* are an important predator in tropical Asian and African ecosystem, playing a key role in food web dynamics by regulating prey population size and prey behavior, thus indirectly affecting the health of the whole ecosystem.

The leopard is a solitary animal except for mating periods and in the case of females raising dependent offspring. Because of its elusive, nocturnal nature coupled with its considerable attacking capabilities, it is often considered a fearsome and dangerous animal. In fact, the leopard is like other animals that fight for survival in the wild, and the role of the leopard, like other top carnivores, has been shaped by natural processes and millions of years of evolution.

The leopard distribution is the widest of any of the large cats and occupies a variety of habitats, from rainforests to mountains (Kitchener, 1991; Nowell and Jackson, 1996). It is more ecologically tolerant than other large cats and has great adaptability throughout its range (Nowell and Jackson, 1996). However, leopards are endangered, with populations showing marked declines due to habitat loss, depletion of prey and direct hunting. It has been listed as the Protected species by WARPA B.E. 2535 and is also listed on Appendix I of the Convention of International Trade of Endangered Species of Wild Fauna and Flora (CITES) since 1983.

The majority of past leopard research has taken place in sub-Saharan Africa, India, Sri Lanka, and Nepal. In Southeast Asia, there has been little research concerning leopard abundance, behavior and ecology.

Detailed knowledge of leopard diet, prey abundance, home range characteristics, and their relationship to environment factors have not been well studied in Southeast Asia. Information on these aspects of leopard ecology are needed for its management and conservation in the wild. In addition, estimating the abundance and density of leopards will help us to understand their present status in the study area.

OBJECTIVES

1. Evaluate home range size, site fidelity, conspesific overlap and movement patterns

2. Investigate habitat selection to identify resources important for leopard survival and reproduction

3. Estimate leopard abundance and density

4. Investigate prey selection from leopard’s fecal analysis

5. Assess prey composition and abundance

LITERATURE REVIEW

1. Taxonomy and evolution

Leopards (*Panthera pardus*) are one of 271 extant species of carnivore. The felidae family, of which leopards are a member, is thought to have branched off from the other carnivore families 35-40 million years ago (Beninder-Emonds *et al.,* 1999; Mattern and Mclennan, 2000). Leopards are grouped into the *Panthera* genus, which diverged from a common ancestor 2-3 million years ago (Johnson and O'Brien, 1997), and places them with the other big cats that are capable of roaring. Yu and Zhang (2005), studying pantherine mitochondrial and nuclear DNA, concluded that, of the 5 members of the pantherine group, leopards were the last to diverge and were closely related with snow leopards (*Panthera unica*).

The earliest fossils of leopards, dated at 3.5 Ma years ago, were found in Tanzania (Turner and Anton, 1997). The oldest in Asia, reported as 2 Ma years old were discovered in Indian Siwalik Hills (now in Pakistan) (Hemmer, 1976).

This supports other molecular evidence suggests modern leopard lineages probably originated in Africa about 470,000–825,000 years ago, after which they radiated into and across Asia 170,000–300,000 years ago (Uphyrkina *et al.*, 2001). The best estimates, constructed from molecular analysis, suggest the existence of a minimum of 9 recognized sub-species (Uphyrkina *et al.*, 2001); one African, *Panthera pardus, pardus*, and eight Asian subspecies, *P. p. saxicolor*, *P.p.nimr, P. p. fusca*, *P. p. kotiya*, *P. p. melas*, *P. p. delacouri*, *P. p. japonensis*, and *P. p. orientalis*.

Uphyrikina et al. (2001) found that leopards have comparable genetic diversity compared to lions, cheetahs (Driscoll, 1998), jaguars (Eizirik *et al.*, 2001), and pumas (Culver *et al.*, 2000). There is significant genetic variation for leopards across their geographic range (Uphyrina *et al.*, 2001). The highest level of genetic variation was found in the African specimens, and the lowest in the Southeast Asian specimens (*P. p. orientalis*; Uphyrina *et al.*, 2001).

2. Range

The leopard (*Panthera pardus)* has the widest range of any wild cat in the old world (Lekagul and McNeely, 1977). It lives in a diverse array of terrestrial habitats, from rain forest to desert and from sea level up to more than 5,500 m (Kitchener, 1991).

Leopards are found across most of sub-Saharan Africa. The countries with high numbers (est. > 10,000) of leopard are in central and eastern Africa and the countries with estimated 1,000-10,000 are in the part of Eastern, Western and Southern Africa (Martin and Meulenaer, 1988; Nowell and Jackson, 1996). In north Africa, leopards occur in small populations in Algeria and Morocco (Nowell and Jackson, 1996).

In the Middle East, leopards are found in Iran, confined to Montane Areas. Small populations of leopard are found in Egypt, Israel, Oman, Saudi Arabia, Yemen (Nowell and Jackson, 1996). Harrison and Bates (1991) believe that the leopards are absent from the true desert of the central Arabian peninsula.

Leopards are found in most of tropical Asia, throughout the Indian sub-continent, southeastern China and mainland Southeast Asia (Nowell and Jackson, 1996) (Figure 1).

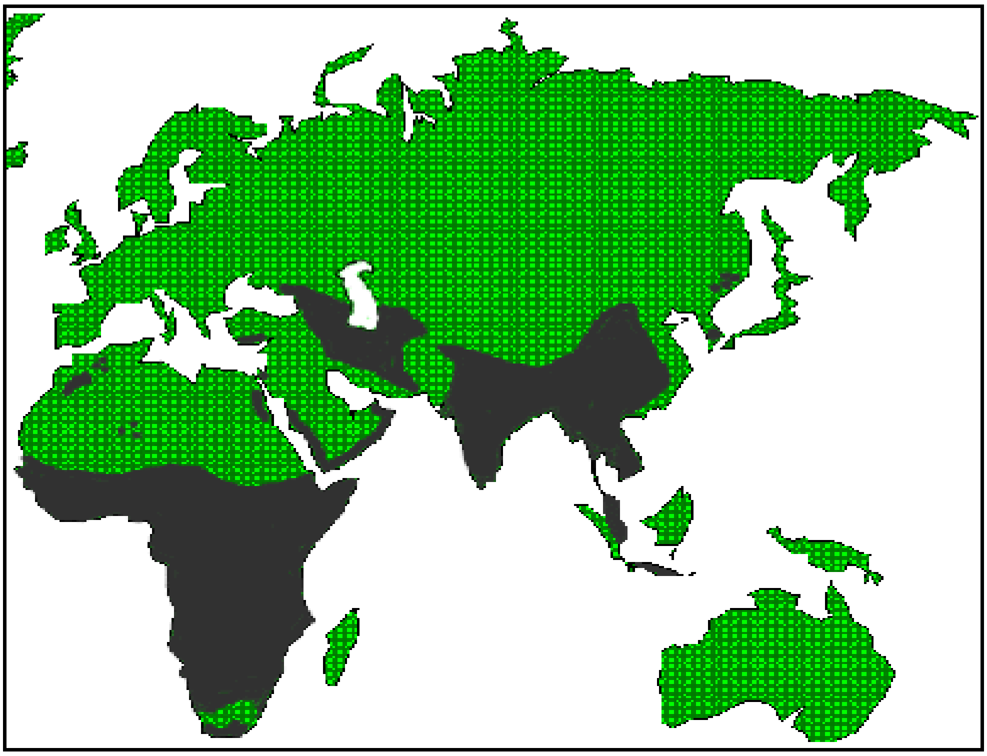


Figure 1 Map of distribution of leopard *(Panthera pardus).*
Source: Nowell and Jackson (1996)

3. Pelage

The leopard is the third largest of the great cats. It is dimorphic in pelage color, occurring in the wild as either spotted or black (melanistic; Kitchener, 1991). The common pattern is a golden yellow base color that is covered with a scattering of black spots arranged in rosettes. On the legs and head, these rosettes become single spots. The ears are black with a central white spot (Kitchener, 1991). Both color and rosette pattern vary considerably within and between populations (Prater, 1971; Kitchener, 1991; Nowell and Jackson, 1996). Coat pattern varies across the leopard's range in relation to climate and habitat type (Kitchener, 1991; Nowell and Jackson, 1996; Uphyrkina *et al.*, 2001).

In Africa, Pocock (1932) observed leopard pelage as rufous to ochraceous in savannah leopards, pale cream to yellow-brown in desert leopards with more gray from cooler regions, dark deep gold in rain forest leopards and darker in high mountain leopards. Leopard's coloration makes it well camouflaged in its natural environment, increasing its stalking and escaping abilities (Jackson, 1996).

A black phase is caused by an autosomal recessive gene and is a condition more frequently seen in tropical Asia, especially in Java, Malay peninsula, Burma and Thailand (Robinson, 1970; Lekagul and McNeely, 1977; Kitchener, 1991; Daniel, 1996). Rosettes are present in the black form and can be seen in strong light or when old black leopard coats start to fade.

4. Morphology

Average size and other morphological characteristics vary across the leopard's range (Prater, 1971; Kitchener, 1991; Nowell and Jackson, 1996). Variation in size can be compared using either weight or body length.

There is substantial sexual dimorphism in leopards and adult male leopards weigh approximately 30-60% more than females (Ilani, 1981; Stuart, 1981; Bailey, 1993; Grassman, 1997; Odden and Wegge, 2005). In Kruger National Park, South Africa, mean weights for adult male and female leopards were 58.2 kg (n=3) and 37.5 kg (n=5), respectively (Bailey, 1993). The same study found notable variation in the size of females within a single breeding population; females from the Nwaswitshaka River 5 km upstream from Skukuza were smaller than those from Kenya and Zambia. Bailey (1993) concluded that females in the Nwaswitshaka area might have been smaller because of subsistence on smaller prey, but was unclear whether this is a genetic or nutritional response.

Figure 2 Spotted and black leopard *(Panthera pardus)* in HKK.

Male leopards from the coastal mountains of South Africa's Cape Province averaged only 30.9 kg (n=27) and 21.2 kg (n=9) in females (Stuart, 1981). Norton (1984) suggested that similarly, leopards were smaller due to selection for feeding on the relatively much smaller prey that occurs in these mountains.

Some of the largest leopard specimens recorded were found in the mountains of Iran and Central Asia, where males weighed up to 90 kg (Harrington, 1977). In contrast, leopards from the Arabian Peninsula are notably smaller than average (Harrison and Bate, 1991). In the Judean Desert, Ilani (1981) recorded an adult male leopard that weighed only 29.5 kg and two adult females averaged 22.8 kg.

In Nepal, Odden and Wegge (2005) reported average weight of two males as 51 kg and a female as 36 kg. In Sri Lanka the average weight of males was 56 kg and the average for females was 29 kg (Pocock, 1939). In Kaeng Krachan National Park Thailand, a prime adult male weighed 40 kg and a prime adult female weighed 25 kg (Grassman, 1997). In Huai Kha Khaeng Wildlife Sanctuary Thailand, two male leopards weighed 60 and 70 kg and a female leopard weighed 21 kg (Rabinowitz, 1989).

In Kruger National Park, South Africa, average body length was 131.7 cm (n=3) for adult males and 122 cm (n=5) for adult females; tail length was 79.8 and 76.4, respectively (Bailey, 1993). Stuart (1981) reported average body and tail lengths of 110.7 cm and 67.8 (n=21), respectively, for adult males and 103 cm and 67.7 cm (n=8), respectively, for adult females.

In the Judean Desert, Israel, an old adult male was 117 and 82 cm in body and tail length, respectively. Average body and tail lengths of two adult females were 103 and 77.2 cm, repectively (Ilani, 1981). In Nepal, Odden and Wegge (2005) reported male average body and tail length of 124 cm and 89 cm, repectively, and female average body and tail lengths of 96 and 84 cm, respectively.

Body measurements of Thai leopards were reported to range from 108-130 cm body length with a tail length of 80-100 cm (Lekagul and McNeely, 1977). Rabinowitz (1989) reported average male body length and tail lengths of 125 and 77.5 cm (n=2) repectively and female body and tail length of 109 and 74 cm (n=1), respectively. In Kaeng Krachan NP, average males were 132 and 79 cm for body length and tail length and females, 106 and 75 cm (Grassman, 1997) (Table 1).

Table 1 Weight and sizes of leopards in other studies

Study area	Age class	Sex	N	Weight (kg)	Body length (cm)	Tail (cm)	Total length (cm)	Hind foot (cm)	Ear (cm)
Kruger NP, South Africa (Bailey, 1993)	Old adult	M	5	63.1	141.3	78.1	219.4	27.2	8.5
	Old adult	F	6	37.2	121.9	78.2	200.1	24.7	7.7
	Prime adult	M	3	58.2	131.7	79.8	211.5	27.3	8.5
	Prime adult	F	5	37.5	122	76.4	198.4	23.8	7.7
	Sub-adult	M	6	50.9	130.8	77.4	208.2	26.8	8.2
	Sub-adult	F	3	30.1	119.3	73.4	192.7	23.3	7.8
	Large cub	F	2	18.6	106	49.5	155.5	21.5	7.4
Cape province, South Africa (Stuart, 1981)	Adult	M	20-27	30.9	110.7	67.8	178.5	21.9	7.3
	Adult	F	7-9	21.2	103	67.7	170.7	20.6	7
	Sub-adult	M	2	12.45	90	57	147	19.5	7.3
	Sub-adult	F	2	16.25	total 171			-	-
Iran and Central Asia (Harrington, 1977)	Adult	M		90	-	-		-	-
Israel (Ilani, 1981)	Old adult	M	1	29.5	117	82	199	-	7.1
	Adult	F	2	22.75	103	77.2	180.2	-	6.15
Sri Lanka (Phillips, 1935; Pocock, 1939)	-	M	-	29.5	-	-	-	-	-
	-	F	-	22.8	-	-	-	-	-
Bardia Np, Nepal (Odden and Wegge, 2005)	-	M	2	51	124	89	213	-	-
	-	F	1	36	96	84	180	-	-
Thailand (Lekagul and McNeely, 1977)	-	-	-	45-65	108-130	80-100		22-24	6.5-7.5
Huai Kha Khaeng WS,	-	M	2	62.5	125	77.5	202.5	-	-
Thailand (Rabinowitz, 1989)	-	F	1	21	109	74	183	-	-
Kaeng Krachan NP,	young adult	M	1	37	112	76	188	23	7.2
Thailand (Grassman, 1997)	Prime adult	M	1	40	132	79	211	24	5.5
	Prime adult	F	1	25	106	75	181	21	6

5. Behavior

Leopards are solitary, secretive and usually nocturnal. They spend most of their life alone and the main social bond is between females and their offspring. Males and females also associate for a short period during courtship. Leopards appear to be more solitary than other large felids (Schaller, 1972; Sunquist, 1983; Bailey, 1993; Mizutani and Jewell; 1998). They are most active between sunset and sunrise and use keen hearing and vision to hunt their prey (Hamilton, 1976; Bailey, 1993). In Wilpattu National Park, Sri Lanka, where leopards are the only large felid, they are less nocturnal than leopards studied elsewhere (Muckenhirn and Eisenberg, 1973).

Leopards are bold animals that have been known to return to a kill in spite of being shot at and missed. In addition, they are usually cautious and circumspect (Daniel, 1996). They communicate with one another using scent marking and vocalizations. Scent marking includes urine spraying, scrape marking, and tree raking. Urine spraying is primarily done by adult leopards. They spray urine on prominent tree trunks, reeds and rocks. Scrape marking consists of raking earth, dry leaves or gravel with hind feet to form a shadow trapezoidal or triangular-shaped depression. Scrape marks are the best indicator of the present of leopards and are generally found in their core home range, near water sources and along their trails. Tree raking is performed by the animal standing on its hind legs and etching claw marks into the trunks of large tress (Ilani, 1981). Eisenberg and Lockhart (1972) reported acoustic communication in Ceylon leopards, where they emitted loud, brief calls when approaching another leopard's territory.

6. Ecological niche

Leopards are able to coexist with other large felids by reducing spatial and food competition, using habitats not favored by the larger felids, eating different-size prey, and having different diel activity patterns (Seidensticker, 1976; Bertram, 1982).

Leopards are adaptable large carnivores that can survive in a wide variety of habitat types. Their flexibility is due, in part, to their eclectic choice of prey items; sustenance on medium to large ungulates is supplemented by small prey items such as primates, rodents, reptiles and birds (Ilani, 1981; Odden and Wegge, 2005). Some of their prey items are also selected for by larger and smaller carnivores using the same habitat, such as tigers, clouded leopard and wild dog.

Studying leopard diet helps biologists and managers understand which preys are needed for their long term population viability. Furthermore, it provides insight into how the presence of leopards affects an ecosystem.

Studies in Africa have found that leopards tend to select prey items in the 3-70 kg range (Bailey, 1993; Cavallo, 1993; Norton *et al.*, 1986; Hayward *et al.*, 2006). In

Asia, work has been focused on the Indian Sub-continent (Seidensticker, 1976; Seidensticker *et al.*, 1990; Karanth and Sunquist, 1995; Santiapillai and Romono, 1992). In Thailand there have been only a few studies on the ecology and diet of leopard (Rabinowitz, 1989; Grassman, 1997).

Investigation of prey selection normally takes one of two forms, using information gathered by the remains of kills or examining scat contents. Cataloging kill remains is probably the more informative of the two methods since it provides information on the size, sex and age class of the prey. Smaller kills are less likely to be discovered by researcher than larger kills, which imposes a bias toward larger prey being recorded. Scat analysis can record prey of any size, however, and scats are much more frequently encountered than kills. There are, nevertheless, problems with scat analysis that must be accounted for: (a) distinguishing scats from target species and non-target species, (b) correct identification of scat contents, and (c) contribution of one prey item to multiple scats.

There may also be variation in prey selection due to (1) changes in availability due to seasonal environmental fluctuations and (2) individual heterogeneity of metabolic requirements (e.g., females with dependant offspring require more and larger prey than a female without young.).

Leopards have a diverse diet but generally hunt locally abundant medium-sized ungulate species in the 20-80 kg range (Seidensticker, 1991; Bailey, 1993; Hayward *et al.*, 2006). Leopard prey selection probably varies with prey density and availability as well as the individual leopard preference (Bailey, 1993).

In Lope National Park, Central Africa, leopards preyed on ungulates (58.6%), diurnal primates (17.7%), large rodents (17.1%), carnivores (4.1%) and pangolins (0.3%) (Henschel *et al.*, 2005). In Kruger National Park, South Africa, Bailey (1993) found that ungulates composed 94% of 55 kills and occurred in 64% of feces. The weight of preferred prey is 25-30 kg (Bailey, 1993; Hayward *et al.*, 2006), which slightly less than leopard weight (Bailey, 1993). Adult male leopards consumed about 3.5 kg per day and female about 2.8 kg per day (Bailey, 1993).

In the East Africa, leopards most frequently killed Thomson's gazelle, which is abundant in this savanna region (Kruuk and Turner, 1967). In protected areas in east Africa, impala is also an important prey species (Hamilton, 1976; Bailey, 1993). In Zambia, leopards frequently killed reedbuck, puku and waterbuck (Mitchell *et al.*, 1965). In Matopos NP, Zimbabwe, hyraxes, cane rats, springhares and hares were important prey (Grobler and Wilson, 1972). In the Judean Desert of the Middle East important prey animals were hyrax (*Procavia capensis*) and ibex (*Capra ibex nubiana*; Ilani, 1981).

The leopards of tropical Asia have a varied diet but show preference for small to medium size ungulates (Nowell and Jackson, 1996). In India, Karanth and Sunquist (1995) found that 76.5% of the leopard's diet was composed of ungulates; chital deer (*Axis axis*) was the most prevalent (43.7%). In Sri Lanka, 60% of leopard diet consisted of chital and wild pig (*Sus scrofa*) (Muckenhirn and Eisenberg, 1973). In Thailand, 43% of the leopard's diet is barking deer (*Muntiacus munjak*) (Rabinowitz, 1989).

Despite specializing on ungulates, leopards are known to feed opportunistically on a great variety of species, such as birds, lizards and rodents. Rabinowitz (1989) found that primate remains in 12% of leopard scats in Thailand's HKKWS. The high percentage of primate in the leopard's diet in HKK may be because of the open canopy, which forces primates to travel on the ground. Small mammals, such as rodents and hares, are also important leopard prey, particularly in areas where small mammals are abundant (Bailey, 1993; Eisenberg and Lockhart, 1972).

In the areas that leopard coexists with other large felids, they segragate by vegetation type, activity period and prey size. Leopard preyed on a wider range of prey species than other cat species and in some places leopards cache large kills in trees (Seidensticker, 1976; Bertram, 1982; Bailey, 1993). But in Sri Lanka, where the leopard is the biggest cat, it hunts and kills a much higher proportion of large prey species (Muckenhirn and Eisenberg, 1973). Leopards are noted for their versatility and they are more tolerant than the tiger of arid environments (Satiapillai and Romono, 1992; Nowell and Jackson, 1996).

Primates are a major part of leopard prey in parts of their range. In the Seronera Valley, Serengeti National Park, Tanzania, leopards attack and kill olive baboon *(Papio anubis)* in trees at night (Cavallo, 1993) but are frequently attacked by baboons during the day (Cavallo and Blumenschine, 1989; Cavallo, 1990). In Java, leopards preyed on long-tailed macaque *(Macaca jascilaris)*, silver leaf-monkey *(Presbytis cristata)*, crab-eating macaque *(Macaca fascicularis)* and Javan gibbon *(Hylobates moloch)* (Seidensticker and Syuono, 1980; Santiapillai and Romono, 1992). In Thailand, leopard have been documented preying on Rhesus macaque *(Macaca mulatta)*, White-handed gibbon *(Hylobates lar)* and Phayre's Langur *(Presbytis phayrei)* (Bhumpakpan, 1988).

7. Reproduction and survival

Leopards are capable of breeding anytime of the year, but peak mating takes place during the dry season, so that cubs are born at the onset of the rainy season (Bailey, 1993). Den sites were located in dense, tall grass cover (Sunquist, 1983). Female leopards are polyestrous. The range of estrous intervals is 20 to 50 days and the average duration of estrous is 6.7 days. Cubs are born after a gestation period of

90-105 days (Crandall, 1964; Sadleir, 1966; Bailey, 1993). In the wild there are 1-4 cubs in a litter (Robinson, 1970; Schaller, 1972; Seidensticker *et al.*, 1990; Bailey, 1993). Seidensticker *et al.* (1990) reported mean size for litters at 1/3 of adult size was 2.3 (n=3) and at 1/2-2/3 of adult size was 1.3 (n=6). Le Roux and Skinner (1989) observed five litters that averaged 2.2 cubs/ litter. During the first 2-3 months, the mother will hunt alone while her cubs remain in the protected places (Seidensticker, 1977). Bailey (1993) found that when the young leopards are 6 months old, they follow their mother to kills. The cubs live with their mother for at least 12 months (Eisenberg and Lockhart, 1972), and as long as 20 months (Schaller, 1972). Shaller (1972) observed a 13-month-old female cub independent of its mother and a male cub that remained with its mother until 20 months old. Young leopards are usually independent of their mother by 13-18 months of age (Schaller, 1972; Eisenberg and Lockhart, 1972; Hamilton, 1976).

Sunquist (1983) found 13-month-old leopards still residing in their natal area. But their movements infrequent together with their siblings were confirmd to a small area (1.5-2.0 km^2) and their rest sites were separated by 0.8 km. A month later, they expanded their range to 8 km^2 but still remained within their natal area. Two males left their natal home range at 15-16 months old and another left his natal home range at 18 months old. A female leopard may allow her cubs to stay in her home range if resources are adequate for survival (Mizutani and Jewell, 1998). Ilani (1981) reported a female leopard that hunted for her 2-year-old daughter until she became pregnant again.

Male cubs almost always disperse from their natal home range but female cubs may remain within their natal home range (Bailey, 1993). Furthermore, male cubs disperse farther than female cubs and establish territories in poorer quality habitat (Smith, 1993).

Bailey (1993) found that young dispersing animals and old leopards have higher mortality (43% and 43% percent per year, respectively) than adults (7%) and large cubs (7%). Bailey posited that a lack hunting experience among dispersing juveniles and poor physical condition among old animals resulted in their higher mortality. An estimated 64% of leopard mortality is caused by starvation and 36% from other causes, including poisoning, poaching for skins, retaliation for livestock depredation, and habitat loss (Myers, 1976; Bailey, 1993; Nowell and Jackson, 1996; Marker and Dickman, 2005). Causes of death are different between sexes; female leopards die from starvation more frequently than males. Annual mortality rates were 18% for adults, 32% for sub-adults and 50% for cubs. Mortality rate of adult males is higher (25%) than adult females (13.5%) and old adults higher (23%) than prime adults (13%). Sub-adult females had higher mortality rate (40%) than sub-adult males (25%; Bailey 1993).

8. Conservation status

The leopard (*Panthera pardus*) is a widespread but endangered large felid. Habitat destruction, poaching and prey depletion have created an often discontinuous patchwork of leopard populations throughout Asia, Sub-Saharan Africa, and the Middle East (Bailey 1993; Uphyrkina *et al.* 2001). Their general persecution has lead to the species being listed on Appendix 1 of the Convention of International Trade of Endangered Species of Wild Fauna and Flora (CITES). North China leopard (*P. p. japonensis*), Sri Lanka leopard (*P. p. kotiya*), Java leopard (*P. p. melas*) and Persian leopard (*P. p. saxicolor*) are listed as *Endangered* by the International Union for the Conservation of Nature and Natural Resources (IUCN). Arabian leopard *(P. p. nimr)*, Amur leopard *(P. p. orientalis)*, Barbary leopard *(P. p. panthera)* and Anatolian leopard *(P. p. tulliana)* are considered *Critically Endangered*. Indian leopard *(P. p. fusca)* and African leopard *(P. p. pardus)* are considered *Least Concern* (The International Union for the Conservation of Nature and Natural Resources [IUCN], 2006).

In Thailand, leopards are protected under teh *Conservation and protection of Wildlife Act B.E. 2535*; poaching, commercial trade and possesion (including the carcass) are illegal (Ratchakitchanubeksa, 1992).

In the Middle East, Arabian leopards are under threat from trade in Yemen (Environment and Protected Areas Authority [EPAA], 2003). In Israel, a small population of leopards may be one of the last on the Peninsula (Spalton *et al.*, 2006) and has declined because of a lack of suitable habitat, limited prey availability, low breeding success, accidents, and management errors (Ilani, 1990; Timna, 2000).

In Asia, illegal hunting for pelts and bones (used in Asian traditional medicine) and prey depletion are major threats to leopards (Santiapillai and Romono, 1992). Furthermore, leopards are persecuted when they prey on domestic livestock (Nowell and Jackson, 1996). Small populations, such as the Amur leopard population, are additionally prone to inbreeding depression (Uphyrkina and O'Brien, 2003).

In Thailand, reduction of prey and poaching remain threats to leopard with habitat loss probably the most serious long-term problem (Grassman, 1999).

9. Home range

A home range must be sufficient to meet energy requirements for the animal in question together with any dependent offspring (Gittleman and Harvey, 1982). In some cases, the home range will be restricted in size, either by the distribution of resources or the need to defend those resources from conspecifics (Buskirk, 2004).

The home range size reflects social organization and mating systems, in some cases also indicating habitat quality (Smith *et al.*, 1987).

There are a multitude of definitions of the home range. Burt (1943) defined home range as the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. According to Burt (1943), occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range. Similarly, Harris *et al.* (1990) defined a home range as a restricted area where an animal moves during its normal activities. More recently researchers have used probabilistic approaches refered to as utilization distributions (Kernohan *et al.* 2001).

The earliest home range calculation, the minimum convex polygon (MCP), was developed by Mohr (1947) and is the most commonly used estimator found in the literature, in part due to its early development and its simplicity of application. It is constructed by drawing a polygon connecting the outermost locations observed for an animal. As the sample size of animal observations increases, so too does the estimated MCP. The MCP calculation, therefore, underestimates home range size when sample size is small (e.g., when $n<50$). Furthermore, by connecting extreme or outlying locations, MCP can incorporate areas clearly never utilized by the animal (Worton, 1989; Burgman *et al.*, 1993).

To overcome this weakness several probalistic approaches were developed. The first of these was the bivariate normal estimator, which is less dependent on sample size than the MCP (Jennrich and Turner, 1969). This parametric analysis assumes an underlying bivariate distribution of locations. It is biased in that locations closer to the center of the range are weighted more than those further away. Graphically, this estimator creates an ellipse around a calculated center of the range. This ellipse and center construction is often an unrealistic representation of an animal's use of space, so the bivariate normal technique is infrequently used.

An alternative, non-parametric approach was suggested by Van Winkle (1975) that estimates a utilization distribution based on the probability that an animal is located in each cell of a grid. The harmonic mean estimator (HME; Dixon and Chapman, 1980) was one of the first of these probabilistic, non-parametric techniques. It estimates the probability of an animal being encountered at each intersection of a grid. Intersections of equal probability are then joined to create isopleth contours. One advantage of this method is that it allows inferences of more than one center of activity. Problems with this method include sensitivity to grid size choice (Worton, 1989) and possible issues when observed locations are at similar distances apart. Furthermore, home ranges tend to be both overestimated for large sample sizes and underestimated for small sample sizes.

Another grid based estimator that is becoming more popular in the literature, is the kernel-based method, which has two versions: the adaptive kernel (AK) and fixed kernel (FK; Worton, 1989; Silverman, 1986). In the Kernal method, a grid is superimposed onto the location data. Each animal point is covered with a three defined, taking into account estimated error. Adaptive and fixed kernels differ in that adaptive kernels allow the smoothing factor to vary over the entire surface, so that low density areas receive more smoothing. As the value of the smoothing factor increases, so to does the influence of distant locations to each grid intersect density estimate (Seaman and Powell, 1996). A robust means of selecting optimal band width is Least Squares Cross Validation (LSCV), which selects the smoothing factor that minimizes error (Seaman and Powell, 1996). Unlike the harmonic mean, kernel home ranges are not sensitive to grid size or placement. Furthermore, kernels are least effected by sample size and variance can be calculated by bootstrapping (Silverman, 1986).

For all methods it is possible to investigate the affect of sample size using area curves. As sample size increases, so will the area, until at some point, the gain in area is negligible (where the curve reaches the asymptote). At this point there can be reasonable confidence that the full extent of the home range has been properly estimated.

Each method has strengths, weaknesses and inherent assumptions. Selection of the appropriate method may include consideration of (a) sample size, (b) independence of serial locations, (c) previous application, (d) comparability to other studies and (e) general underlying theoretical framework.

10. Teritorial behavior and spatial dynamics

Territoriality is an important behavioral trait which affects the spatial organization of population (Mizutani and Jewell, 1998). Noble (1939) defined a territory as any defended area. Davies (1978) defined territoriality as occurring when animals were spaced further apart than would be expected from a random occupation of suitable habitats. Brown and Orians (1970) defined territory as ‘a fixed, exclusive area with the presence of defense that keeps out rivals’ and proposed three criteria for this designation: little overlap between home ranges, scent marking behavior and antagonistic interactions.

Among carnivores, the defended resource for females is an area that provides food and a secure place to raise young and for males it is access to estrous females. This results in a polygamous mating system with smaller female territories overlapped by larger male territories.

Bailey (1993) found evidence for a polygamous mating system and for territoriality among resident male leopards. Leopards at Kruger National Park, South Africa showed little overlap between adjacent home ranges and exhibited scent marking and vocalizing behavior.

Leopards call, scent mark and make conspicuous movements through their home range to establish their territories and reduce the chance of aggressive encounters (Muckenhirn and Eisenberg, 1973; Bailey, 1993). Most scent marks are deposited along frequently used trails and conspicuous places such as trail intersections, edges of bridges, and along dry stream beds.

Size of leopard home ranges are highly variable depending up on age, sex, reproductive status, habitat quality, and prey distribution and density (Bertram, 1982; Rabinowitz, 1989; Bailey, 1993; Grassman, 1997; Mizutani and Jewell, 1998). Prey density is main factor driving home range size among female leopards, particularly during cub-rearing (Cavallo, 1993).

In Africa the home ranges of adult males are much larger (16.4-96.1 km^2) than adult females home ranges (5.6-29.9 km^2). Home ranges of adult females were established in higher quality habitat than those of adult males because females required sufficient prey and denning sites for their kittens (Bailey, 1993). When females live in low quality habitat, they frequently have larger home ranges (Mizutani and Jewell, 1998).

The largest known home ranges (1,137.0 km^2) of male leopards occur in the Kalahari Desert (Bothma *et al.*, 1997), which is approximately 6 times larger than the home range of leopards in Kruger National Park (36.4 km^2) and Tsavo National Park (36.3 km^2) (Bailey, 1993; Hamilton, 1976). Schaller (1972) suggested that the large ranges of leopards are probably linked to food scarcity in the Kalahari. Mizutani and Jewell (1998) posit that if prey availibility is seasonally or inter-annually variable, leopard home ranges must be large enough to meet their energy requirements when prey availability is lowest.

In Huai Kha Khaeng Wildlife Sanctuary and Kaeng Krachan National Park, Thailand, male home range size was 17-37 km^2 and female home range size was 9-37 km^2 (Rabinowitz, 1989; Grassman 1997). In Nepal, female home range size was 13-16.9 km^2 (Seidensticker, 1976; Odden and Wegge, 2005) and male home range size was 16.9 km^2 (Odden and Wegge, 2005).

Home range overlapping depends on many factors such as sex, age, habitat quality, season and relationship between sympatric individuals. Intra-sexually, leopard home ranges usually overlap only slightly. Near the Nwaswitshaka River, Krugar National Park, South Africa, however, Bailey (1993) reported that in areas with a surplus of food male and female leopard home ranges had 19% and 18% overlap, respectively. Mizutani and Jewell (1998) observed four males using the same area, which had a surplus of food for most of the year.

Inter-sexual home range has been documented across the leopard's range (Le Roux and Skinner, 1989; Bailey, 1993; Stander *et al.*, 1997; Mizutani and Jewell, 1998; Grassman, 1999) (Table 2). A male's territory typically overlaps >2 female ranges, which results in a polygamous mating system (Kitchener, 1991; Mitzutani and Jewell, 1998).

Sandell (1989) observed mother and daughter home ranges that overlapped in an area of concentrated resources. In Kruger National Park, South Africa, sub-adult male leopard home ranges temporarily overlapped with adult males prior to their dispersal and establishment of separate home ranges (Bailey, 1993). In Kaeng Krachan National Park, Thailand, Grassman (1997) found more than 40% home range overlap between 2 males and between a male and female. These individuals, however, were never observed within within 1 km of each other (Grassman, 1997).

Table 2 Home range overlap of leopards in other studies

Study area	**Home range site**			**Source**
	F-F	**M-F**	**M-M**	
Huai Kha Kheang WS,Thailand		overlap	Overlap	Rabinowitz (1989)
Kaeng Krachan NP., Thailand		overlap	Overlap	Grassman (1999)
Royal Chitawan NP,Nepal		overlap		Seiensticker (1976)
Bardia NP, Nepal		overlap	Overlap	Odden & Wegge (2005)
Londolozi Game Reserve,South Africa		overlap		Le Roux & Skinner (1989)
Kruger NP,South Africa	overlap	overlap	Overlap	Bailey (1993)
North-eastern Namibia	overlap	overlap	Overlap	Stander *et al.* (1997)
Lolldaiga Hills ranch, Kenya	overlap	overlap	Overlap	Mizutani & Jewell (1998)
Taï NP, Ivory Coast	overlap	overlap		Jenny (1996)
Cape Province,South Africa			Overlap	Norton & Henley (1987)

11. Movement

The movement of animals provides information about their home range use, how individuals respond to each other, and patterns of patrolling territorial boundaries and hunting. Movements of leopards are influenced by sex, age, physical condition, reproductive status and prey abundance (Bailey, 1993).

Adult males traveled greater distances than adult females. Bailey (1993) reported the average daily movement of adult males as 2.8 km and adult female movement as 1.5 km. Males took several days to completely circumnavigate their territory but females, because of their with smaller home ranges, averaged only 2 days (Mizutani and Jewell, 1998). Females moved the minimum distances required to obtain prey and rear their young, while the males moved greater distances in order to defend larger territories from conspecific males and maximize their reproductive success (Mizutani and Jewell, 1998).

In the Kalahari Desert, adult male leopards traveled an average of 14.4 km per day and females with cubs averaged 13.4 km per day (Bothma and Le Riche, 1986). In contrast, a female with cubs in the Nossob river valley moved only an average of 3.8 km per day (Bothma and Le Riche, 1986). The Kalahari leopards moved longer distances than those in the Nossob River valley because of the lower prey density in desert versus riverine habitats (Bothma and Le Riche, 1984). Bailey (1993) also observed that leopard daily movement is related to prey abundance.

Age also influences the daily movements of leopards. Bailey (1993) reported an average daily movement of 2.8 km for adult males, 1.6 km for sub-adult males, 1.5 km for adult females, and 1.1 km for sub-adult females. Additionally, average daily movement of leopards in good physical condition was 2.6 times that of individuals in poor physical condition (Bailey, 1993).

Leopards increased their daily movement in breeding period. Maximum daily distance of male leopards in Namibia was greater during breeding period (33 km) than during the nonbreeding period (27.3 km; Bothma and Le Riche, 1984). Hamilton (1976) reported that female leopards increased their movements during estrous cycle. During breeding periods, average daily distance of leopards increased from 2.7 to 3.0 km for males and from 1.8 to 2.5 km for females (Bailey, 1993). Females with cubs traveled less(1.2 km/day) than females without cubs (1.9 km/day). Similarly, females traveled more before partrition (1.4 km/day) than after (1.1 km/day) (Bailey, 1993).

In Huai Kha Khaeng Wildlife Sanctuary, Thailand, the average daily movement of a radio-collared adult male leopard was 2.0 km (n=1) (Rabinowitz, 1989) and 1.6 and 2.8 km for two adult male and 1.8 km for an adult female in Kaeng Krachan National Park (Grassman, 1997).

12. Abundance

Capture-recapture is a common approach to investigating abundance of marked animals; capture histories of animals can be used to determine the number of undetected animals present. Different statistical models can be applied to estimate population sizes for open and closed populations. In a closed population, there is assumed to be no births, deaths, immigration, or emigration during the time of the survey.

Because of Leopards' nocturnal and elusive behavior, camera trapping is used to generate capture histories, which can be analyzed in capture-recapture software such as CAPTURE (Otis *et al.*, 1978; White *et al.*, 1982) and MARK (White and Burnham, 1999). This approach has already been used to estimate leopard abundace in Namibia (Stander *et al.*, 1997), Armenia (Khorozyan, 2003), Ivory Coast (Jenny, 1996), Oman (Spalton *et al.*, 2006), Russia (Kostyria *et al.*, 2003) and has also been applied to other cryptic felids such as tigers (*Panthera tigris*; Karanth, 1995; Karanth and Nichols, 1998, 2000; Kawanishi and Sunquist, 2004), jaguars (*Panthera onca*; Silveira *et al.*, 2003; Wallace *et al.*, 2003; Maffei *et al.*, 2004; Silver, 2004), snow leopards (*Uncia uncia;* Spearing, 2002) and ocelots (*Leopardus pardalis*; Trolle and Kerv, 2003).

Estimating abundance of leopards is necessary to evaluate population viability and for collecting base line data for wildlife managers to monitor changes in population size. Estimating abundance requires a direct count of the study animal directly or of its secondary sign. Any count (C) of animals will be some proportion of the total number of animals (N) present. Therefore, the number of animals present but undetected will also need to be estimated. Density (D) can then be derived by dividing N by the area (A).

In the past, methods for estimating abundance of wild cat using used track counts in which individual animals were distinguished by track measurements (Riordan, 1998) and track shape (Panwar, 1979). However, this method has met with considerable criticism regarding its accuracy, bias, and repeatability (Karanth 1985, 1987, 1988). Measurement inconsistancy among observers and variability of track visibility across substrate types are two factors leading to bias in this method (Karanth 1985, 1987, 1988).

Felid biologists have also used radio telemetry to derive estimates of wild cat densities by estimating the carrying capacity of a region based on the known home range sizes of a sub-sample of the population (Seidensticker, 1976; Hamilton, 1981; Sunquist, 1981; Bailey, 1993; Smith, 1993; Karanth and Sunquist, 1995, 2000; Mizutani and Jewell, 1998; Grassman, 1999; Marker and Dickman, 2005). The accuracy of this method is generally limited by a small sub-sample of radio-collared animals due to the high cost and effort required in capture and radio tracking operations (Karanth, 1995; Karanth and Nichols, 1998).

Camera trapping has been widely used to assess patterns of abundance movement, distribution, activity patterns, habitat use and reproductive information (Karanth and Nichols, 1998; Silveira *et al.*, 2003), which are important for wildlife conservation (Spalton *et al.*, 2006; Silveira *et al.*, 2003). Silveira *et al.* (2003) conclude that camera trapping is the most appropriate method for surveying mammals rapidly across heterogeneous environmental conditions. In addition, camera trapping is an efficient method for estimating abundance of cryptic animals, such as tigers, leopards and jaguars, that are individually recognizable because of natural pelage variation (Karanth, 1995; Karanth and Nichols, 1998; Carbone *et al.*, 2001; Kostyria *et al.*, 2003; Silveira *et al.*, 2003, Ngoprasert, 2004). Capture and recapture frequencies of individually recognizable animals can used in the framework of mark-recapture theory to estimate capture probabilities, population size, animal density, and other parameters of animal populations (Karanth, 1995) using the computer program CAPTURE (Rexstud and Burnham, 1991).

In contrast, density estimates based on radio telemetry may more accurately reflect carrying capacity. If a female leopard is to successfully raise young, her territory must be large enough to supply the nutritional requirements of her and her young. In the Kalahari Desert of South Africa, Bothma and Le Riche (1984) estimated densities of 0.6 leopards/100 km^2. In Serengeti National Park, Tanzania, leopard densities were estimated at 4.7 leopards/100 km^2 (Cavallo, 1993) in woodland habitat. The density of leopards in East of Tsavo National Park, Kenya, was estimated at 7.69 adults/100 km^2 (Hamilton, 1976). In Cape Province, South Africa, Norton and Henley (1987) estimated 6-9 adult leopards/100 km^2 in the mountainous Cedarberg Wilderness Area and Norton and Lawson (1985) estimated 1.54 leopards/100 km^2 in Stellenbosch. In Kruger National Park, South Africa, Bailey (1993) reported a population density of 16.4 leopards/100 km^2 adult leopards in the Sabie River study area and 9.5 leopards/100km^2 in the Nwaswishaka River study area.

Table 3 Leopard densities in other studies

Study area	Leopard Density (animals/100 km^2)	Method	Source
Huai Kha Kheang WS, Thailand	4	Spoor*	Rabinowitz (1989)
Kaeng Krachan NP, Thailand	4.78	Capture	Ngoprasert (2004)
Wilpattu NP, Sri Lanka	3.33	-	Eisenberg & Lockhart (1972)
Sri Lanka	5	Sightings	Clark (1901)
Serengeti NP, Tanzania	3.5	Sightings	Schaller (1972)
Serengeti NP,Tanzania	4.7	Radio-tracking	Cavallo (1993)
Stellenbosch,Cape Province,South Africa	1.54	Radio-tracking	Norton & Lawson (1985)
Cedarberg ,Cape Province, South Africa	6-9	Radio-tracking	Norton & Henley (1987)
Kruger NP, South Africa	3.5	Radio-tracking	Bailey (1993)
Kalahari Desert, South Africa	0.6	Radio-tracking	Bothma & Le Riche (1984)
Tsavo NP, Kenya	7.69	Radio-tracking	Hamilton (1976)
North-eastern Namibia	1.5	Spoor	Stander *et al.* (1997)
Taï NP, Ivory Coast	7.14-11.11	Capture & radio-tracking	Jenny (1996)
Russian Far East	1.2	Capture	Kostyria *et al.* (2003)

Jenny (1996) used both capture-recapture and radio-tracking methods to generate an estimate of 7.14-11.11 leopards/100 km^2 in Tai National Park, Ivory Coast. Bailey (1993) found leopard density to be highest in riparian forests, where prey density is also highest. Similarly, Martin and de Meulenaer (1988) conclude that leopard density is lowest in arid environments.

In Thailand, Rabinowitz (1989) estimated 4 leopards/100 km^2 using total track count (Table 3).

13. Capture techniques

There are many methods for catching leopards, including wooden and steel mesh box traps, leg-hold traps, cable snares, culvert traps, coil spring traps, darting from a vehicle, darting on a bait, drugged meat and Boma trapping. Box traps have been used for Bobcat (Chamberlain and Leopold, 2005; Nielsen and Woolf, 2001), Black-footed cat (Sliwa, 2004), Leopard cat (Rabinowitz, 1990), Clouded leopard (Austin and Tewes, 1999), Malayan Sun Bear (Wong, 2002), Coyote *(Canis latrans)*, and grey fox (Chamberlain and Leopold, 2005). Leg-holds have been used for Ocelot (Crawshaw and Quigley, 1989), Bobcat (Chamberlain and Leopold, 2005; Benson *et al.*, 2004), Wolverine (Bailey and Hornocker, 1973) and coyote (Windberg *et al.*, 1997; Bromley and Gese, 2001; Atwood and weeks, 2003). Cable snare have been used for Snow leopard (Jackson, 1996; McCarthy *et al.*, 2005), Alaskan brown bear (Ben-David *et al.*, 2004). Culvert and barrel traps have been used for Malayan Sun Bear (Wong, 2002) and Sloth bear (Joshi *et al.*, 1999). Coil spring traps were used for Bobcat (Lovallo, 1999). Darting from a vehicle were used for wild dog, lion, cheetah and spotted hyena (Mills, 1996). Darting on bait was used for wild dog and lion (Mills, 1996). Drugged meat was used for brown hyena, spotted hyena, lion and leopard. Boma trapping was used for wild dog (Mills, 1996).

For felids, the most common methods used are box traps, leg-hold traps, cable snares and drugged meat (Mills, 1996; Frank, 2001). Cable snares are highly efficient and easily transported (Citation needed here). However, proper use of this method requires considerable training and snare designs could benefit from additional improvements (Frank, 2001).

Box trapping is the most widely used capture technique for leopard (Norton and Lawson, 1985; Rabinowitz, 1989; Rabinowitz and Walker, 1991; Bailey, 1993; Grassman, 1999; Marker and Dickman, 2005; Odden and Wegge, 2005). The strengths of box traps are ease of use, facilitation of animal immobilization, and low danger to researchers and animals. Moreover, this method requires only simple darting equipment and a small capture team. The considerable weight and size of box traps, however, limit the locations where they can used (Bailey, 1993; Frank, 2001).

14. Immobilization

A wide variety of different drugs have been used for immobilizing felids. Ketamine hydrochloride is commonly used for on snow leopard (McCarthy *et al.*, 2005), bobcat (Chamberlain and Conner, 2003; Chamberlain and Leopole, 2005), Lavollo, 1999; Benson *et al.*, 2004), and pallas's cat (Munkhtsog *et al.*, 2004). A combination of ketamine hydrochloride and acetyl-promazine were used on black-footed cat (Sliwa, 2004). A mixture of ketamine hydrochloride and xylazine hydrochloride were used on ocelot (Crawshaw and Quigley, 1989), puma (Franklin *et al.*, 1999). A mixture of ketamine hydrochloride and medetomidine hydrochloride were used on leopard (Jenny, 1996; Odden and Wegge, 2005). Snow leopards that were immobilized with ketamine hydrochloride without tranquilizers, exhibited tolerance to this drug and with two cases that also required atropine sulfate because excessive salivation (McCarthy *et al.*, 2005). Kreeger *et al.* (2002) suggested that immobilizing with ketamine and tiletamine without tranquilizers produced rough inductions and recoveries, with poor muscle relaxation.

Curro *et al.* (2004) compared xylazine and medetomidine in combination with midazolam and ketamine on captive Siberian tigers (*Panthera tigris altaica*). Both drugs were safe and effective, but a smaller effective dose of medetomidine resulted in faster induction and recovery times.

A combination of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®) were used on tiger (Smith *et al.*, 1993), leopard (Rabinowitz, 1989; Marker and Dickman, 2005), snow leopard (McCarthy *et al.*, 2005), leopard cat (Rabinowitz, 1990), cheetah *(Acinonyx jubatus)* (Marker, 2002; Broomhall *et al.*, 2003), and geoffroy's cat *(Oncifelis geoffroyi)* (Manfredi *et al.*, 2006). A combination of tiletamine hydrochloride and zolazepam hydrochloride and xylazine were used on leopard (Stander *et al.*, 1997) and cheetah (Broomhall *et al.*, 2003)

Grassman *et al.* (2004) compared a combination of ketamine hydrochloride and xylazine hydrochloride and a combination of tiletamine hydrochloride and zolazepam hydrochloride on wild felids in Thailand, including leopard cat *(Prionailurus bengalensis)*, clouded leopard *(Neofelis nebulosa)*, Asiatic golden cat *(Catopuma temminckii)* and marble cat *(Pardofelis marmorata).* They concluded that both of them are safe and effective immobilizing agents for these felids, but a smaller effective dose for tiletamine hydrochloride and zolazepam hydrochloride resulted in a shorter time to induction and an absence of prolonged muscle rigidity.

Captured leopards were anesthetized with Telazol® at 4–10 mg/kg of estimated body mass (Rabinowitz, 1989; Marker and Dickman, 2005). In addition, a combination of Zoletil® (tiletamine hydrochloride and zolazepam hydrochloride) and xylazine was used as immobilizing agent for leopard (Stander *et al.*, 1997). Leopards were immobilized with a mixture of ketamine hydrochloride and medetomidine hydrochloride at a rate of 6 mg/kg and 0.03 mg/kg of body weight, respectively (Jenny, 1996) and 3.6-5.9 mg/kg and 0.07-0.12 mg/kg (Odden and Wegge, 2005) and a combination of 8.7-10.4 mg/kg ketamine hydrochloride and 4.35-6.2 mg/kg xylazine hydrochloride (Odden and Wegge, 2005).

Bailey (1993) used a mixture of 13 mg/kg ketamine hydrochloride and 1.4 mg/kg xylazine hydrochloride to anesthetize leopards; recumbence and head up time averaged 9.3 and 95.2 minutes, respectively. Grassman (1999) immobilized with 12 mg/kg ketamine hydrochloride (Calypso®); recumbence and head up time averaged 5.8 and 72 minutes respectively.

Kreeger *et al.* (2002) recommended 3mg/kg ketamine plus 0.07 mg/kg medetomidine with supplemental 2 mg/kg ketamine. Alternative drugs were 6.6 mg/kg Telazol®.

15. Habitat selection

For management purposes it is necessary to understand how leopards are using a particular ecological setting, so that important resources that relate to their survival can be identified and protected (Alldredge and Ratti, 1992; Marker and Dickman, 2005). Understanding the ecological needs of leopards will help prioritize sites for additional survey. The first step to discerning the leopard's needs is to identify what resources or habitat types it is selecting, with the presumption that the animals are selecting that which will maximize survival and reproduction.

When attempting to characterize selection, there may be problems associated with the two main underlying assumptions: (1) that recorded observations can be used to infer habitat selection, and (2) that evidence of selection is related to fitness (Porter and Church, 1987; Alldredge and Ratti, 1992; Garshelis, 2000). Investigating how a species selects different features of its environment, however, is an essential step towards assigning importance to those features, with the acknowledged caveat that subsequent measurements of survival and reproduction parameters will be needed.

There are a number of variations on the definitions associated with study of an animal's resource use. For the purposes of this study, the definitions are as follows:

Habitat use: the quantity of that component utilized.

Habitat selection: the process by which an animal chooses that component.

Habitat preference: a reflection of the likelihood of that component being chosen if offered on an equal basis with others.

Habitat importance: habitat quality relative to other habitat and its contribution to the sustenance of the individual/population.

There are several statistical issues regarding habitat selection that need to be taken into account. A major issue is the potential error that can be generated by inappropriate level of sampling and sample size. Some analysis approaches use the animal locations themselves as the sample unit, normally with all locations pooled across individuals to represent the sample size. This is a problem because serial correlation and individual variation is not accounted for. When sequential locations are not independent, the second location may be dependant of the position of the first (Aebischer *et al.*, 1993; Alldredge *et al.*, 1998). Also, two individual animals may use the same habitat differently even if they are both of the same sex, age, condition and are faced with the same environmental conditions. Non-independence and variation of individual preference inflate the apparent number of degrees of freedom in the analysis, thus increasing the likelihood of making a Type I error (Aebischer *et al.*, 1993, Alldredge *et al.*, 1998).

Another issue to overcome is the non-independence of proportions: because the habitat proportions sum to 1 (the unit sum constraint), the use of one habitat is linked to the use of other types (Aebischer *et al.*, 1993). A third issue is that animals may use habitat differently depending on age, sex, condition, etc. A forth issue is the arbitrary definition of habitat availability; the choice of study area and home range are largely subjective and dependent on the spatial analysis technique employed (Aebischer *et al.*, 1993).

The number of analysis techniques for investigating habitat selection continues to grow. Traditionally the most often used methods are the Chi-square test, Neu's method and Johnson's method. None of these methods account for all of the issues mentioned above. A more recent method, compositional analysis, overcomes the first three issues by (1) using individual animals as the sample unit, (2) taking into account that use of one habitat is not independent of use of other habitats, and (3) placing individual animals into groups where appropriate (Aebischer *et al.*, 1993).

Although there is no totally objective way of overcoming arbitrary delineation of study area and home range, this problem can be overcome to a certain extent by studying habitat selection hierarchicaly (Johnson, 1980):

1st order habitat selection: selection of habitat across the landscape (Distribution)

2nd order habitat selection: selection of home range within landscape

3rd order habitat selection: selection of habitat patches within home range

4th order habitat selection: selection of items (e.g. rest sites, hunting locations) within habitat patches

Inference of habitat selection will be greatly influenced by the choice of data collection and analysis methods employed. Radio telemetry provides a means to investigate both habitat use and home range dynamics for leopards, in spite of their elusive nature and naturally occurring low densities. Telemetry has been used extensively for leopard research in African range, where the animal's relationship with its environment has been well documented (Hamilton, 1981; Norton and Lawson, 1985; Bailey, 1993; Jenny, 1996; Mizutani and Jewell, 1998; Marker and Dickman, 2005). In South Asia, radio telemetry has been used to study leopards in Nepal (Seidensticker, 1976; Sunquist, 1983; Odden and Wegge, 2005), and India (Karanth and Sunquist, 1995, 2000). To date, the only studies of this kind documented in Southeast Asia have been in Thailand (Rabinowitz, 1989; Grassman, 1999). If leopards are going to be successfully conserved in this region, further information is urgently needed on leopard resource needs and population status.

MATERIALS AND METHODS

1. Capture procedure

Leopards were captured using wooden box traps (0.8 x 2.0 x 1.0 m) baited with live or dead chickens. The door of the trap closed when a leopard inadvertently pulled a string attached to the bait (Rabinowitz, 1989; Simcharoen, 1990; Grassman, 1997). A total of ten traps were placed along the main roads and animal trails where leopard tracks and other secondary sign were frequently found (Bailey, 1993). Foot pad and scrape measurements were used to identify leopard sign (Ilani, 1981; Phetdee, 2000). Width of front foot pad of leopards averaged 5.2 cm for female and 6.2 cm for a male and hind foot pad averaged 4.9 cm and 5.8 cm respectively (Ilani, 1981). Scrapes were reported to range from 5.5-9.5 cm width and 16-42 cm length (Phetdee, 2000). All traps were checked each day in the early morning.

2. Immobilization

Either (1) a combination of 5 mg/kg ketamine hydrochloride (Ketaset®) and 2 mg/kg xylazine hydrochloride (Rompun®), or (2) a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil® and Telazol®) at 5 mg/kg was injected intramuscularly to leopards using a pole mounted syringe (Smith per. comm.). The animals were then weighed, measured (total body length along curves) and fitted with a radio collar (Telonic Inc., Mesa, Arizona), set in the 164-166 MHz frequency range. The Xylazine was antagonized with Yohimbine (0.05 mg/kg) and the processed animals were placed back in the trap while they recovered from the effects if the drugs. The animals were monitored from a safe distance until they were able to leave the trap.

3. Radio tracking

Radio tracking was conducted using standard methodology outlined by Mech (1983). Tracking was often performed from hill tops or high elevation ridges to increase the range of the receiver. Whenever possible, three teams took bearings of a particular leopard simultaneously, in order to minimize error in location estimation due to leopard movement during location acquisition. An attempt was made to locate all collared leopards at least three times a week during daylight hours. Telemetry error was calculated using the distance between estimated and known locations of spare radio collars. All radio locations were plotted on 1:25,000 scale topographic maps in Universal Transverse Mercator (UTM) coordinates and processed using Arcview® v3.3 [ESRI, Redlands, California, USA] (Figure 3).

Figure 3 Tracking equipment and radio collars.

4. Home range estimation

To understand the spatial extent of an animals ranging pattern, home range can be delineated as a two dimensional polygon, constructed by a mathematical formula that incorporates locations, recorded in coordinate form. For the leopards in this study, the Minimum Convex Polygon (MCP; Mohr, 1947) method was chosen to calculate home range. The MCP approach has been used extensively in the literature, so its use in this analysis will allow direct comparison with past studies. Because home range size increases positively with the number of locations recorder, home range size is estimated when additional locations increase home range size <1%. Area curves were generated in BIOTAS (Ecological Software Solutions) for each animal to determine (a) the full home range had been recorded, and (b) how many locations were needed to establish this home range.

Normally some sub set of the total locations for an animal are used to estimate home range; outlying locations may represent exploratory excursions rather than presence in an area used for essential activities (Burt, 1943; Smith, 1993; Mizutani and Jewell, 1998). Burt (1943) used 95% of locations to define overall home range, and 50% of locations to identify core zones of high activity. These 95% and 50% levels are arbitrary, but have been used in a wide range of studies on animal spatial dynamics (Mizutani and Jewell, 1998; Karanth and Sunquist, 2000; Broomhall *et al.*, 2003; Munkhtsog *et al.*, 2004; Marker and Dickman, 2005). Home range was calculated separately for 3-, 6- and 12-month periods in order to investigate home range change over time and to classify leopards as resident or dispersing animals.

Seasonal home ranges were calculated for the dry season (November to April) and for the wet season (May to October). Home range size and movement analysis were conducted using ArcView® v3.3 software (ESRI, Redlands, California, USA). Seasonal difference was tested using the Wilcoxan Paired Rank *t*-test.

Leopard densities, measured as number of individuals/100 km^2, were estimated annually using adult home range size and overlap estimates.

5. Estimating overlap

Mean overlap of 95% and 50% MCP home ranges was calculated for each pair of leopards in the same demographic group (Mizutani and Jewell, 1998; Broomhall *et al.*, 2003; Munkhtsog *et al.*, 2004):

$$\text{Mean overlap} = \{[AO \times 100)/Alep1] + [AO \times 100)/Alep2]\}/2 \qquad (1)$$

Where AO is the size of overlap between two home ranges, and $Alep1$ and $Alep2$ are the sizes of the respective individual leopard's home ranges.

This can be considered a minimum mean overlap since not all animals in the area were collared. Mean annual overlap of home range was calculated separately for dry season, rainy season, and full-year datasets.

6. Estimating movement

An index of leopard movement was estimated using the straight line distance between sequential daily locations. However, the actual daily distance will be greater than this estimate due to the effects of topography and non-linear route probably taken between sequential locations.

7. Assessing site fidelity and home range shifts

Site fidelity can be considered the propensity of an animal to return to a previously occupied location or, in the case of territorial animals, their defense of a particular area (Jakob *et al.*, 2001). In this study, fidelity was measured as return to the same territory (Switzer, 1997). Site fidelity was investigated using activity radius and the degree of shift in home range center. Activity center was calculated by the averaging the coordinates of all locations in a given period of time (Odden and Wegge, 2005). Activity radius was calculated in 3 month increments using the distance between activity center and all radio locations. Home range center shift was measured in distances between activity centers calculated for each 3 month period.

Accumulative area curves were constructed to determine the adequate number of locations for calculating home range size. Home range size was estimated by visually interpreting accumulative area curves to determine when size reached an asymptote where size does not increase significantly with more locations. Accumulative home range was also used to detect when an animal's home range shifted. For example, a shift that a mother made to accommodate her daughter or a shift an individual made when it was forced to give up part or all of its home range to another animal.

8. Camera trapping

Camera trapping was carried out for 3 years (1996-1999) over a 115.88 km^2 area (A) around Khao Nang Ram Wildlife Research Station, Huai Kha Khaeng Wildlife Sanctuary (Figure 5). The area (A) was determined by a polygon around all camera locations. Camera traps were deployed for 3-4 months a year.

Trailmaster® (Goodson Associates, Inc., Kansas, USA) camera traps were set on the trails and roads where leopard tracks or other secondary signs were frequently found. Camera traps were mounted on trees 3-4 m from the path, with the infrared beam set 45 cm above the ground (Karanth, 1995; Karanth and Nichols, 1998; Korstyria, 2003) (Figure 4). Camera traps were set out in pairs to capture the opposing, asymmetrical spot patterns of the passing leopards (Karanth, 1995). The distance between unit pairs was 1.0-3.0 km. GPS locations were taken for all sites. Cameras were checked every 2-3 days to change batteries and film and to document the presence of animal tracks.

Figure 4 Camera trap were mounted on trees.

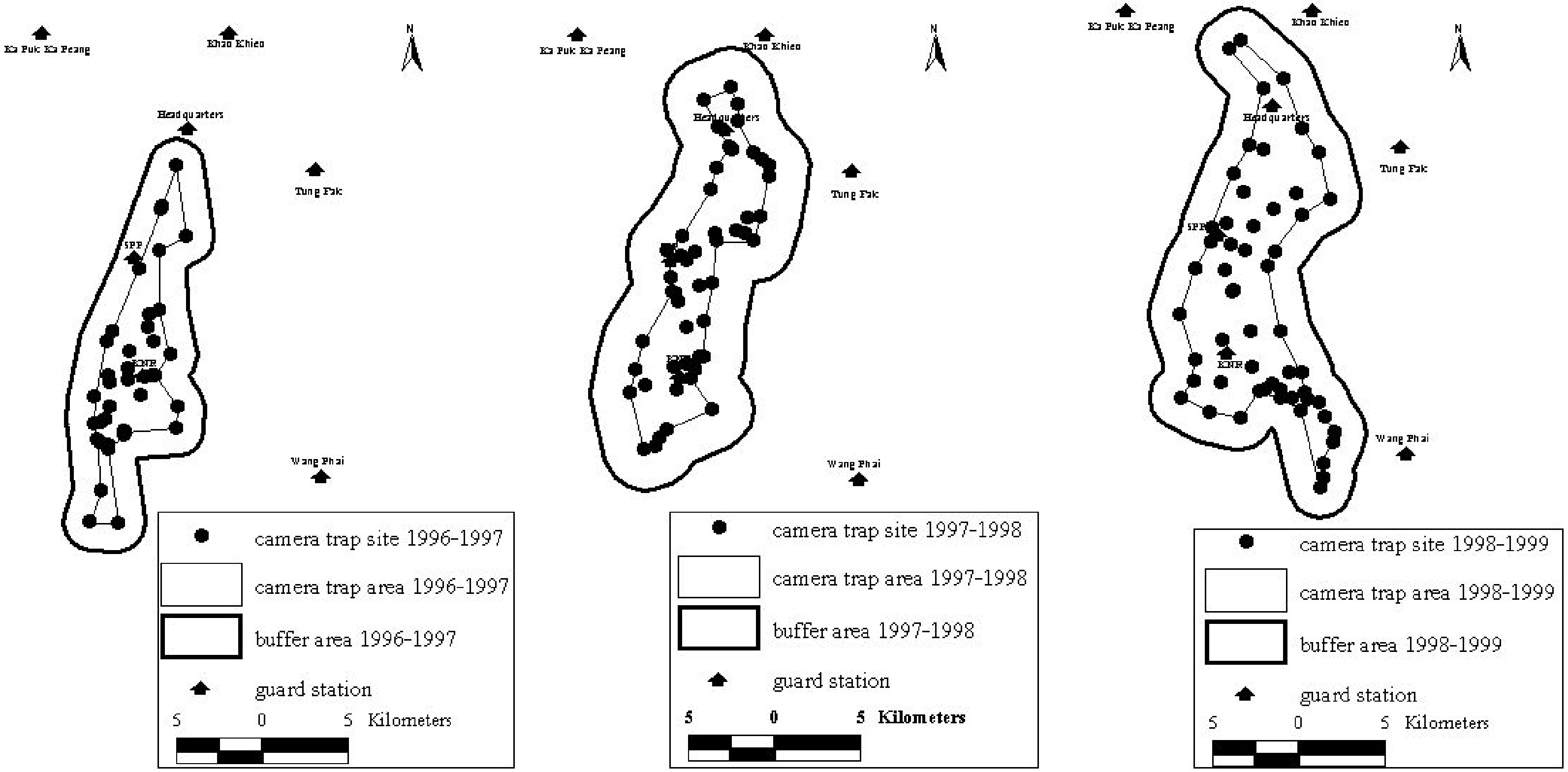


Figure 5 Camera trap sites, camera trap areas, and buffer areas.

9. Leopard identification

Leopards exhibit natural variation in their pelage spot patterns that allowed individuals to be identified diagnostically. Because rosettes and spot patterns of individual leopards are asymmetrical on their left and right flanks, both sides of an animal had to be photographed simultaneously to ensure its recognition upon resighting. Once an animal had been photographed on both sides, however, future photographic attempts obtaining only on one side could be matched to the left or right profile of existing photos to positively identify individual leopards. Unclear animal photographs on one side were not used for analysis. Black leopards could not be identified clearly by their spot pattern. However, they were identified by their size, sex and photograph time and location (Figure 6).

Animal photographs were organized separately for each individual leopard and the date, time, photograph location, age class and sex were recorded. Colalred animsals were given IDs based on their collar number and non-collared animals were given novel IDs.

10. Estimating abundance

Capture history was used to generate capture frequencies. Data were recorded in an X matrix consisting of *i* animals in rows and *t* trapping occasions in columns, assuming a value of either “0” if the animal was not photographed or a “1” if it was photographed. Five trapping occasions were used for all sites, with each occasion containing 3 days of field visits. The capture histories of individual leopards were used in the framework of capture-recapture theory to estimate capture probabilities and population size using the computer program CAPTURE (Otis *et al.*, 1978; White *et al.*, 1982; Rexstud and Burnham, 1991). CAPTURE estimates abundance of closed populations under seven models (M_h, M_b, M_t, M_{bh}, $M_{th,}$ M_{tb}, M_{tbh}), which vary by *h*-heterogeneity, *b*-behavior, and *t*-time. M_0, in which the probability is constant, is the null hypothesis (White *et al.*, 1982). In CAPTURE, the *closure test* is used to assess whether the number of individual is constant during the overall study period and is computed for the subset of the data defined by the capture frequencies. The *validity test* cannot be devised because of problems in behavioral responses and time trends (White *et al.*, 1982). A closed population was assumed, however, because of the bevity of the study period (3-4 months), which did not allow enough time for birth, death, immigration or emigrationt to significantly alter the results. In this study, model M_h in which capture histories vary by individual heterogeneity, was used to estimate abundance because the estimator for this model (the jackknife, $\hat{N}_h$) is the most robust of the four estimators $(\hat{N}_{bh}, \hat{N}_b, \hat{N}_t, \hat{N}_0)$(White *et al.*, 1982). This model has been widely used in previous studies to estimate abundance of large cats (Karanth and Nichols, 1998; Kostyria *et al.*, 2003) and is well suited to territorial species in which home range size and trapping rate are dependent on social position and spatial location of the animal (Karanth, 1995).

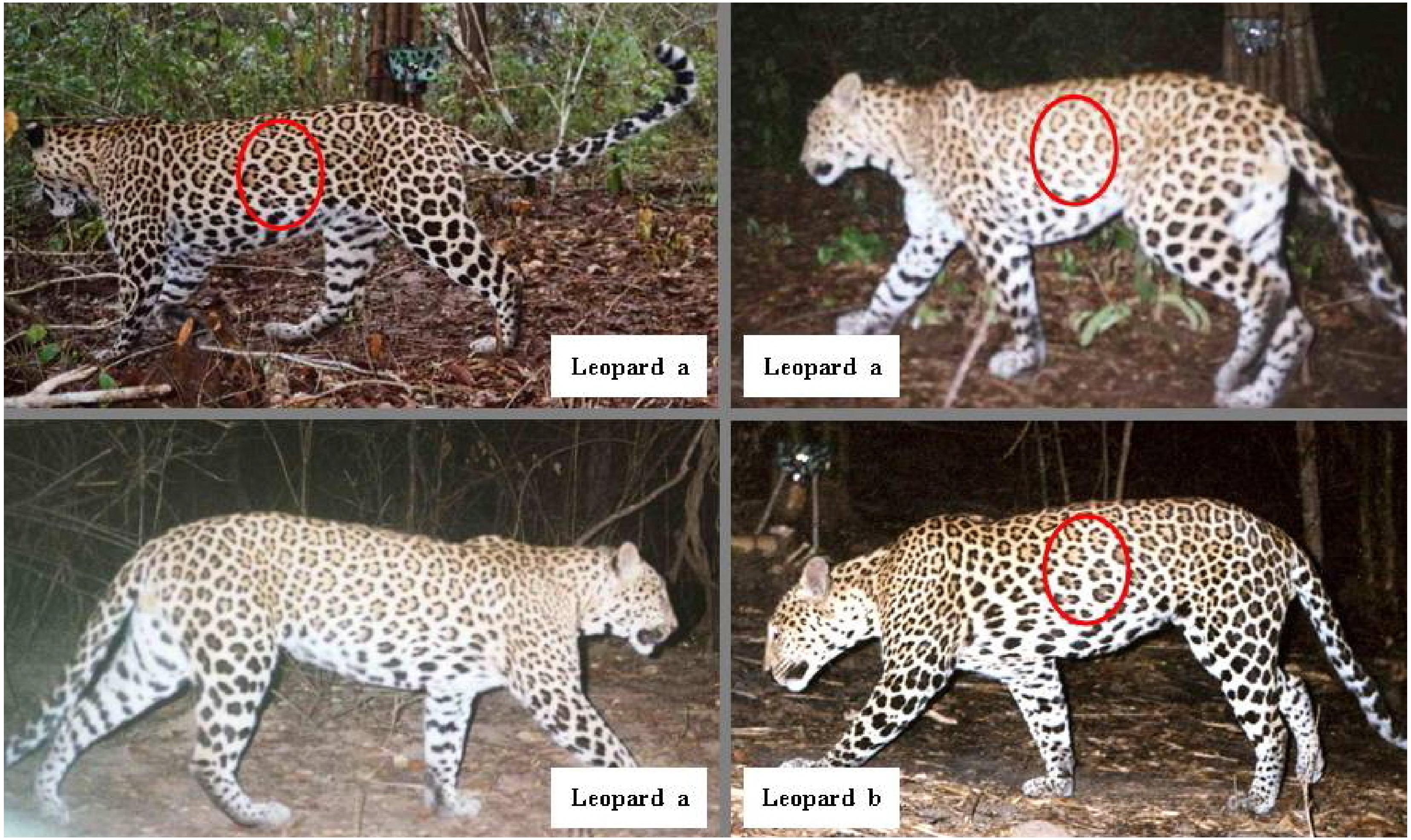


Figure 6 Asymmetrical rosettes and spot patterns of individual leopard on two flanks and leopard identification**.**

11. Estimating density

Animal density can be estimated using abundance estimates from CAPTURE. Density is defined as:

$$\hat{D} = \hat{N} / \hat{A}(W) \tag{2}$$

$\hat{D}$ is the estimated animal density, $\hat{N}$ is the estimated abundance and $A(\hat{W})$ is the estimated effective area in which photographed animals live; W is the boundary strip of width that is added around the perimeter of the area in which the camera traps were set.

Variance in animal density is calculated from variance in estimated abundance and effective area:

$$\mathrm{v\hat{a}r}(\hat{D}) = \hat{D}^2 \left[\frac{\mathrm{v\hat{a}r}(\hat{A}(W))}{[\hat{A}(W)]^2} + \frac{\mathrm{v\hat{a}r}(\hat{N})}{\hat{N}^2} \right] \tag{3}$$

Variance in estimated abundance was computed by program CAPTURE. The effective area includes the area where camera trap sites were plotted and connected on the edge to form the perimeter and the buffer area. The buffer width $(\hat{W})$ was calculated using the mean maximum distance moved by leopards $(\hat{\bar{d}})$ between camera trap sites divided by two (Karanth and Nichols, 1998).

$$\hat{W} = \hat{\bar{d}} / 2 \tag{4}$$

Variance in buffer width was calculated using variance in mean maximum distance moved by leopards. Let d_i denote the maximum distance moved between camera trap sites for animal *i* and *m* denote the number of animals that cameras trapped at least twice:

$$\mathrm{v\hat{a}r}(\hat{W}) = 0.25 \times \mathrm{v\hat{a}r}(\hat{\bar{d}}) \tag{5}$$

$$\mathrm{v\hat{a}r}(\hat{\bar{d}}) = \frac{\sum_{i=1}^{m} (d_i - \hat{\bar{d}})^2}{m(m-1)} \tag{6}$$

Variance in estimated effective area was calculated following Karanth and Nichols (1998):

$$\hat{\text{var}}(\hat{A}(W)) = 4\pi^2 (c + \hat{W})^2 \ \hat{\text{var}}(\hat{W}) \tag{7}$$

This estimation approximates each of the sampled areas as a circle in which c is a constant that is calculated from $\hat{A}(W) = \pi(c + \hat{W})^2$; $\hat{A}(W)$ is the estimated effective area that includes the camera trap area and the buffer area and $\hat{W}$ is the buffer width.

12. Scat collection

Radio telemetry provides a means to locate kill remains, but for leopards in HKK this proved problematic because due to the small prey items selected (a) prey was consumed fast, giving less indication of a kill from locational data and (b) the odor needed to locate the kill was less detectable. Thus, using kill remains for prey selection analysis will lead to a small and biased sample in which larger prey items will be found more often. To avoid this bias, this study used the scat analysis method to study leopard prey selection.

Scat collection took place between 1996 and 1999. Leopard scats were collected along trails. Tiger and leopard scats were distinguished using the size of track and scrape (Figure 7). Scats collected without a corresponding track or scrape were not included in analysis. The range of track sizes of adult leopards and tigers does not overlap (Phetdee, 2000). Pad widths range from 4.2-6.0 cm for leopards and 7.0-9.2 cm for tigers (Phetdee, 2000). Leopard scrapes are 4.5-10 cm in width and 16-42 cm in length (Phetdee, 2000). The scats were stored individually in a plastic bag and labelled with the date and GPS location.

Figure 7 Leopard scat and scrape.

13. Identifying scat contents

Scats were carefully washed in fine mesh and strained to separate remains such as hair, bones, hooves and teeth. Hardened scats were boiled or soaked in warm water prior to separation. Hairs from scats were identified following Phetdee (2000). Cleaned and dry hair was examined by light microscope and prey species identification was based on diagnostic hair properties, such as cuticle pattern, medulla structure and medulla width.

Hair samples were embedded in paraffin in order to cross-section and mount on a glass side. In order to study the medulla structure of each hair, the sample was placed in xyline until the pigments were removed. In the case of heavily pigmented hair such as wild pig and hog deer, the sample was placed in hydrogen peroxide and then mounted on slides. The cuticle pattern of hair was characterized at the base, middle and end of the hair. Hair diameter and cross section morphology were used to further distinguish prey species. Hair samples were compared to a reference collection for cross-validation (Phetdee, 2000).

14. Estimating prey selection

The scat data was analysed with several different approaches:

14.1 relative frequency of food item (RF).

$$RF = \left(\frac{f_i}{\sum_{i=1}^{n} f_i} \right) \times 100 \tag{8}$$

Where f_i denotes the number of scats in which item i appears.

14.2 Seasonal diet. The relative frequency of preys was compared between dry season (November-April) and wet season (May-October).

14.3 The comparison of leopard’s diet and tiger’s diet. Leopard’s diet in this study was compared with tiger’s diet from Phetdee (2000).

14.4 Diet comparison. A comparison between leopard and tiger diets was considered. The prey species of more than 2% of percentage occurrence were drawn on a graph. The x-axis was the percentage occurrence of leopard diet and y-axis was the percentage occurrence of tiger diet. A cluster of points near the 45 degrees line means that prey species were consumed by both species. The points above the line show which prey species tigers consumed more than leopards. In contrast, the points below the line show those prey species that were consumed by leopards more than by tigers.

15. Home range estimation for habitat selection

"Habitat class" was used to signify a physical or biological spatial coverage (e.g., vegetation or slope), and "habitat type" to signify areas representing the variation in characteristics within a class (e.g., diptorpcarp forest or evergreen forest). Johnson's (1980) definition of "selection" for the process of choosing resources was used for this study, as opposed to "preference", which is the likelihood of a resource being chosen if offered on an equal basis with other resources.

To improve the likelihood of serial independence of locations, only one radio location per day was used for each leopard.

Program BIOTAS^{TM} 2.0a (Ecological Software Solutions) was used to determine fixed kernel (FK) 95% home ranges (Worton, 1989), with a smoothing factor determined by least squares cross validation (LSCV). Seaman and Powell (1996) found that FK estimators gave little bias using smoothing by LSCV and made good distribution estimates compared to the adaptive kernel approach.

Kernel estimators are nonparametric and robust to autocorrelation. They allow more than one *center of activity* to be generated and create a utilization distribution (UD) rather than a simple home range outline (Kernohan *et al.*, 2001). The least-squares cross validation method is based on properties of the data.

Leopard home ranges were determined for each study year (annual) and for each season (wet and dry) within a study year. Home ranges were only calculated data sets containing a minimum of 50 locations (Mitchell, 2006). A mean home range size was estimated for each leopard and a grand mean for all leopards in the same demographic group. A Wilcoxon signed rank *t*-test was used to test whether wet and dry home range sizes were significantly different ($\alpha=0.05$).

Telemetry error was estimated by measuring the distance between estimated (generated by radio telemetry and program LOAS^{TM} 4.0b, Ecological Software Solutions) and actual (recorded using a GPS) locations of a radio collar placed in variety of terrain and habitats to simulate actual tracking conditions.

16. Habitat selection

Habitat selection analysis followed the hierarchical habitat framework outlined by Johnson (1980) and described in the introduction. In this study, data collection focused on investigating selection at the second and third order levels. Each day, an attempt was made to locate all radio collared leopards using standard telemetry procedures (Mech, 1983). To minimize possible error resulting from a moving animal, three teams, positioned at different locations, took bearings of the same leopard simultaneously.

For statistical inference, the compositional analysis approach (Aitchison, 1986; Aebischer *et al.*, 1993), which overcomes the problems that can result from assessing habitat selection without taking into account non-independence of proportions (also known as the unit sum constraint), and inappropriate level of sampling and sample size, was used to examine habitat selection of leopards. Compositional analysis has gained in popularity since its formulation, and has been used to investigate habitat selection for a variety of taxa (Pendleton *et al.*, 1998; Conner *et al.*, 1999; Gabor and Hellgren, 2000; Miller *et al.*, 2000; Dickson and Beier, 2002).

Compositional analysis (Aebischer *et al.*, 1993) was carried out on the recorded available and used habitat proportions using program Resource Selection for Windows 1.00, © Fred Leban, 1999.

This program first tests for difference between proportional use and availability for each animal. Within each habitat class there are D habitat types and an animals habitat use is (x_{u1}, x_{u2}… x_{uD}), so the corresponding log ratios (using the D^{th} element as the denominator) for proportion of habitat used are $y_{uD} = (y_{u1},\ldots, y_{uD-1})$ and for available are $y_{aD} = (y_{a1},\ldots, y_{aD-1})$. Each animal's proportional use of habitat type i (measured in a log ratio y_{iu}), is paired with y_{ia}, the log ratio of the available habitat. Random use of habitat types will result in the pair wise differences d (calculated by $y_1u - y_1a$) following a multivariate normal distribution so that $d \equiv 0$. If the pair wise differences d_D (given by d_1,,…, d_{D-1}) for each habitat type is different to d, then that is an indication of use more ($d_j > 0$) or less ($d_j < 0$) than expected, relative to the use of all other habitat types.

Analysis of all animals together is expanded by forming a matrix of differences between used and available habitat log ratios for each leopard. The matrix is made up into D-1 columns and n rows, where n is the number of study animals. This matrix is used to create *R1* (matrix of mean corrected sum of squares and cross-products) and *R2* (matrix of raw sum of squares and cross products).

Let x_{ai} denote the difference between used and available habitat log ratios for each leopard.

Let $\overline{x_a}$ denote the mean difference in habitat type a.

Matrix of mean corrected sum of squares and cross-products (R1) and matrix of raw sum of squares and cross products (R2) calculate as follows:

$$R1 = \begin{bmatrix} \text{mean corrected Sum SQ of habitat type1} & \text{cross products} \\ \text{cross products} & \text{mean corrected Sum SQ of habitat type2} \end{bmatrix} \tag{9}$$

$$\text{Mean corrected Sum SQ of habitat type1} = \sum_{i=1}^{n} (x_{1i} - \overline{x_1})^2 \tag{10}$$

$$\text{Mean corrected Sum SQ of habitat type2} = \sum_{i=1}^{n} (x_{2i} - \overline{x_2})^2 \tag{11}$$

$$\text{Cross products} = (x_{11} - \overline{x_1})(x_{21} - \overline{x_2}) + ... + (x_{1n} - \overline{x_1})(x_{2n} - \overline{x_2}) \tag{12}$$

$$\text{R2} = \begin{bmatrix} \text{raw Sum SQ of habitat type1} & \text{cross products} \\ \text{cross products} & \text{raw Sum SQ of habitat type2} \end{bmatrix} \tag{13}$$

$$\text{Raw Sum SQ of habitat type1} = \sum_{i=1}^{n} (x_{1i})^2 \tag{14}$$

$$\text{Raw Sum SQ of habitat type2} = \sum_{i=1}^{n} (x_{2i})^2 \tag{15}$$

$$\text{Cross products} = (x_{11})(x_{21}) + ... + (x_{1n})(x_{2n}) \tag{16}$$

The Wilks' lambda statistic λ (calculated by determinant (det) of matrix) is a multivariate test statistic which measures the difference between used and available habitats:

$$\lambda = \frac{\det(R1)}{\det(R2)} \tag{17}$$

This test statistic can be converted into a chi-square distribution with degrees of freedom equal to the number of habitat types minus one. Use was considered significantly non-random when the resulting $p < 0.05$.

$$\chi^2 = -n \times \ln(\lambda) \tag{18}$$

If overall use is significantly non random, the habitat types are ranked from most to least used, using a matrix of mean and standard deviation of log ratio differences for all habitat types.

A t-value (derived from the ratio mean/standard error) indicates which differences from non-random use between two habitat types are significant (Aebischer *et al.*, 1993).

Habitat classes analyzed were vegetation, slope, and water courses. Vegetation class included main three broad types; dry dipterocarp, dry evergreen and mixed deciduous forest. There was also a small amount of hill evergreen, but since this comprised <1% of the study area it was merged with dry evergreen; the habitat type with most similar characteristics (Figure 8).

The slope class was created using a 20 m elevation contours to define slope angle for each 30 m grid square using ArcView 3.3 (ESRI, Redlands, California, USA). Slope class was divided into three types measured in degrees from level; flat slope type was 0-12, moderate was 13-24, and steep was 25-49 degrees (Figure 9).

The water course class was constructed using a 150 m buffer around all streams and rivers in the study area. Area within this buffer was termed stream type, whilst outside was termed dry type (Figure 10). Not all water courses had running water year round, but they could still be used as potential travel routes and hunting areas, as well as sources of water for both leopard and its prey. Furthermore, mineral licks detected in the study area seem to be found predominantly along water courses; another associated factor that could potentially affect the distribution of leopard prey species (Naksathit, 1994).

The study area was defined by creating an MCP around the collective locations derived from all radio-collared leopards.

To circumvent the problems associated with using point data for habitat selection analysis (Rettie and McLoughlin, 1999), a buffer (of radius equal to the mean estimated telemetry error) was created around each leopard location. This was done to take into account both telemetry error and the potential importance of habitat close to the animal's position (Rettie and McLoughlin, 1999; Dickson and Beier, 2002).

The second order selection was look at using compositional analysis to compare proportions of available habitat types in the study area to used habitat within 95% FK home ranges for combined, wet (April-September) and dry (October-March) season locations.

For third order selection the proportion of available habitat in multiyear 95% fixed kernel home ranges (for combined, wet and dry locations) were compared to the used habitat encompassed by the buffered locations within the home range (Dickson and Beier, 2002).

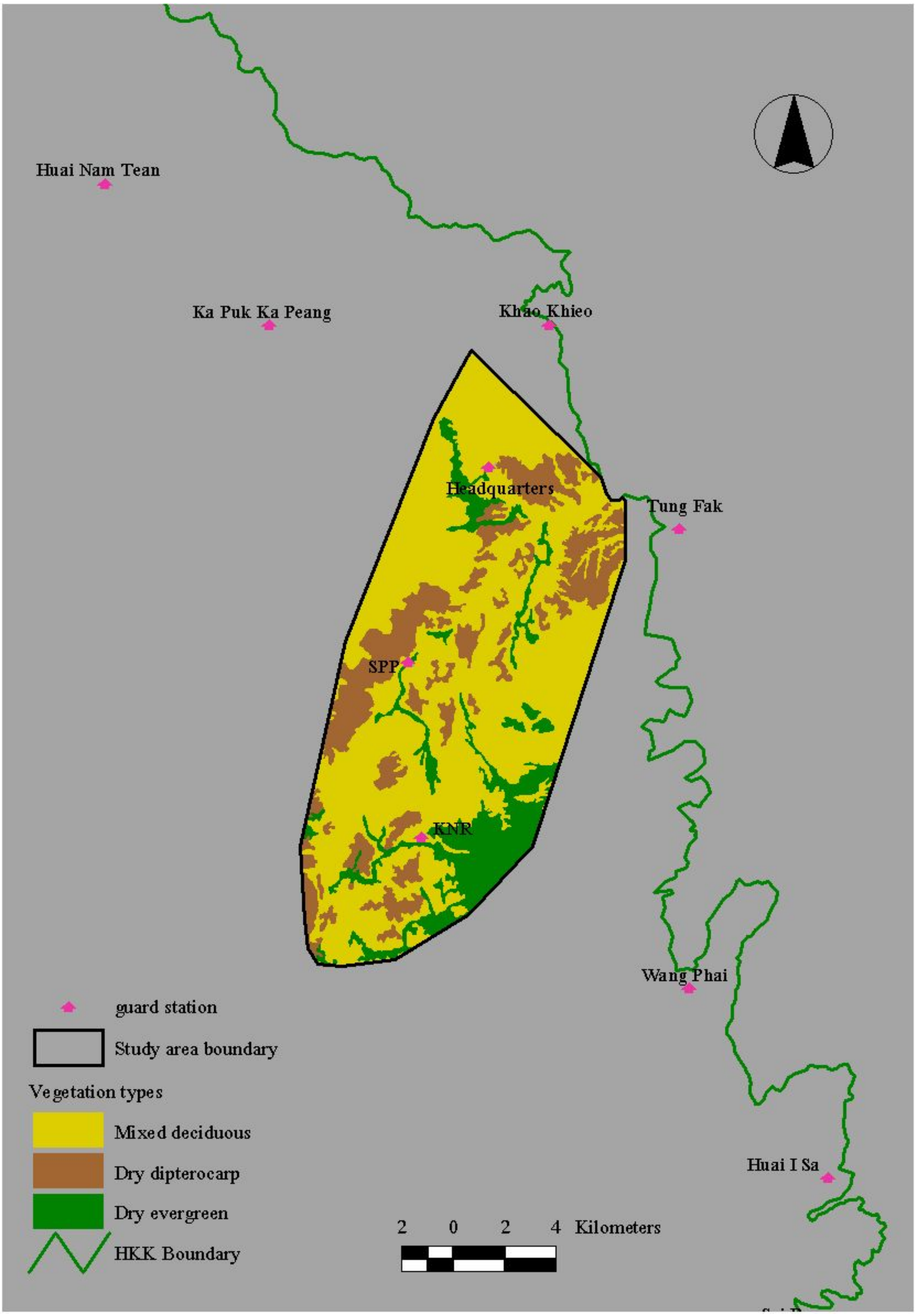


Figure 8 Vegetation types in the study area.

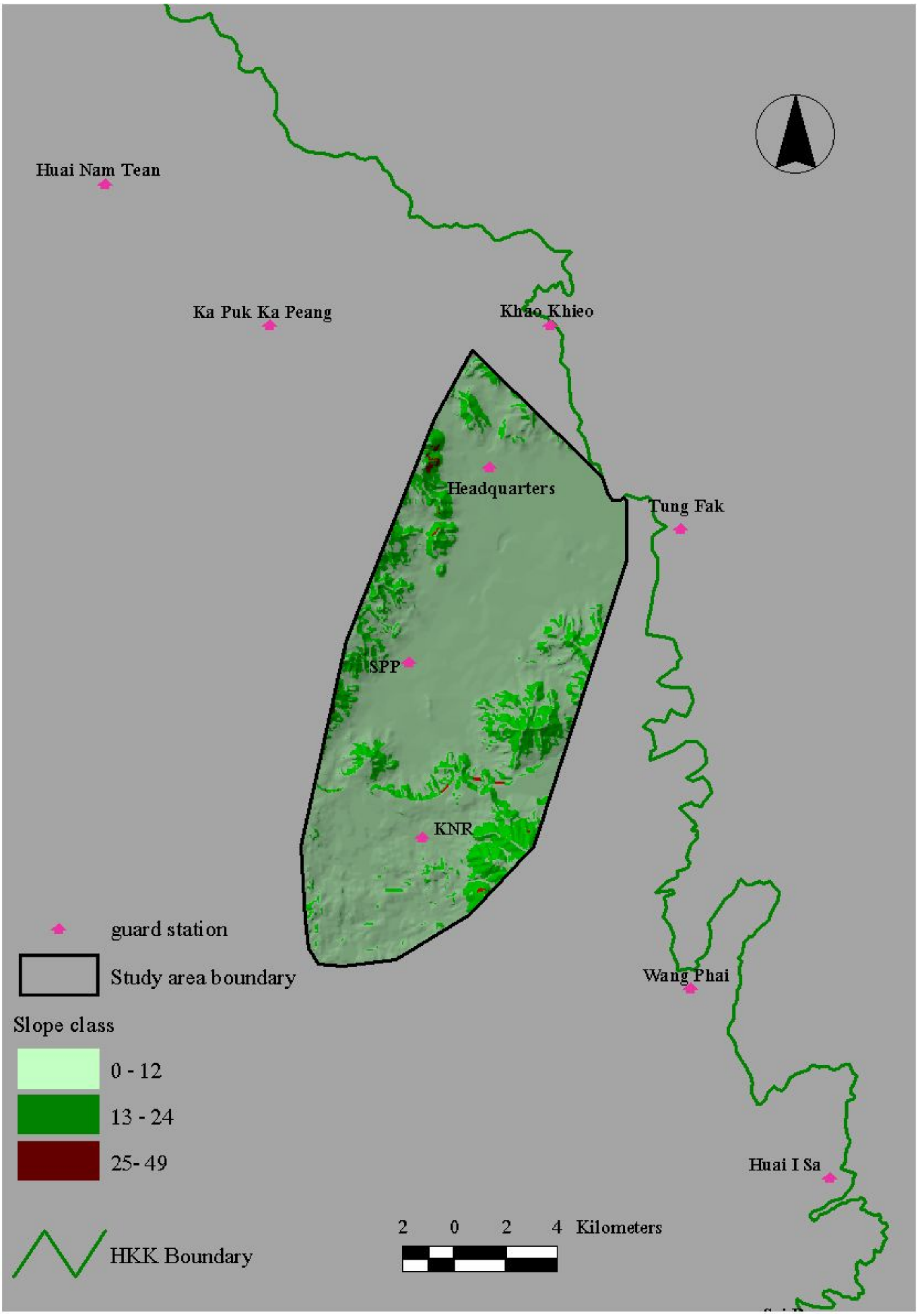


Figure 9 Slope classes in the study area.

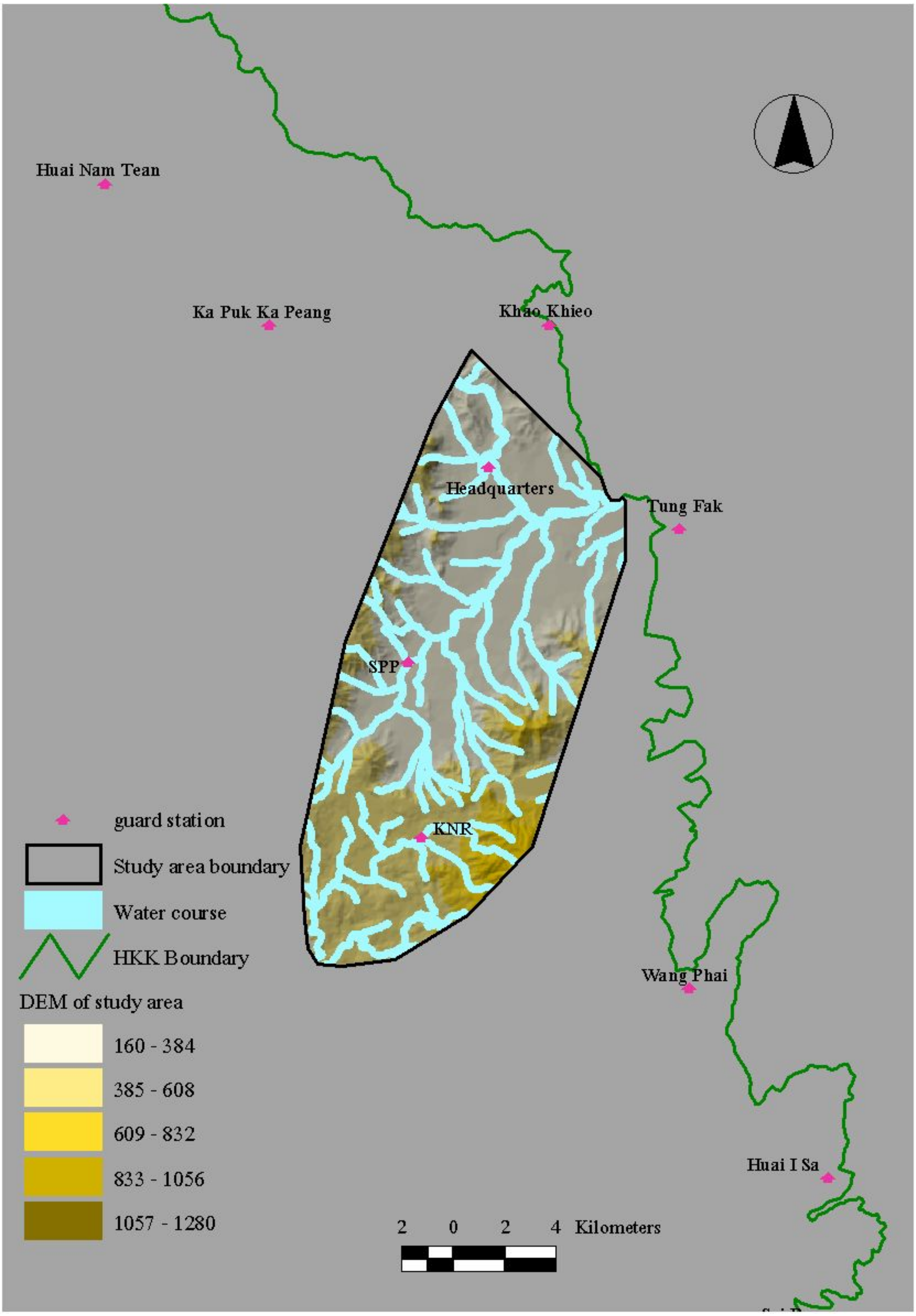


Figure 10 Water courses of the study area.

17. Study area

Huai Kha Khaeng Wildlife Sanctuary (HKK) was established in 1972. In 1991 the sanctuary was announced as a natural world heritage site by UNESCO. HKK lies between 14º56′ and 15º48′ north latitudes and 90º27′ and 99º28′ east longitudes in Lansak, Banrai and Huai Kod districts of Uthai Thani province, and Umpang district of Tak province. HKK covers approximately 2,800 km^2. Khao Nang Rum Wildlife Research Station (KNR) was established in 1976.

The study area covers HKK Head office, Sub Fa Pa Guard Station and KNR, with an area of approximately 181 km^2. This area is defined by the MCP of all leopard radio locations collected during the study (Figure 11).

17.1 Topography The topography of the area is composed of rugged mountains ranging from 160-1687 m above sea level separated by valleys of undulating terrain. This mountainous area is the part of Khao Thanon Thongchai system, which includes the peaks Khao Plai Huai Kha Khaeng (1687 m) Khao Yai (1554 m) and Khao Nam Yen (1530 m). Many of the mountains are oriented from the north to the south. The Huai Kha Kheang River is the main waterway of the sanctuary flowing from north to south and separating the area into two halves.

17.2 Climate. The climate of HKK is classified as *Tropical Savanna Climate*, (Aw) in the Koppen system. The dry season occurs from November to April and the wet season from May to October. The sanctuary is affected by a Southwesterly Monsoon during the rainy season. During 1986-2005 KNR experienced an average annual rainfall of 1447.15 mm and mean annual temperature was 24.6°C. The mean minimum temperature was 20.3°C in December, due to the influence of the northeast monsoon. The mean maximum temperature was 27.6°C in April. Mean annual humidity from 1995 to 2005 was approximately 63.7%.

17.3 Vegetation. Vegetation in the area encompasses five forest types: dry evergreen forest 3.08%, hill evergreen forest 0.05%, mixed deciduous forest 83.01%, dipterocarp forest 13.25% and secondary forest 0.16% (The Western Forest Complex ecosystem management project [WEFCOM], 2003).

17.3.1 Dry evergreen forest. Dry evergreen forest is found at elevations between 400-1000 m. This forest type is very tall and dense. The dominant tree species are *Dipterocarpus alatus, Dipterocarpus turbinatus, Hopea odorata, Afzelia xylocarpa, Lagerstroemia loudonii, Lagerstroemia ovalifolia.* Ground cover consists of seedlings, palms, ferns, shrubs and grasses such as *Lygodium Flexuosum, Entada pursaetha, Homonoia riparia*.

17.3.2 Hill evergreen forest. Hill evergreen is found at elevations over 1000m. It is dominated by trees of family Fagaceae (genus *Lithocarpus*, *Castanopsis* and *Quercus*), Podocarpaceae and Cephalotaraceae.

17.3.3 Mixed deciduous forest. Mixed deciduous forest occurrs on moderately sloping and flat areas. The canopy of this forest type is open. The dominant tree species are *Afzelia tylocapa*_*Lagerstroemia tomentosa*, *Lagerstroemia calyculata*, *Pterocarpus macrocarpus*. Ground cover in this forest type consists of shrubs and creepers including *Viburnum* o*doratissimum*, *Ixora sp*., *Harrisonia perforata* and *Congea tomentosa*. Annual fires occur in the dry season, playing an important role in the ecosystem.

17.3.4 Dry dipterocarp forest. Dry dipterocarp forest is found scattered throughout the sanctuary where drought stress is highest. This forest has a more open canopy. Canopy tree species include *Shorea obtuse*, *Shorea siamensis*, *Shorea floribunda*, *Dipterocarpus obtusifolius* and *Dipterocarpus tuberculatus*. The ground is covered with grasses, seedlings, cycads and shrubs. Ground fires occur during the dry season.

17.3.5 Secondary forest. This forest is found in the eastern and southern part of the sanctuary. It is the result of the actions of local people who planted bamboo and destroyed the existing mixed deciduous forest.

17.4 Wildlife. There are many species of mammals living in the study area due to the high diversity of topography and vegetation. Based on a report produced by KNR, there are 623 species of vertebrate comprising of 64 species of mammals, 355 species of birds, 65 species of reptiles, 65 species of amphibians and 74 species of freshwater fish. Among these species are wild water buffalo (*Bubalus bubalis*), gaur (*Bos gaurus*), banteng (*Bos javanicus*), Asian tapir (*Tapirus indicus*), tiger (*Pantera Tigris*), Asiatic elephant (*Elephus maximus*), marbled cat (*Felis marmorata*), clouded leopard (*Neofelis nebulosa*), Fea's barking deer (*Muntiacus feae*) and green peafowl (*pavo muticus*) and leopard *(Panthera pardus).*

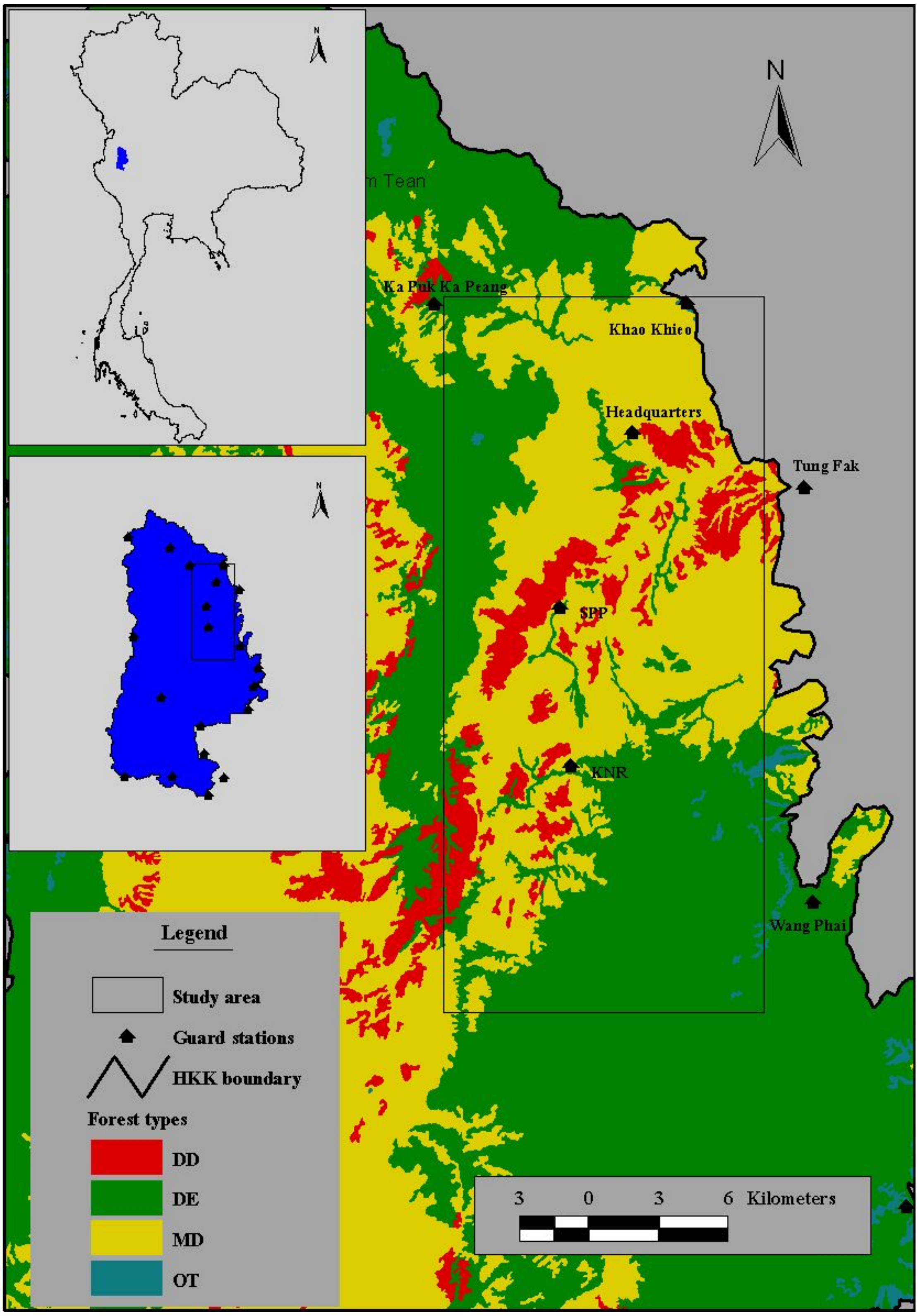


Figure 11 Study area around Khao Nang Rum Wildlife Research Station.

RESULTS AND DISCUSSION

Results

1. Capture and telemetry

A total of 16 leopards (7 females and 9 male) were captured using box traps from 1994 to 1999. One male and three females were melanistic. With the exception of one adult female, all leopards were weighed, measured, and evaluated with regard to sex, age class, and physical condition. All animals recovered from immobilization.

Figure 12 Captured leopard being fitted with a radio collar.

The adult females (n=4) had total body lengths (nose to tail tip along curves) of 179.5-183.0 cm (181.1±1.7), and weights (n=5) of 27.0-34.9 kg (mean 30.3±3.1). Two sub-adult (judging by their teeth) females had total body length of 170.7-178.0 cm (mean 174.4±5.2), and mean weight of 22.5-24.5 kg (mean 23.5±1.4). Adult males had total body lengths of 191.0-220.0 cm (202.9±11.8; n=7), and weights of 36.0-43.5 kg (mean 40.2±3.1; n=6). Two sub-adult males had body length 189.0-202.0 cm (mean 195.5±9.2) and weights were 32.1-34.0 kg (mean 33.1±1.3) (Table 4). Adult male leopards were significantly longer (t=4.799, DF=6.404, p=0.003) and heavier (t=5.316, DF=9, p<0.001) than adult female leopards. Sub-adult males were significantly heavier than sub-adult females (t=6.924, DF=2, p=0.020) but the difference between their lengths was not significant.

Eleven leopards were radio-collared, including three adult males, five adult females, one sub-adult male and two sub-adult females (Figure 12). There was also a considerable variety of non-target animal by-catch, including large Indian civet (*Viverra zibetha*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*), large spotted civet (*Viverra megaspila*), leopard cat (*Prionailurus bengalensis*), Asian golden cat (*Felis temminicki*), yellow throated martin (*Martes flavigula*), crab-eating mongoose (*Herpestes urva*), clouded monitor (*Varanus nebulosus*), elongated tortoise (*Indotestudo elongata*), crested serpent eagle (*Spilornis cheela*) and changeable hawk eagle (*Spizaetus cirrhatus*).

Radio collared leopards were followed over five years (1994-1999). Individuals leopards were tracked for 3-55 months (30.5±18.0). A total of 4,070 locations were recorded. The mean number of total locations collected for each leopard was 403.2±255. All leopards were tracked until the collar signal was lost. Mean telemetry error, calculated by distance between estimated and actual collar positions (n=28) was 154±76 m. A mean telemetry error of 150 m was used during subsequent analyses.

Table 4 Size and weight of captured leopards

No.	Collar frequency	Age class	Sex	Weight (kg)	HB (cm)	Tail (cm)	Neck (cm)	Ear (cm)	Upper canine (cm)	Lower canine (cm)	Front pad width (cm)	Front total width (cm)	Front total length (cm)	Hind pad width (cm)	Hind total width (cm)	Hind total length (cm)
1	L046	Adult	F	27	-	-	-	-	-	-	4.5	5.7	6.6	4.5	5.4	6.9
2	L390	Adult	F	28.5	106	76	35	6.4	2.9	2.5	4.9	6.4	6.3	4.5	5.3	6.9
3	L195	Adult	F	29.6	107	72.5	34.5	6.1	3.2	2.5	4.5	6.8	6.3	4.5	5.8	7
4	L025	Adult	F	31.7	102	78	27.7	5.5	2.7	2.15	4.7	5.8	6.5	4.5	5.3	6.6
5	L345	Adult	F	34.9	110	73	33.5	5.3	-	-	4.6	6.5	6.7	4.3	5.3	6.8
$\bar{x}$				30.34	106.25	74.88	32.68	5.83	2.93	2.38	4.64	6.24	6.48	4.46	5.42	6.84
S.D.				3.07	3.3	2.59	3.37	0.51	0.25	0.2	0.17	0.47	0.18	0.09	0.22	0.15
6	L055	Adult	M	36	112.5	85.5	40	6	-	-	5.3	-	-	-	-	-
7	L550	Adult	M	37.5	131	89	41	6.5	3.1	2.7	5.5	7.2	6.8	4.9	6	7.3
8	L855	Adult	M	41.5	121	83	39	6.4	3	2.6	5.9	7.3	7.6	5.5	6.4	7.7
9	L800	Adult	M	43.1	112	82	45.5	7	3.16	2.49	5.8	7.3	7.2	5.3	6	7.5
10	L055	Adult	M	43.5	132	86.2	40	6	2.4	3	6	7.4	7.8	5.8	6.3	8.2
11	L538	Adult	M	39.5	117	78	38.5	7.2	3.41	3.15	5.7	7.4	8	5.4	6.7	7.8
12	Lkbd-kk	Adult	M	-	105	86	41	-	3.5	3.2	5.9	8.5	8	-	6.2	7
$\bar{x}$				40.18	118.64	84.24	40.71	6.52	3.1	2.86	5.73	7.52	7.57	5.38	6.27	7.58
S.D.				3.05	10.06	3.57	2.31	0.5	0.39	0.3	0.25	0.49	0.48	0.33	0.27	0.42
13	L467	Sub-adult	F	22.5	109	69	35	5.3	-	-	4.5	5.7	6.5	4.3	5.5	6.5
14	L035	Sub-adult	F	24.5	100	70.7	-	6.2	2.7	2.3	4.6	6.2	6	4.2	5	6.5
$\bar{x}$				23.5	104.5	69.85	35	5.75	2.7	2.3	4.55	5.95	6.25	4.25	5.25	6.5
S.D.				1.41	6.36	1.2		0.64			0.07	0.35	0.35	0.07	0.35	0
15	L159	Sub-adult	M	34	110	79	-	6	-	-	5.3	7.1	7	4.8	6	7.1
16	L256	Sub-adult	M	32.1	122.3	79.7	37.3	7.4	3.3	2.7	5.4	7.2	7.1	5.2	6.2	8.2
$\bar{x}$				33.05	116.15	79.35	37.3	6.7	3.3	2.7	5.35	7.15	7.05	5	6.1	7.65
S.D.				1.34	8.7	0.49		0.99			0.07	0.07	0.07	0.28	0.14	0.78

2. Home range size

2.1 Home range size The home range of radio-collared leopards tracked from 3-55 months showed a strong sexual dimorphism in size. The mean accumulative home ranges of 7 adult females was 27.1 (SD=6.5) km^2 (Table 5). The mean accumulative home range of adult males was 48.7 (SD=7.8) km^2, which was significantly larger (approximately 1.8 times) than female range size (t=-4.576, DF=8, p=0.002). However, the difference in size of their 50% MCP core areas was not significant (t=-1.744, DF=2.174, p=0.213).

From our visual inspection of accumulative area curve, it required a mean of 13.4 months (SD=9.0) and 202.2 locations to determine home range size. Home range sizes were estimated when the mean change in home range size between 3 month periods ranged from 1.51-6.68 % (3.64±1.78) (Figure 13-21). The accumulative home range size was compared to annual and overall to examine site fidelity and shifts in home range (Table 5).

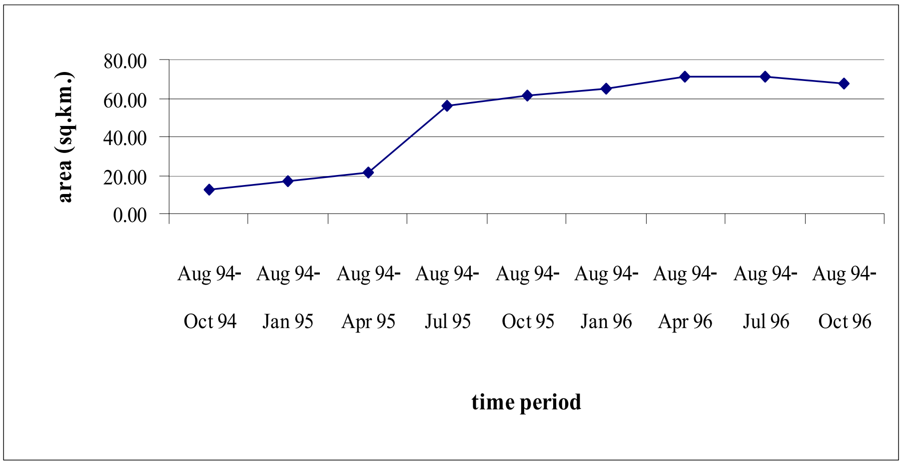


Figure 13 Accumulative home range area curve of L025.

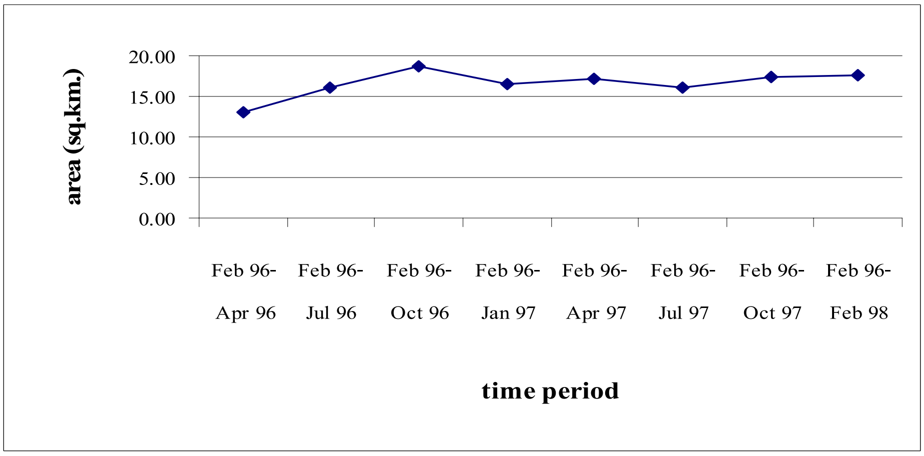


Figure 14 Accumulative home range area curve of L035.

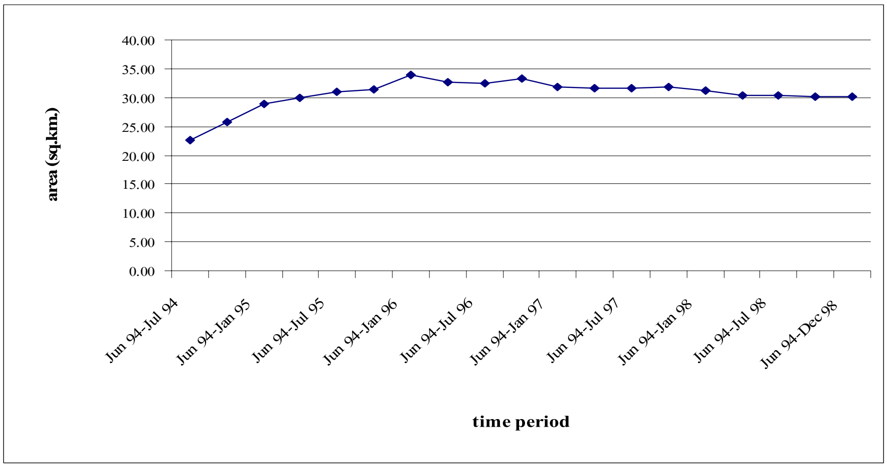


Figure 15 Accumulative home range area curve of L046.

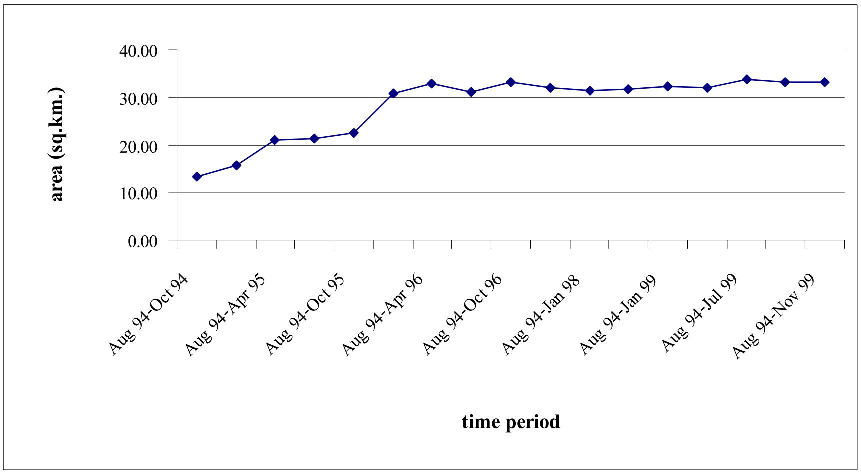


Figure 16 Accumulative home range area curve of L195.

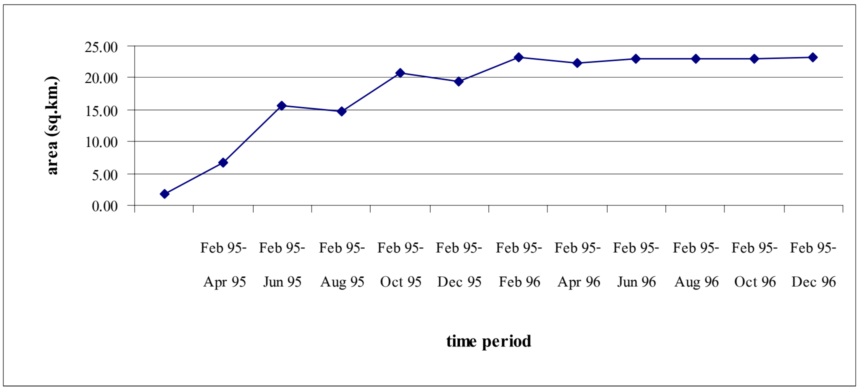


Figure 17 Accumulative home range area curve of L 345.

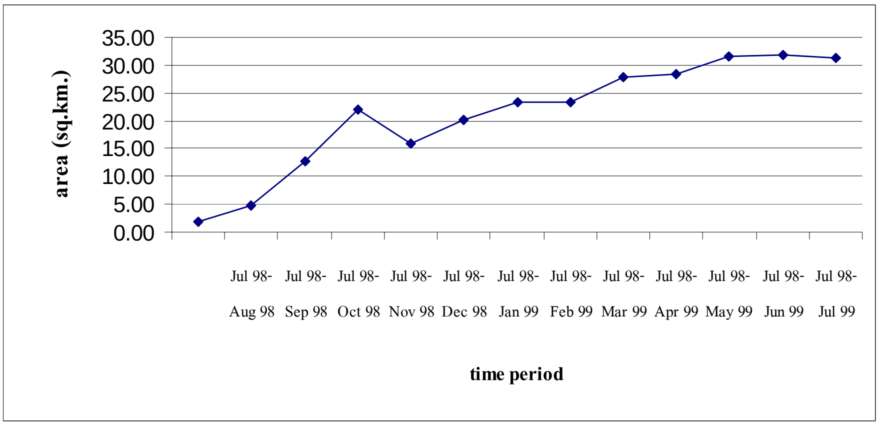


Figure 18 Accumulative home range area curve of L390.

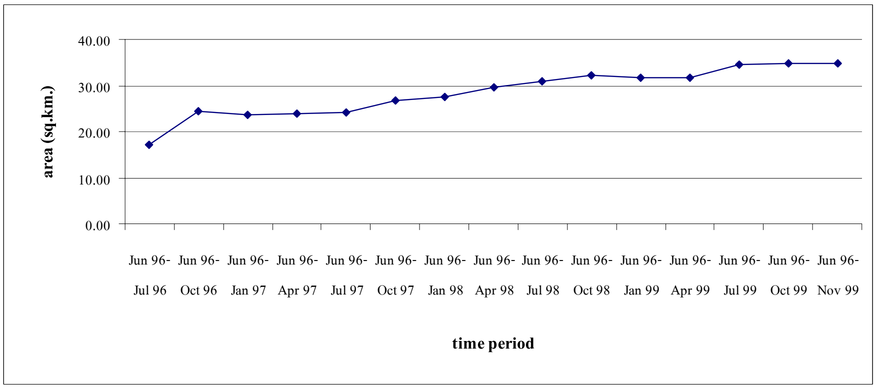


Figure 19 Accumulative home range area curve of L467.

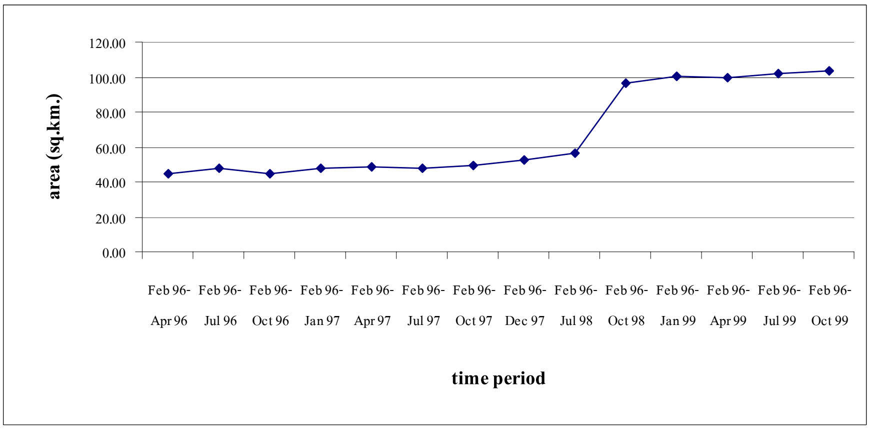


Figure 20 Accumulative home range area curve of L055.

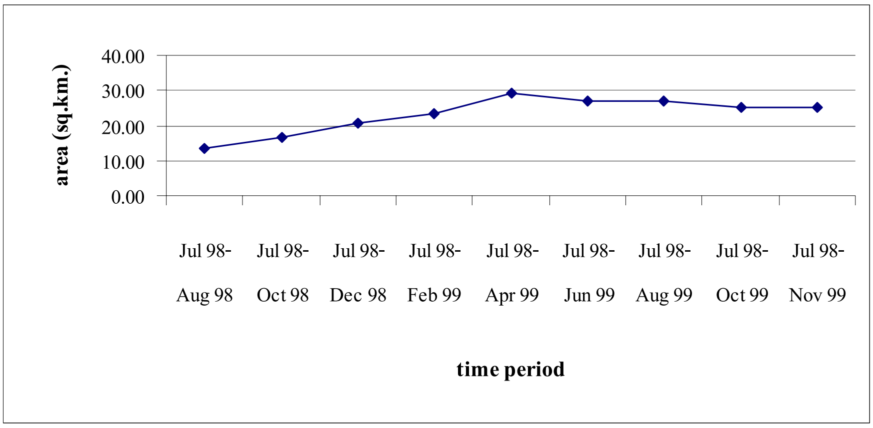


Figure 21 Accumulative home range area curve of L550.

Table 5 Home range size of females and 3 males leopard

Collar frequency	Sex	Age class	Duration (months)	No. locations	Overall home range size (95% MCP)	Accumulative home range	Annual home range (95% MCP)	Annual home range size (50%)
L046	F	Adult	55	848	30.1	31.6	23.5	8.0
L390	F	Adult	14	160	31.2	30.7	31.8	6.2
L195	F	Adult	52	659	33.2	32.5	21.5	5.8
L025	F	Adult	27	412	**67.3**	21.4	21.4	6.5
L345	F	Adult	24	368	23.2	22.9	20.1	4.0
L467	F	Adult	42	529	34.9	33.6	23.3	4.4
L035	F	Adult	43	393	**41.4**	17.2	14.6	4.6

Collar frequency	Sex	Age class	Duration (months)	No. locations	Overall home range size (95% MCP)	Accumulative home range	Annual home range (95% MCP)	Annual home range size (50%)
L055(1)	M	Adult	47	449	**103.2**	56.6		
L055(2)	M	Adult	47	449	**103.2**	48.6	49.5	14.2
L800	M	Adult	12	38	41.0		41.0	11.1
L550	M	Sub-adult	17	181	29.4	26.8	26.9	5.4

Notes: The overall home ranges in bold indicate home range shift.
L055(1) indicate home range before shift.
L055(2) indicate home range after shift.

Table 6 Leopard seasonal home ranges

Collar frequency	Sex	Age class	Average dry season home range size					Average wet season home range size				
			No. location	100%MCP (km^2)	95%MCP (km^2)	50%MCP (km^2)	n	No. location	100%MCP (km^2)	95%MCP (km^2)	50%MCP (km^2)	n
L046	F	Adult	355	27.2	19.5	6.4	4	470	24.5	18.2	5.9	5
L390	F	Adult	69	27.8	24.4	4.1	1	45	26.3	22.1	3.0	1
L195	F	Adult	312	26.5	19.6	5.0	4	251	27.9	17.3	4.2	3
L025	F	Adult	182	38.0	31.9	8.6	2	175	48.5	42.5	20.4	2
L345	F	Adult	88	28.2	19.1	2.6	1	202	20.4	16.9	3.3	2
L035	F	Adult	86	13.5	10.6	4.1	1	174	17.4	14.0	3.1	2
L467	F	Adult	86	18.3	13.6	3.2	1	165	32.2	24.2	6.6	2
Mean			168.3	25.7	19.8	4.9	7	211.7	28.2	22.2	6.6	7
S.D.			119.4	7.8	7.0	2.1		129.8	10.2	9.6	6.2	
L467	F	Sub-adult	132	20.2	18.1	7.5	2	173	22.3	20.0	7.5	2
L055	M	Adult	143	45.2	37.2	15.6	2	259	43.9	36.6	12.0	4
L550	M	Adult	76	32.6	27.2	5.1	1	101	21.3	14.4	3.4	2
Mean			109.5	38.9	32.2	10.4	2	180.0	32.6	25.5	7.7	2
S.D.			47.4	8.9	7.1	7.4		111.7	16.0	15.7	6.1	

2.2 Seasonal home ranges Dry season female home ranges averaged 19.8 km^2 for adults (SD=7.0, n=7) and 20.2 km^2 for the one sub-adult. The dry season adult male home range averaged 32.2 km^2 (SD=7.1, n=2). Wet season, female home ranges averaged 22.2 km^2 (SD=9.6, n=7) for adults and 20.0 km^2 (n=1) for one sub-adult. Wet season adult male home ranges averaged 25.5 km^2 (SD=15.7, n=2). Home range sizes (95% MCP) were not significantly different between wet and dry seasons for males (t=1.098, DF=1, P=0.470) and females (t=-1.043, DF=6, P=0.337) (Table 6).

3. Home range overlap

Ninety five percent MCP overlap was high between sexes (mean=54.2%, SD=19.1%) and similarly their core areas had a high degree of overlap (mean=34.4%, SD=16.9%). Most of the overlap between sexes was by Male L055 who overlapped with the ranges of all females. In contrast the home range of male leopard (L550) overlapped with only two females (L195 and L467) and his core area only overlapped with female L195 (Figure 22). Females established their home range within male home ranges which resulted in a male's home range overlaping two or more female ranges. Because males were able to successfully excluded other males and their territory included 2 to several females, leopards had a polygamous mating system.

Among females overlap was also extensive. The mean 95% MCP overlap was 38.6% (SD=25.4%) and the 50% MCP overlap was 16.5% (SD=26.7%) (Figure 24). The highest overlap observed among females was between L046 and L467. The latter was capture as a sub-adult (weight 18.1 kg) in side the home range of L046. During her capture L046 was located near by where she remained while L467 was fitted with a radio collar. Based on her weight and the proximaty of L046 that L467 probably was L046's daughter. These 2 animals maintained a high degree of overlap for 2 years and 2 months. The first year their overlap of their 95% MCP home ranges was 88.6% in the second year it declined to 69.1% (Figure 23). For the first 9 months their activity centers were very close to each other. Gradually these centers diverged (Figure 26). In contrast L046 had a low degree of 95% MCP overlap with 2 of her neighbors L195 and L345 (Figure 24).

There was more 95% MCP overlap in the dry season among adult females (43%, SD=24.3%, n=8) and among adults and sub-adult females (63.8%,(SD=18.7%, n=3) than in the wet season where home range overlaps were 33.1% (SD=25.1, n=21) for adults and 43.30% (SD=33.3, n=8) for adults and sub-adults. Among males there was no overlap overall and no overlap in the dry season, but 13.9% (n=1) during the wet season.

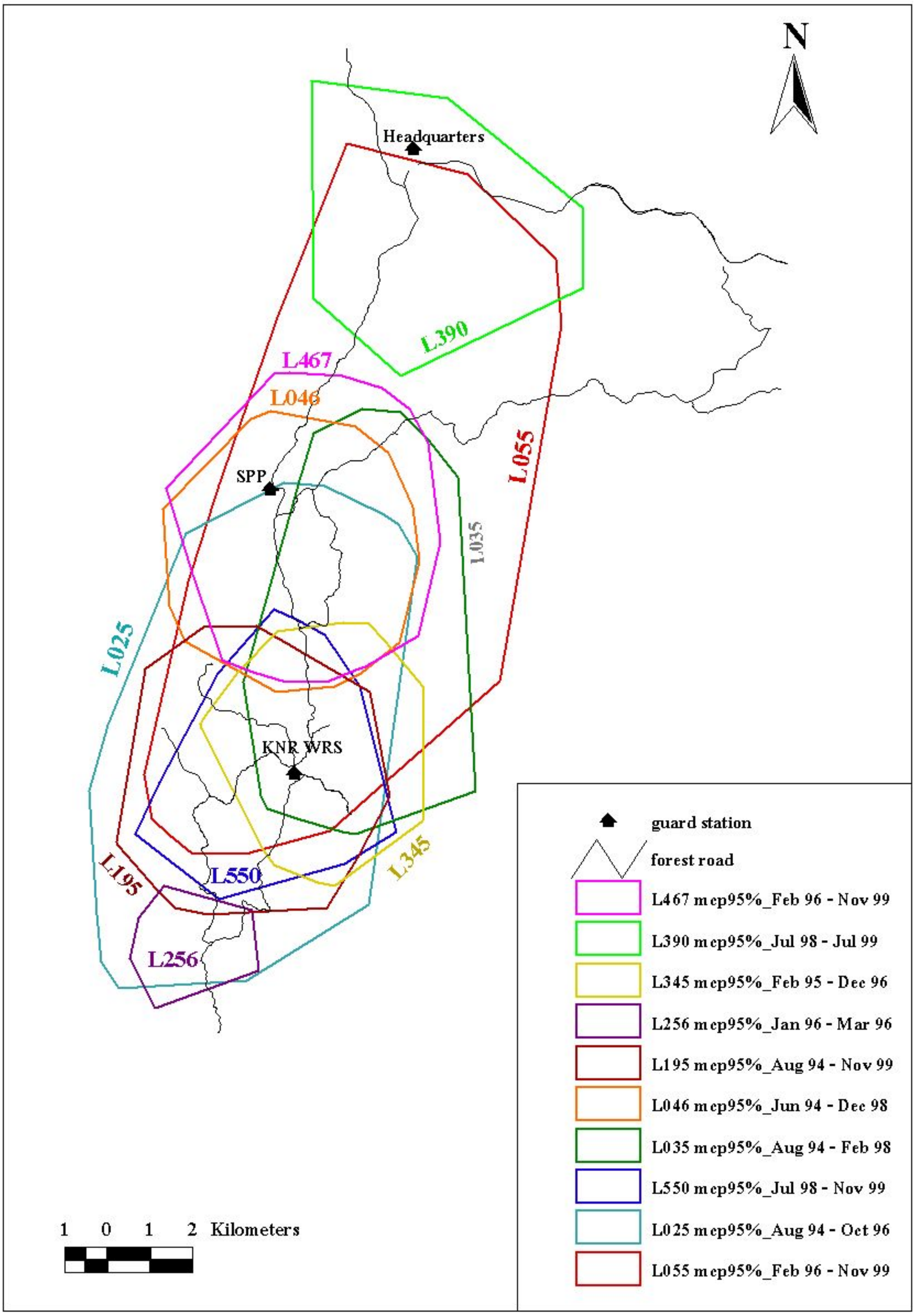


Figure 22 High overlapping of the overall leopard 95% MCP home ranges.

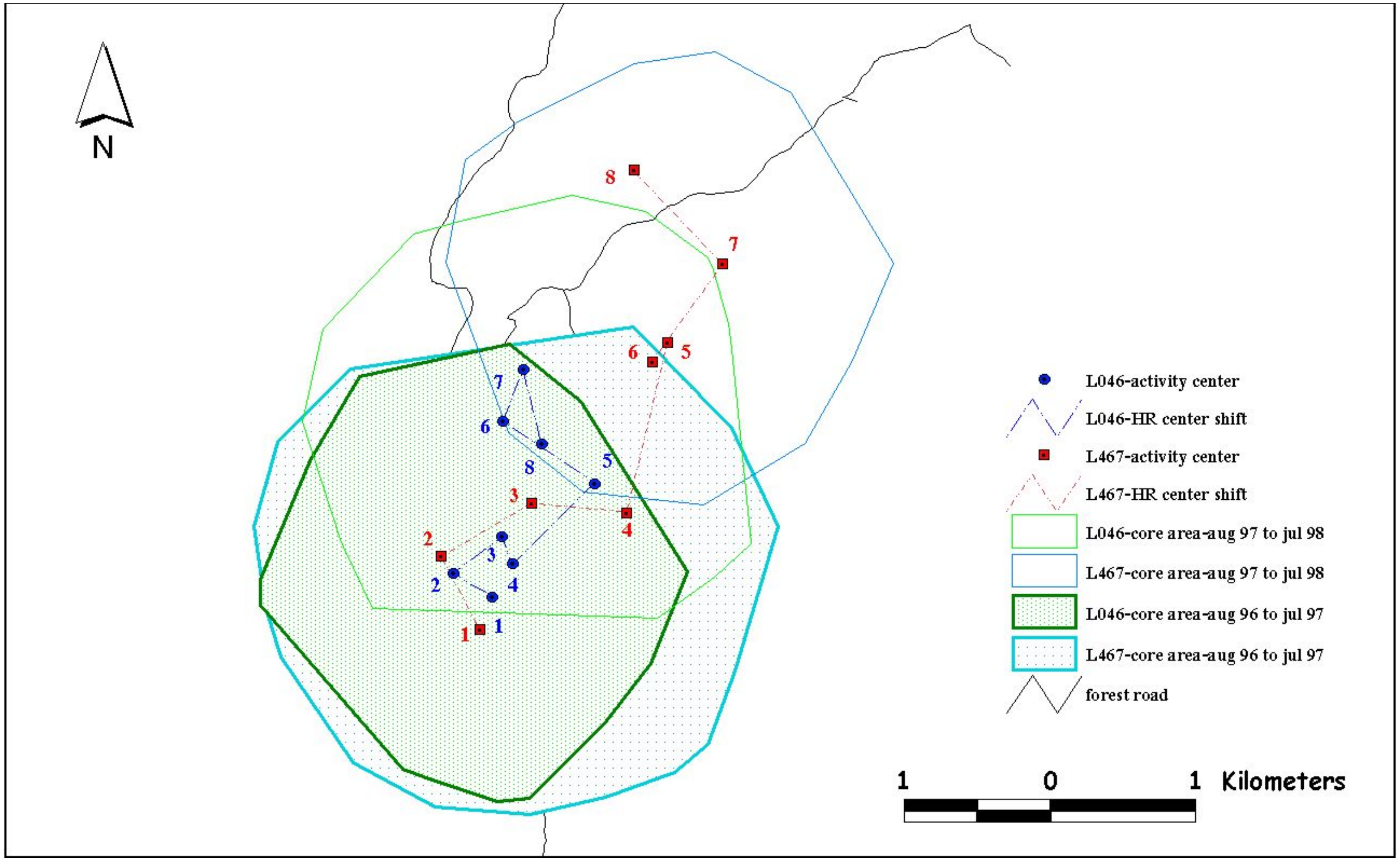


Figure 23 Overlapping core areas (50% MCP) of L046 and L467.

95% MCP overlap

	L025	L035	L046	L195	L345	L390	L467	L055	L550
L025		52.5%	45.6%	71.1%	43.7%	-	-	75.7%	-
L035	52.5%		44.6%	12.2%	15.7%	-	59.7%	52.6%	-
L046	45.6%	44.6%		7.0%	8.5%	-	78.9%	62.8%	-
L195	71.1%	12.2%	7.0%		53.9%	-	8.2%	63.6%	60.1%
L345	43.7%	15.7%	8.5%	53.9%		-	-	59.5%	-
L390	-	-	-	-	-		-	61.6%	-
L467	-	59.7%	78.9%	8.2%	-	-		43.6%	8.8%
L055	75.7%	52.6%	62.8%	63.6%	59.5%	61.6%	43.6%		-
L550	-	-	-	60.1%	-	-	8.8%	-	

50% MCP overlap

	L025	L035	L046	L195	L345	L390	L467	L055	L550
L025		-	-	68.5%	4.3%	-	-	44.8%	-
L035	-		28.1%	-	-	-	46.2%	32.0%	-
L046	-	28.1%		-	-	-	66.9%	37.6%	-
L195	68.5%	-	-		0.9%	-	-	42.2%	70.6%
L345	4.3%	-	-	0.9%		-	-	11.5%	-
L390	-	-	-	-	-		-	23.5%	-
L467	-	46.2%	66.9%	-	-	-		47.0%	-
L055	44.8%	32.0%	37.6%	42.2%	11.5%	23.5%	47.0%		-
L550	-	-	-	70.6%	-	-	-	-	

Figure 24 Overall home range overlap (95% and 50%MCP)

Table 7 Annual and seasonal home range overlap

Percent

95%MCP	**Adult female**			**Adult male**			**Sub-adult female**		
	Annual	**Dry**	**Wet**	**Annual**	**Dry**	**Wet**	**Annual**	**Dry**	**Wet**
Adult female	35.4	43.0	33.1	52.5	53.3	49.3	72.5	63.8	43.3
Adult male	52.5	53.3	49.3	0.0	0.0	13.9	70.1	67.3	69.1
Sub-adult female	72.5	63.8	43.3	70.1	67.3	69.1	-	-	-

50%MCP	**Adult female**			**Adult male**			**Sub-adult female**		
	Annual	**Dry**	**Wet**	**Annual**	**Dry**	**Wet**	**Annual**	**Dry**	**Wet**
Adult female	28.3	30.1	30.1	36.9	40.0	35.1	60.0	48.6	52.1
Adult male	36.9	40.0	35.1	0.0	0.0	0.0	47.0	37.1	40.1
Sub-adult female	60.0	48.6	52.1	47.0	37.1	40.1	-	-	-

4. Site fidelity and home range shifts

4.1 Constancy of home ranges. Average home range center shift for L046, L195, L345, L390 and L467 showed a high degree of home range constancy (Table 8, 9); the mean activity radii was 0.81 km. In contrast, females L025, L035 and male L055 showed greater activity radii and home range shifts, which were 3.63, 1.18 and 1.63 km respectively. A typical example of home range constancy are females L046 and L195 (Figure 25). Both of their activity radii and home range shifts were in the range of 0.72 to 0.76 km.

Table 8 Leopard activity radii

Kilometers

Collar frequency	**Mean**	**Max**	**Min**	**S.D.**	**N**
L025	2.84	4.13	0.49	1.17	9
L035	1.60	4.81	0.55	1.39	10
L046	0.74	1.42	0.25	0.35	17
L195	0.72	1.38	0.31	0.32	15
L345	0.55	1.18	0.30	0.31	7
L390	0.96	1.39	0.23	0.51	4
L467	1.09	1.87	0.52	0.43	13
L055	3.80	6.53	1.01	1.70	12

Table 9 Shift in leopard home range centers

Kilometers

Collar frequency	Mean	Max	Min	S.D.	N
L025	3.63	7.46	0.10	2.94	8
L035	1.18	5.11	0.22	1.53	9
L046	0.73	2.17	0.20	0.48	16
L195	0.76	1.72	0.10	0.57	14
L345	0.60	0.91	0.10	0.31	6
L390	1.39	2.06	0.98	0.59	3
L467	0.79	1.59	0.17	0.39	12
L055	1.63	4.49	0.55	1.08	11
L550	0.83	1.38	0.38	0.48	4

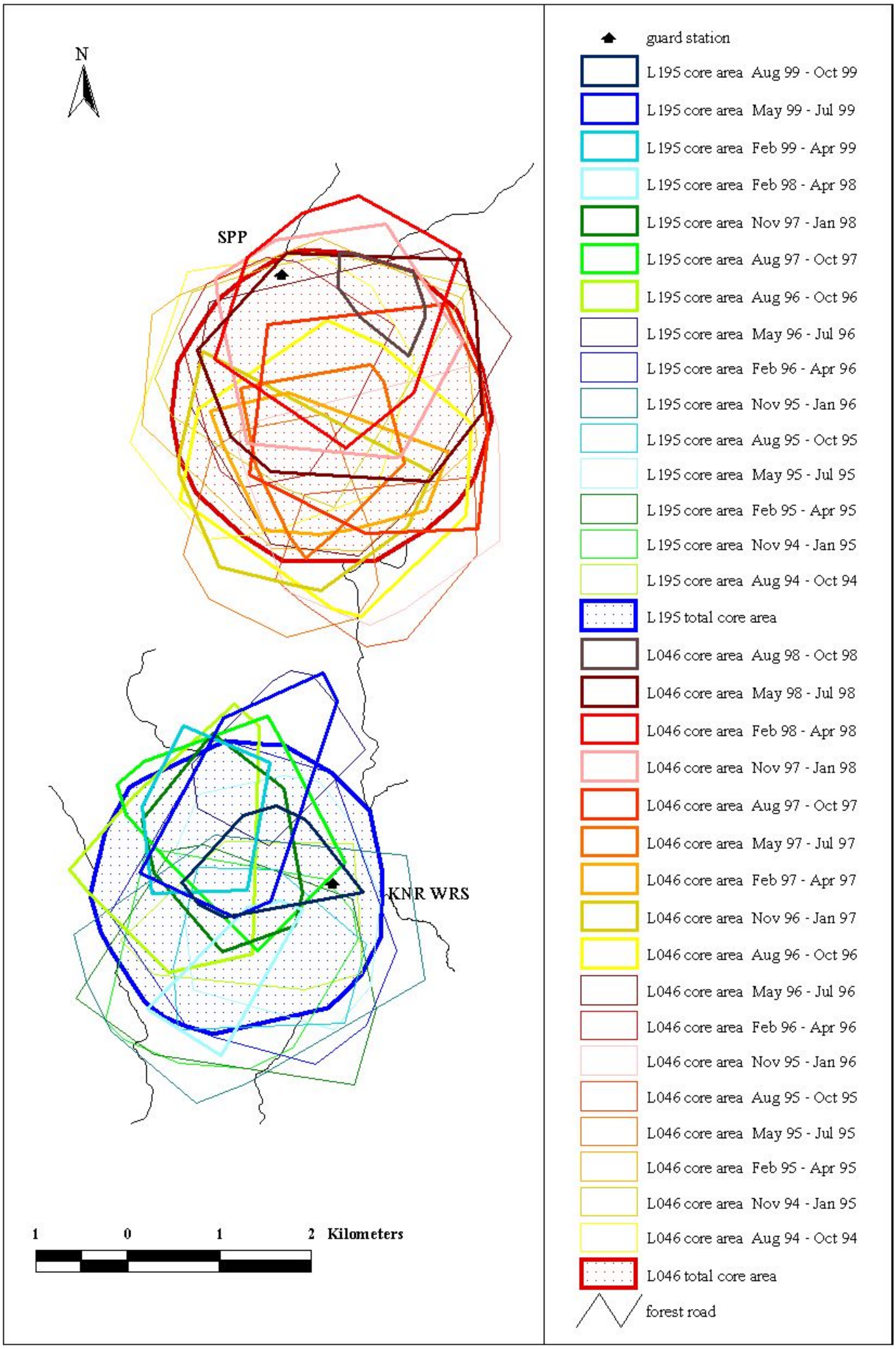


Figure 25 Leopards L195 and L046 50% MCP home ranges for every 3 month segment.

4.2 Shift in home ranges Two females shifted their home range during this study. The first was L025. She was an older female based on her tooth wear and after tracking her for 9 months she shifted her home range to the north approximately 6 km into the home range of L046. Her mean home range center from May, 1995 to January, 1996 averaged 6.80 km. During this period she moved back and forth 4 times between the territories of females L046 and L195 (Figure 26). Her 50% minimum convex polygon in relation to those of females L046 and L195 show considerable overlap during five time periods. During the last time period, August to October 1996, she moved to the southwest part of L195's range and their 50% MCP home ranges did not overlap (Figure 26).

The other female L035 was a sub-adult daughter of L345. She was collared within L345's territory and remained there for 5 months and then shifted to the north to establish a home range with no MCP overlap with L345. Her activity radii before and after the move shifted 5.1 km in 13 months.

One male, L055 made a territorial shift. He began moving north of his home range he used for 15 months and shortly after leaving his previous home range another male was radio collared and this animal's subsequent home range coincided with the preshift home range of L055. The movement of male L055 and the subsequent settle of L550 was also influenced by 2 other male leopards. These animals were camera trapped in L055's former territory when he first started his gradual shift to the north (Figure 27). In the initial stage of L055's shift he moved 2.60 km north) was capture in February, 1996 when it was the resident male. From the camera trap data, it was the only male in the area. He initially settled between KNR to Sub Fa Pha Guard Station. After 15 months he began to shift to the north. His activity radius before the shift was 0.90 km and after the shift it was 0.96 km, as compared to an overall activity radius of 3.8 km. The small radii before and after the shift shows that the male had a high degree of site fidelity. He, however, moved north a distance of 6.2 km vacating his old territory that was eventually taken over by L550 (Figure 28).

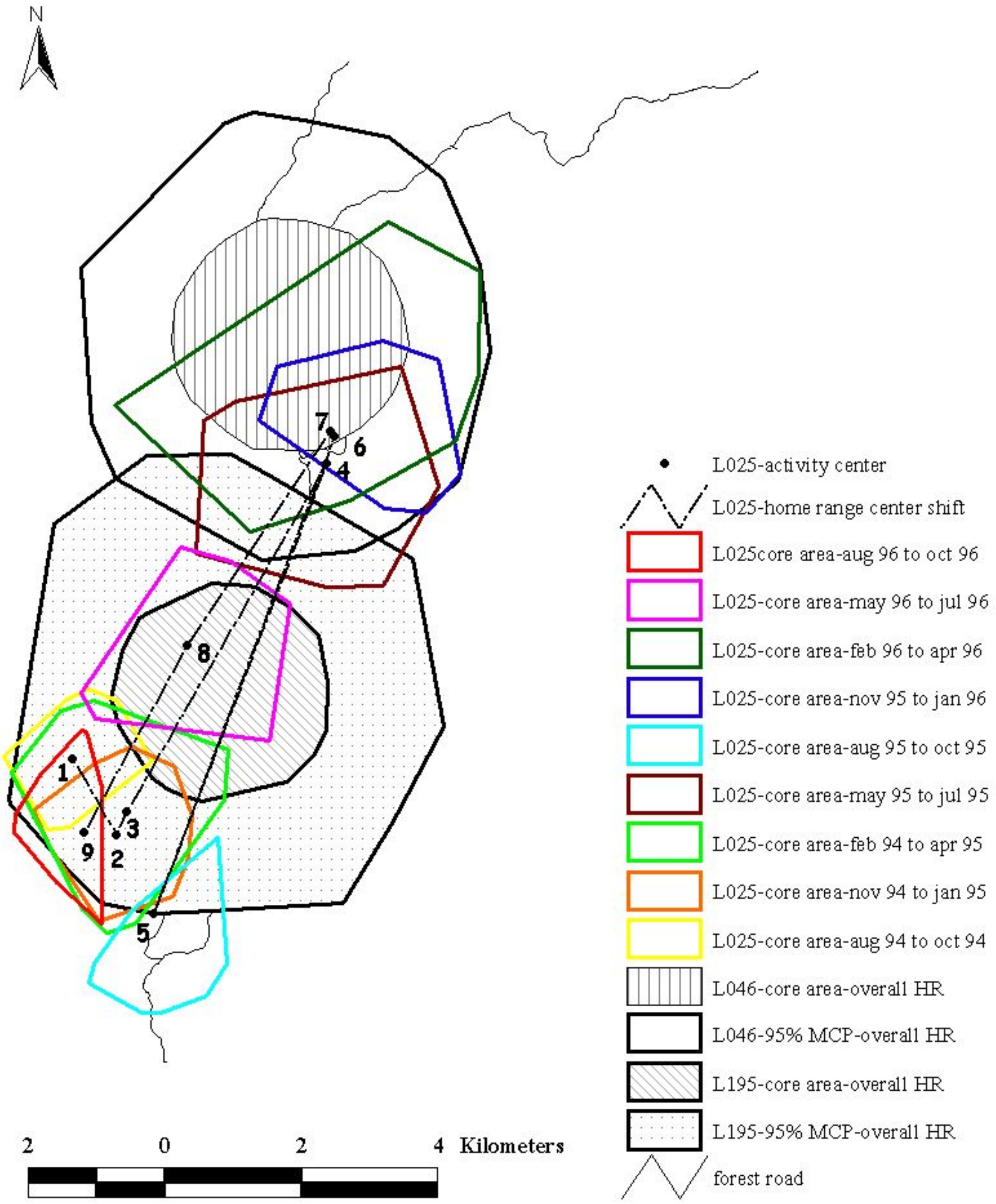


Figure 26 In may 1995 female L025 began a series of home range shifts between the home range of L195 and L046.

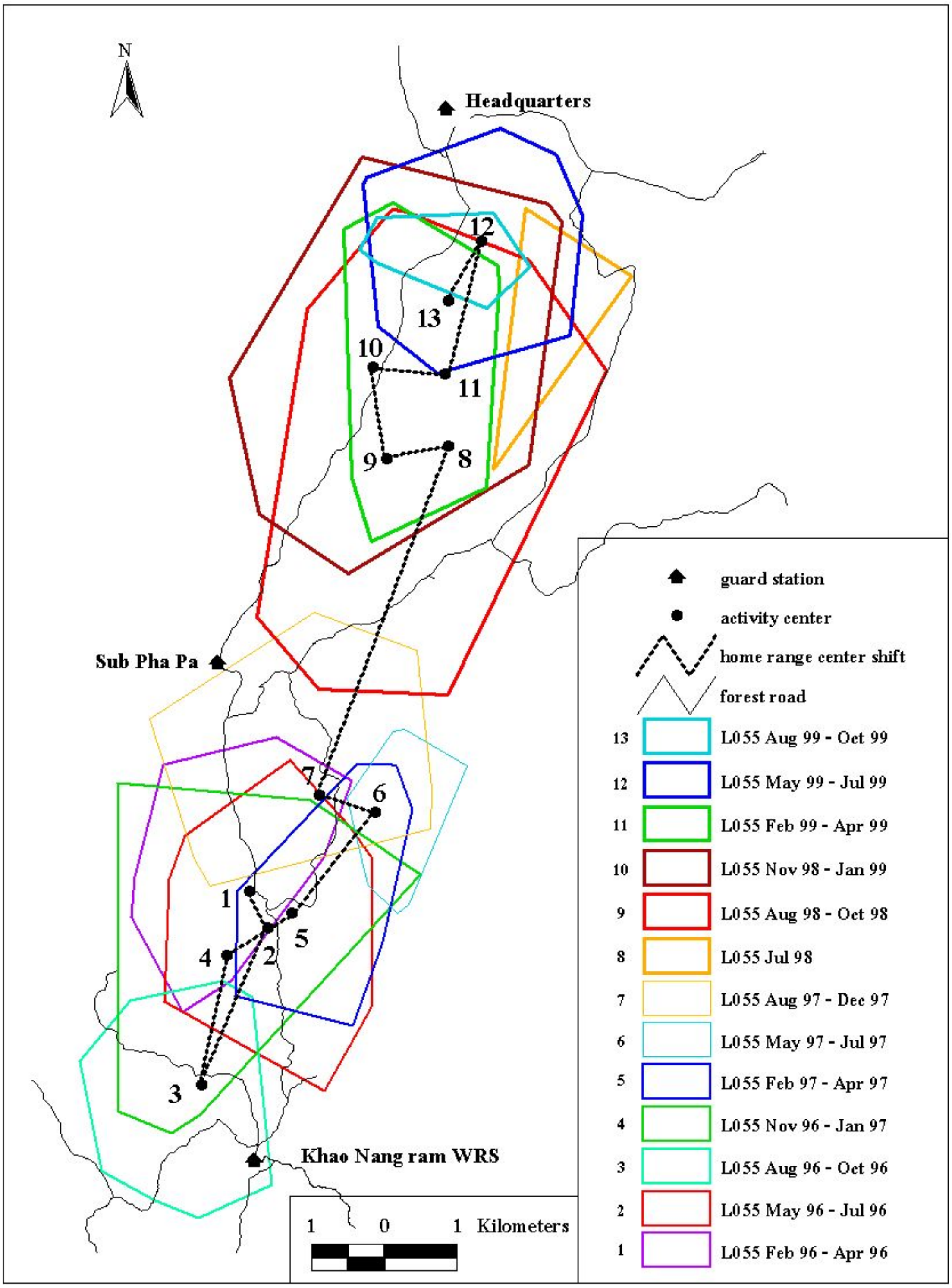


Figure 27 Home range center shifts of L055.

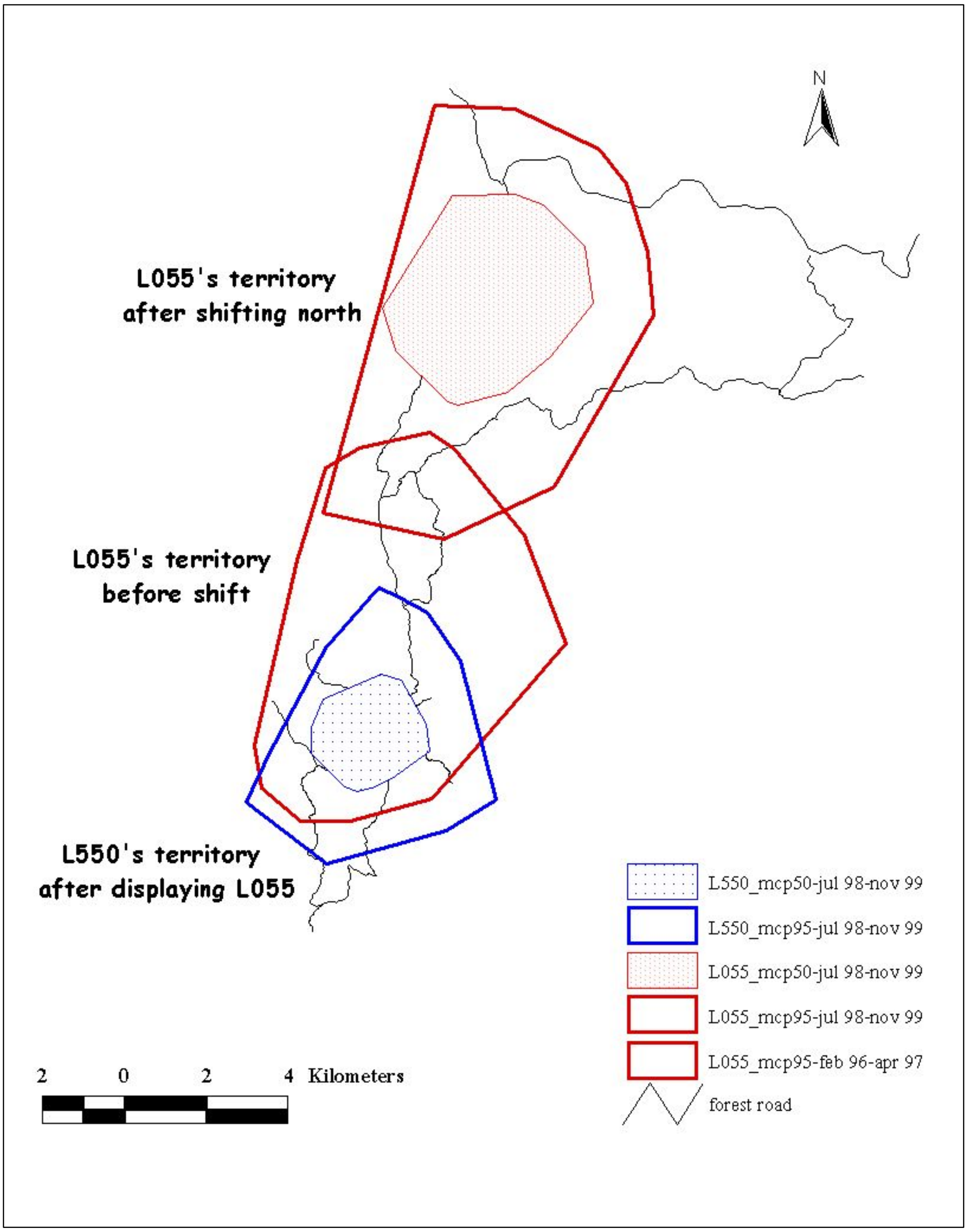


Figure 28 Male L550 occupied the previous core area of L055 and Male L055 established a new territory with no overlap with L550.

5. Movement

Despite a high degree of home range overlap the average daily distance between each leopards was 4.71 km (SD=2.84, n=3126) among females and 11.30 km (SD=3.72, n=92) among males. Between sexes, average distance was 5.33 km (SD=3.79, n=1,197). These distances appear to be over dispersed indicating that despite high home range overlap.

Nine leopards, including sub-adult and adult for both sexes, were radio located once-daily for 74 to 448 days. The average straight line distance between consecutive daily locations for adult males was 2.30 km/day (SD=1.83, n=320) and 1.67 km/day (SD=1.19, n=1602) for females. Daily distance of sub-adult females averaged 1.71 km (SD=1.27, n=195) (Table 10). The maximum daily distances recorded were 13.24, 10.37 and 6.19 km for adult males, adult females and sub-adult females respectively. Minimum daily distance was 44.72, 10.00 and 22.36 m for adult males, adult females and sub-adult females, respectively. Adult male daily movement was significantly different from that of adult female (Wilcoxon rank-sum test, $p<0.001$) or sub-adult female (Wilcoxon rank-sum test, $p<0.001$). The difference between the average daily distance of adult and sub-adult female was not significant (Wilcoxon rank-sum test, $p=0.951$).

Table 10 Daily distance traveled by leopards

Kilometers

Leopard	Mean	Max	Min	S.D.	N
Adult female	1.67	10.37	0.01	1.19	1,602
Adult male	2.30	13.24	0.04	1.83	320
Sub-adult female	1.71	6.19	0.02	1.27	195

6. Camera trap effort

Camera traps were applied in the study, they were set up in a 115.9 km^2 area around Khao Nang Rum WRS. 39-56 cameras were installed for 3-4 months during the dry season of three consecutive years. A total of 2,094 trap nights were conducted: 650 trap nights between Dec 96 and Mar 97, 620 trap nights between Dec 97 and Feb 98 and 824 trap nights between Dec 98 and Mar 99. Camera traps sampled each location for an average of 15 days. Leopards were detected 106 times during 2,094 trap-nights; 43, 39 and 24 times for the three sampling periods, respectively (Table 11).

7. Abundance

Eighteen leopards were photo-captured including 4 adult females, 3 sub-adult females, 3 adult males, 3 sub-adult males and 5 males that could not be identified to age class. From a total of 27 black leopard photographs, 15 photographs were diagnostic for 4 individual leopards; one leopard had a collar and three leopards were identified by their size, sex, and photograph time and location. L055 and L195 were captured every session. Five leopards were captured for two sessions and 11 leopards were capture during only one session.

Capture frequency between sexes was different: males were photographed 1.81 times more than females. The mean male capture rates were 0.77 and 0.18 detections/100 trap nights for adult and sub-adult, respectively. The mean female capture rate was 0.43 and 0.10 detections/100 trap-nights for adults and sub-adults respectively. The average number of photograph locations for individual leopards were 0.56, 0.28, 0.13 and 0.10 locations/100 trap nights for adult males, adult females, sub-adult males and sub-adult females respectively. The highest capture rate male was L055, which was photographed 1.88 detections/100 trap-nights. L390, the highest capture rate female, was photographed 0.61 detections/100 trap-nights.

Closure tests indicate that leopard population was closed (Table 12). The estimates of population size of leopard using model M_h are 10, 10 and 11 leopards for the three sessions respectively. Log-normal-based 95% confidence interval ranged from 10 to 29 leopards for the first session, from 9 to 17 leopards for the second session and from 11 to 26 leopards for the third session. Estimated capture probability over all sampling occasions varied between 0.80 and 0.91. Estimates of average capture probability varied between 0.33 and 0.44 (Table 12).

8. Density

For the three sessions, the camera trap areas were 42.05, 57.86 and 96.93 km^2 respectively. The number of animals which the camera trapped at least twice was six for all three sessions. Average maximum distances moved by photographed leopards ranged from 3.19 to 4.65 km. The estimate boundary strip widths were 1.59(SD=0.72), 2.33(SD=0.98) and 1.81(SD=0.37) km respectively (Table 13). The estimated effective area, which included the camera trap area and the boundary strip, were 126.93, 191.76 and 226.44 km^2 for the three sampling periods, respectively. In these areas, the estimated population sizes were 10, 10 and 11 leopards, respectively. These estimates were used in conjunction with Equation 1 to estimate leopard density. The estimated leopard densities were 7.9±5.8 to 5.2±3.1 and 4.9±2.3 leopards/100 km^2 for the three sampling periods, respectively (Table 14). The average leopard density in this study was 6.0 leopards/100 km^2.

Table 11 Summary statistics for camera trap data on leopards in HKK

Session	**Sampling period**	**No. locations**	**Effort (trap nights)**	**No. detec-tions**	**No. photo-graphs**	**No. individual caught (M_{t+1})**	**No. occasions**
1	12/1996-3/1997	39	650	43	44	9	5
2	12/1997-2/1998	49	620	39	50	8	5
3	12/1998-3/1999	56	824	24	32	10	5

Table 12 Estimated abundance and capture probabilities of leopards in HKK under model M_h of program CAPTURE

		Estimates based on M_h			
Session	**Closure test (p)**	$\hat{p}$	***M(t+1)/N***	***N(SE(N))***	**95% CI**
1	0.81	0.44	0.90	10 (3.01)	10-29
2	0.95	0.42	0.80	10 (1.76)	9-17
3	0.37	0.33	0.91	11 (2.48)	11-26

Notes: M(t+1) is the total number of leopards captured in all occasions, M(t+1) is the probability of a leopard present being caught over the whole sample period and $\hat{p}$ is mean probability of each leopard being caught in each occasion. SE(N) was calculated by the jacknife estimator used in CAPTURE.

Table 13 Calculated effective area using half the mean maximum distance moved by leopards caught on more than one occasion

Session	**camera trap area (km^2)**	***M***	**Maximum distance moved (km)**		**Buffer width (km)**		**Effective area (km^2)**	
			$\bar{d}$ **(km)**	**SE(d)**	W **(km)**	**SE(W)**	**$\hat{A}(W)$ (km^2)**	**SE($\hat{A}(W)$)**
1	42.05	6	3.19	0.59	1.59	0.30	126.93	11.80
2	57.86	6	4.65	0.80	2.33	0.40	191.76	19.56
3	96.93	6	3.62	0.30	1.81	0.15	226.44	8.09

Notes: camera trap area is the area enclosed by the perimeter camera traps, m is the number of tigers caught on more than one occasion.

Table 14 Estimated leopard density and detectable change using program CAPTURE and calculated effective area A(W)

Session	***D* (leopards/100km^2)**	**SE(*D*)**	**95% CI**
1	7.9	2.9	2.1 to 13.7
2	5.2	1.6	2.1 to 8.3
3	4.9	2.6	2.6 to 7.2

9. Prey selection

A total of 367 leopard scats were collected: 239 scats in dry season and 128 scats in wet season. The average diameter of scat was 2.59±0.59 cm. The result of leopard scats analysis showed that 2.48% of hair could not be identified, while 78.47%, 19.35% and 1.09% of scats contained one, two, and three types of prey respectively. Three scats (0.81%) contained only grass and one scat (0.27%) contained only soil. A total of 26 prey species were recorded. Sambar deer (*Cervus unicolor*) was the highest percentage occurrence (25.96%). The percentage occurrence of Malayan porcupine (*Hytrix brachyura),* wild boar (*Sus scrofa*) and barking deer *Muntiacus muntjak),* was 13.77%, 12.87 and 12.19% respectively. Ungulates were consumed the most (58.92%), particularly sub-adult ungulates. Primates were found in 15.80% of scats. In addition, reptiles, carnivores and insects were found, but with low percentage occurrences (Table 15).

9.1 Seasonal diet. The scats collected during November-April were categorized as dry season samples, and those collected during May-October as wet season samples. The diet compositions of wet season and dry season were different. The highest percentage occurrence of prey species in the dry season was sambar deer. Wild boar was the highest percentage occurrence in the wet season. The minor prey species during both seasons were barking deer, Malayan porcupine, banteng and macaque. Hairs and hooves of sambar deer and wild boar found in scats revealed that leopards consumed sub-adult prey more than adult prey. The principal preys were split into two categories: ungulate (sambar deer, wild boar, serow, banteng and gaur) and primate (macaque and leaf monkey). There was a negative relationship between these two groups with respect to the leopard's diet. In the dry season, the percentage occurrence of ungulates was 62.91% whereas the percentage occurrence of primate was 13.07%. Ungulate occurrence decreased in the wet season (51.89%) whilst the percentage occurrence of primate increased (20.63%) (Table 16).

Table 15 Frequency of the leopard's preys according to fecal analysis (n=367)

Species		**Frequency**	**Percentage occurrence**
Sambar deer	*Cervus unicolor*	105	25.96
Wild boar	*Sus scrofa*	57	12.87
Barking deer	*Muntiacus muntjak*	54	12.19
Banteng	*Bos javanicus*	30	6.77
Serow	*Capricornis sumatraensis*	3	0.68
Gaur	*Bos gaurus*	2	0.45
Langur	*Presbytis* spp.	24	5.42
Stump-tailed macaque	*Macaca arctoides*	13	2.93
Pig-tailed macaque	*Macaca nemestrina*	10	2.26
Slow loris	*Nycticebus coucang*	10	2.26
White handed gibbon	*Hylobates lar*	6	1.35
Rhesus macaque	*Macaca mulatta*	5	1.13
Crab-eating macaque	*Macaca fascicularis*	4	0.90
Malayan porcupine	*Hystrix brachyuran*	61	13.77
Rat	F.Muridae	4	0.90
Bamboo rat	*Rhizomys sumatraensis*	2	0.45
Siamese hare	*Lepus pegueensis*	2	0.45
Bay bamboo rat	*Rhizomys badius*	1	0.23
Malayan pangolin	*Manis javanica*	3	0.68
Small Indian civet	*Viverricula malaccensis*	2	0.45
Asiatic jackal	*Canis aureus*	1	0.23
Unknown mammal		11	2.48
Snake		8	1.81
Clouded monitor	*Varanus bengalensis*	2	0.45
Commom butterfly lizard	*Leiolepis belliana*	1	0.23
Beetles	*F.Cerambycidae*	1	0.23
Termites	*Macrotermes* spp.	7	1.58
Grass and soil		4	0.90
Total		443	100.00

Table 16 Comparison of the leopard's seasonal diet

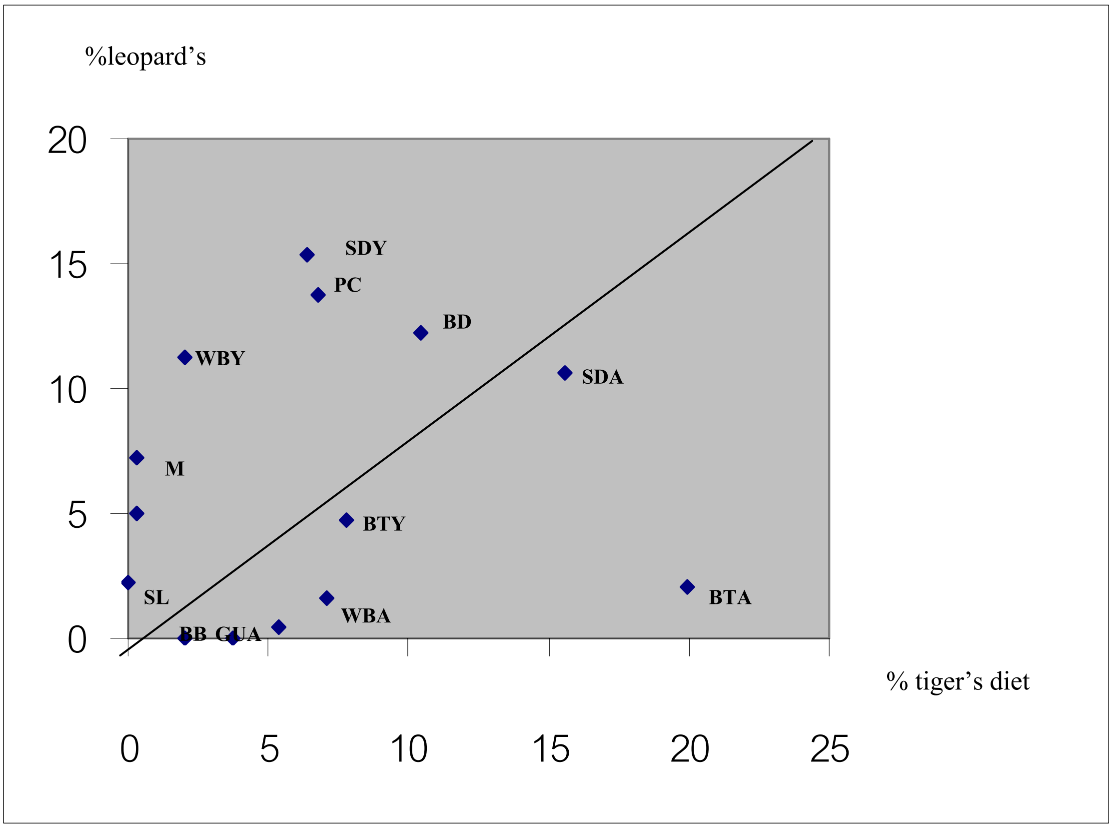
Species		Occurrence (%)	
		dry season	**wet season**
Sambar deer(young adult)	*Cervus unicolor*	20.21	6.92
Sambar deer(adult)	*Cervus unicolor*	14.54	3.77
Wild boar(young adult)	*Sus scrofa*	2.48	27.04
Wild boar(adult)	*Sus scrofa*	1.77	1.26
Barking deer	*Muntiacus muntjak*	13.48	10.06
Banteng(young adult)	*Bos javanicus*	6.03	2.52
Banteng(adult)	*Bos javanicus*	2.84	0.63
Serow	*Capricornis sumatraensis*	1.06	0
Gaur(young adult)	*Bos gaurus*	0.71	0
Langur	*Presbytis* spp.	4.61	5.66
Macaque	*Macaca spp.*	4.26	12.58
Slow loris	*Nycticebus coucang*	2.84	1.26
White handed gibbon	*Hylobates lar*	1.42	1.26
Malayan porcupine	*Hystrix brachyuran*	12.77	15.72
Rat	F.Muridae	0.35	1.89
Large bamboo rat	*Rhizomys sumatrensis*	0.35	0.63
Siamese hare	*Leppus pegueensis*	0.35	0.63
Bay bamboo rat		2.13	1.26
Malayan pangolin	*Manis javanica*	1.06	0
Small Indian civet	*Viverricula malaccensis*	0.35	0.63
Asiatic jackal	*Canis aureus*	0.35	0
Unknown mammal		3.19	3.77
Clouded monitor	*Varanus bengalensis*	0.71	0
Common butterfly lizard	*Leiolepis belliana*	0	0.63
Termites	*Macrotermes* spp.	2.13	0.63
Beetles	F.Cerambycidae	0	0.63

9.2 Density of principal prey species scats. A total of 1,800 circular plots covering 22,628.57 m^2 were surveyed for the presence of scats of five principal prey species: barking deer, sambar deer, banteng, gaur and wild boar. The results showed that the sambar deer's scats have the highest occurrence (84.31%) and highest density (304.04 scats/ha). The percentage of occurrence of other ungulates ranged from 1.72% to 6.50%. Wild boar scat had the lowest density (Table 17).

Table 17 Density of principal prey species scats

Species	**number of scats**	**Percentage occurrence**	**scat density (scats/ha.)**
Barking deer	53	6.5	23.42
Sambar deer	688	84.31	304.04
Banteng	44	5.39	19.44
Gaur	17	2.08	7.51
Wild boar	14	1.72	6.19

9.3 The comparison between the diet of the leopard and the tiger. The results of the scat analysis were compared to the study of tiger diet by Phetdee (2000). Phetdee's study of tiger diet in Huai Kha Khaeng Wildlife Sanctuary showed that tigers consumed at least 18 prey species. The results of this study showed that leopard consume at least 24 prey species. Comparison of prey species consumed by both cats shows an overlap of 13 prey species as summarized in Table 18. Leopard had 72.22% diet overlap with tiger and tiger had 54.16% diet overlap with leopard.



Notes: WBY=Young adult wild boar, WBA=Adult wild boar, SDY=Young adult sambar deer, SDA=Adult sambar deer, BTY=Young adult Banteng, BTA=Adult banteng, GUY=Young adult gaur, GUA=Adult gaur, SL=Slow loris, LG=langur, MC=Macaque, BB=Asiatic black bear, PC= Malayan porcupine, BD=Barking deer

Figure 29 The relationships between leopard's diet and tiger's diet.

The 10 prey species with a percentage occurrence of more than 2% were Asiatic black bear, Malayan porcupine, slow loris, macaque, leaf monkey, barking deer, wild boar, sambar deer, banteng and guar. These 10 prey species were found in 87.85% of tiger scat and in 86.46% of leopard scat. The percentage occurrences of these prey species are shown a comparison graph (Figure 29). The data show that tigers consume more of the following prey species than leopards: black bear, adult gaur, young adult gaur, adult wild boar, adult banteng, young adult banteng and adult sambar deer. Leopards consume more of the following species than tigers: slow loris, leaf monkey, young adult wild boar, barking deer, Malayan porcupine, young adult sambar deer.

Table 18 Comparative species composition of tiger and leopard scats

Species		**Tiger(%)**	**Leopard(%)**
Banteng(adult)	*Bos javanicus*	19.93	2.04
Sambar deer(adult)	*Cervus unicolor*	15.54	10.66
Barking deer	*Muntiacus muntjak*	10.47	12.24
Banteng(young adult)	*Bos javanicus*	7.77	4.76
Wild boar(adult)	*Sus scrofa*	7.09	1.59
Malayan porcupine	*Hystrix brachyuran*	6.76	13.83
Sambar deer(young adult)	*Cervus unicolor*	6.42	15.42
Gaur(young adult)	*Bos gaurus*	5.41	0.45
Unknown mammal		4.05	2.49
Gaur (adult)	*Bos gaurus*	3.72	0.00
Wild boar(young adult)	*Sus scrofa*	2.03	11.34
Asiatic black bear	*Ursus thibetanus*	2.03	0.00
Malayan pangolin	*Manis javanica*	1.69	0.68
Ants		1.69	0.00
Asiatic jackal	*Canis aureus*	1.01	0.23
White handed gibbon	*Hylobates lar*	0.68	1.36
Grass and soil		0.68	0.91
Water buffalo	*Bubalus bubalis*	0.68	0.00
Hog badger	*Arctonyx collaris*	0.68	0.00
Maccaque	*Macaca* spp.	0.34	7.26
Langur	*Presbytis* spp.	0.34	4.99
Termites	*Macrotermes* spp.	0.34	1.59
Small Indian civet	*Viverricula malaccensis*	0.34	0.45
Common palm civet	*Paradoxurus hermaphroditus*	0.34	0.00
Slow loris	*Nycticebus coucang*	0.00	2.27
Snake		0.00	1.81
Rat	F.Muridae	0.00	0.91
Serow	*Capricornis sumatraensis*	0.00	0.68
Clouded monitor	*Varanus bengalensis*	0.00	0.45
Largebamboo rat	*Rhizomys sumatrensis*	0.00	0.45
Siamese hare	*Leppus pegueensis*	0.00	0.45
Beetles	*F.Cerambycidae*	0.00	0.23
Commom butterfly lizard	*Leiolepis belliana*	0.00	0.23
Bay bamboo rat	*Rhizomys badius*	0.00	0.23
Total		100.00	100.00

10. Home range size for habitat selection

Adult female leopards had a mean annual 95% FK home range (n=6) of 26 km^2 (SD=8.2), a wet season home range (n=5) of 25.8 km^2 (SD=7.8) and a dry season home range (n=6) of 29.2 km^2 (SD=12.5). Mean 95% FK annual home range size for the two sub-adult females still living in their natal areas was 29 km^2 (SD=5.5). One sub-adult female had a wet season home range of 30.6 km^2, and a dry season home range of 27.4 km^2. The two adult males had annual home ranges of 56.1 km^2 (SD=8.5) and 35.2 km^2, and dry home ranges of 55.2 km^2 (SD=21) and 41.3 km^2. The one adult male wet home range recorded was 72.3 km^2.

A Wilcoxon paired rank *t*-test (α=0.05) revealed no significant difference (p=0.059) between 95% wet and dry adult female FK home ranges.

11. Habitat selection

The minimum number of individuals needed for compositional analysis is 6, so all leopards with adequate number of locations (n=9) were pooled together, irrespective of demographic group.

Results can be unsound if one or more animals are not recorded using one of the habitat types within a coverage type, in which case the zero value can be replaced by a number less than 0.1 times the next lowest observed value (Aebischer *et al.*, 1993). However, in this study all leopards were recorded in all classes of all habitat types.

11.1 Vegetation**.** Evaluating second order selection (study area vs. 95% FK), leopards showed significant habitat selection for all time periods (combined, dry and wet). In every case mixed deciduous was selected the most, followed by dry evergreen and dry dipterocarp. The paired *t*-test between habitat types showed a significant difference between selection of dry evergreen and dry dipterocarp.

For third order (95% FK vs. buffered locations within 95% FK), only wet season locations produced a significant result; dry dipterocarp was selected the most, followed by dry evergreen and mixed deciduous. None of the paired *t*-test results testing selection between habitats were significant.

11.2 Slope. At the second order level for combined and wet periods, slope types were selected significantly differently from random. In both cases, moderate slope was ranked first followed by flat and steep slope. Steep slope was selected for significantly less than expected.

Table 19 Combined, seasonal home range size (95% FK) of captured leopard

Collar frequency	Sex	Age class	Locations	Combined season home range size (km)	Dry season home range size (km)	Wet season home range size (km)
L025	F	Adult	412	40.7 ± 32.3	46.4 19.5	38.8 ± 34.5
L035	F	Adult	275	20.7 ± 4.9	22.7	18 ± 5.9
L046	F	Adult	848	28.9 ± 13.3	34.9 ± 7.6	24.7 ± 8
L195	F	Adult	603	26 ± 9.1	38.2 ± 20.9	23 ± 4.4
L345	F	Adult	302	17.8 ± 7	16.7 ± 5.4	24.5
L390	F	Adult	160	22	15.9	-
Mean	**F**	**Adult**	**433**	**26.0 ± 8.2**	**29.2 ± 12.5**	**25.8 ± 7.8**
L035	F	Sub-adult	154	25	-	-
L467	F	Sub-adult	353	32.9 ± 2.6	27.4 ± 4.1	30.6 ± 2.5
Mean	**F**	**Sub-adult**	**254**	**29 ± 5.5**	**27.4**	**30.6**
L055	M	Adult	422	56.1 ± 8.5	55.2 ± 21	72.3 ± 4.16
L550	M	Adult	168	35.2	41.3	-
Mean	**M**	**Adult**	**295**	**45.7 ± 14.8**	**48.3 ± 9.8**	**72.3**

Table 20 Compositional analysis of leopard habitat selection

Habitat class	Selection order	Period	Lambda	P	Habitat type ranking
Vegetation	2nd	Combined	0.10	<0.001	mix. decid >dry EG >>dry dipt
	2nd	Wet season	0.16	<0.001	mix. decid >dry EG >>dry dipt
	2nd	Dry season	0.05	<0.0001	mix. decid >dry EG >>dry dipt
	3rd	Combined	0.80	0.30	-
	3rd	Wet season	0.04	<0.05	dry dipt > dry EG > mix. Decide
	3rd	Dry season	0.74	0.69	-
Slope	2nd	Combined	0.39	<0.05	moderate >flat >>steep
	2nd	Wet season	0.41	<0.05	moderate >flat >>steep
	2nd	Dry season	0.52	0.051	
	3rd	Combined	0.32	<0.05	flat >> moderate >> steep
	3rd	Wet season	0.25	<0.05	flat >> moderate > steep
	3rd	Dry season	0.14	<0.001	flat >> moderate > steep
Stream	2nd	Combined	0.80	<0.05	Stream >> dry
	2nd	Wet season	0.74	<0.05	Stream >> dry
	2nd	Dry season	0.47	<0.05	Stream >> dry
	3rd	Combined	0.69	0.07	-
	3rd	Wet season	0.94	0.49	-
	3rd	Dry season	0.82	0.12	-

Notes: Lambda = Wilk's lamda statistic computed from the matrix of log ratio differences and p = probability of their being no overall habitat selection. Habitats are listed in order of rank, from most to least selected, with >> indicating a significant difference in selection between two habitat types. For vegetation class dry eve. = dry evergreen, mix. dec. = mixed deciduous and dry dip. = dry dipterocarp. For slope class flat = 0-12 degrees, moderate = 13-24 degree and steep = 25-49 degrees For stream class stream = all area within 150 m from water courses and dry = all area not within 150 m from water courses.

Third order selection analysis inferred significant differences for all time periods. As slope increased selection decreased, with flat always being selected for significantly more and steep selected significantly less for combined seasons.

11.3 Water courses For all time periods at the second order level, leopards selected significantly more stream type (the area encompassed by the 150 m buffer surrounding all streams and rivers) than dry type.

At the third order level there was no significant difference between proportion of selected and available habitat types (Table 20).

Discussion

1. Body size

The weights of leopards in this study were within the mid-range of leopard weights across the species range. There are not enough data across the all studies to examine geographic or latitudinal trends in leopard weights (Table 1). However, in this study females were slightly heavier (30.3 kg) than the mean for 7 other studies (27.9 kg) (Table 1) and the weight of males was less (40.2 kg) than elsewhere (49.0 kg) resulting in a lower sexual dimorphism ratio (1:1.3) than the mean of other studies (1:1.8).

2. Home range size and spatial dynamic

Home range sizes in leopards varied from 6 km^2 in Royal Chitwan National Park, Nepal (Seidensticker *et al.*, 1990) to 1,137 km^2 in the Kalahari Desert in Africa. (Bothma *et al.*, 1997). The mean home range size of females (27.1 km^2) and males (48.7 km^2) in Huai Kha Khaeng falls in the mid-range of all studies. Food is main factor to determine home range size among female leopards particularly during cub-rearing (Cavallo, 1993). Karanth *et al.* (2004) found a similar pattern in tigers; home range size decreased as prey increased. Royal Chitwan National Park has the highest prey biomass of any of the leopard studies and the Kalahari has extremely low prey density (Table 21).

If the food resources unsteady, Mizutani and Jewell (1998) said that leopard home range must be large enough to meet the energy requirement when prey abundance is lowest. In Huai Kha Khaeng home range size did not vary yearly or seasonally, which suggests the food supply is stable seasonally.

Table 21 Home range sizes of leopards in other studies

		Home range size (km^2)		**Mean home range size (km$^{2)}$)**			
Study area	**Habitat**	**Total**	**Peeled**	**Adult female**	**Adult male**	**Method**	**Source**
Huai Kha Kheang WS, Thailand	Tropical forest	11.4-27.0		11.4(1)	27.0(1)	radio-tracking	Rabinowitz (1989)
Kaeng Krachan NP., Thailand	Tropical forest	8.8-18.0		8.8(1)	17.7(2)	radio-tracking	Grassman (1999)
Royal Chitawan NP,Nepal	Subtropical forest	8	-	8(1)	-	radio-tracking	Seidensticker (1976)
Royal Chitawan NP,Nepal	Subtropical forest	6.0-13.0		8.7(3)	-	radio-tracking	Seidensticker *et al.* (1990)
Bardia NP, Nepal	Subtropical forest	17.1-50.4	-	17.1(1)	35.3(2)	radio-tracking	Odden & Wegge (2005)
Wilpatu NP, Sri Lanka	Tropical forest	8.0-10.0	-	-	-	radio-tracking	Muckenhirn&Eisenberg (1973)
Serengeti NP,Tanzania	Wooded grassland	-	40.0-60.0	**40.0-60.0**(1)	-	Sightings	Schaller(1972)
Serengeti NP,Tanzania	Wooded grassland	22.5-33.8	-	22.5(1)	-	Sightings	Cavallo (1990)
Serengeti NP,Tanzania	Wooded grassland	15.9-17.8	-	15.9(1)	-	radio-tracking	Bertram (1982)
Rhodes matopos NP, Rhodesia	Wooded grassland	10.0-19.0	-	-	-	spoor & sighting	Smith (1978)
Cape Province,South Africa	Fynbos mountain	444.0-670.0	388.0-487.0	-	444.0,**388.0**(1)	radio-tracking	Norton & Lawson (1985)
Cape Province,South Africa	Fynbos mountain	53.5-127.7	42.1-66.8	-	51.0, **49.5**(3)	radio-tracking	Norton & Henley (1987)
Londolozi Game Reserve,South Africa	Woodland savannah	33	23	33.0, **23.0**(1)		radio-tracking	Le Roux & Skinner (1989)
Kruger NP,South Africa	Woodland savannah	5.6-96.1	-	15.8(6)	**36.4**(7)	radio-tracking	Bailey (1993)
Kalahari Desert,Southern Africa	Semi-arid savannah	800	-	-	800(-)	Spoor	Bothma & Le Riche (1984)
Kalahari Desert,Southern Africa	Semi-arid savannah	-	94.0-1,803.0	**290.8**(5)	**1,137.0**(3)	radio-tracking	Bothma *et al.* (1997)
Lolldaiga Hills ranch, Kenya	Wooded grassland	9.7-109.8	7.0-43.1	**16.9**(3)	**37.1**(2)	radio-tracking	Mizutani & Jewell (1998)
Tsavo NP, Kenya	Semi-arid grassland and savannah	11.5-120.6	9.1-63.4	14.1(-)	**36.3(-)**	radio-tracking	Hamilton (1976)
North-eastern Namibia	Semi-arid savannah	-	88.1-1,163.5	**177.2**(3)	**345.0**(6)	radio-tracking	Stander *et al.* (1997)
Taï NP, Ivory Coast	Tropical forest	12.3	-	-	-	Sightings	Hoppe-Dominik (1984)
Taï NP, Ivory Coast	Tropical forest	22.2-85.6	-	25.4(2)	85.6(1)	radio-tracking	Jenny (1996)

Note: Numbers in bold are peeled mean home range size.

The overall home range of 5 of 7 females was nearly constant throughout the study (L046, L195, L390, L345 and L467). There are small shifts with years (3 month intervals) and between years, but these females remained in the same area throughout their lives (Figure 25). Smith *et al.* (1987) found a similar pattern in tigers. In both species there are slight shifts by the mother that allows the daughter to settle nearby as the case with L046 (mother) and L467 (daughter) (Figure 23).

The home range of L035, a sub-adult when she was collared, shifted as indicated by an overall home range of double her annual home range (Table 5). She may have been a young animal exploring to find a place to settle. When she shifted her annual home range she moved more than 5 km. This pattern is consistent with a dispersing female shifting from her natal area to a breeding home range.

Male L055, an adult male, had a strong site fidelity for 15 months and then 2 males were photographed within his home range at about the time he shifted to the north. His continual shift northward appeared to be in response to these other males and subsequently a third male took over the former home range of L055. The accumulative home range area curve of L055 showed a sudden increase in overall home range size, due to the home range shift. However the pre-home range (48.6 $km^{2)}$ and post-home range (56.6 km^2) were similar. From these data, it is not clear that L055 was pushed out; given than his home range increased 8 km^2, he may have been shifting to increase access to females.

Home range size of male leopards was significantly larger than female home range size in Huai Kha Khaeng and elsewhere (Rabinowitz, 1989; Bailey, 1993; Jenny, 1996; Bothma *et al.*, 1997; Stander *et al.*, 1997; Mizutani and Jewell, 1998; Grassman, 1999; Odden and Wegge, 2005). The ratio of male to female home range size in Huai Kha Khaeng was 1.8 to 1. This differs drastically from tigers where male home range size varies from 2 to 7 times larger than female home range size (Smith *et al.* 1987). One explanation for this species difference is the higher female home range overlap in Huai Kha Khaeng leopards (38.6%) versus the low overlap in tigers (3-7%). In South Africa the home range overlap of female leopards was lower than in Huai Kha Khaeng (18%) (Bailey 1993), but still much higher than tigers. Male leopards can access several overlapping females with a much smaller home range size relative to female home range than a tiger can have.

Highly overlapping home ranges of leopards found in this study may be due to higher habitat quality in the study area. The presence of streams and flat to moderate slopes are prime habitat for sambar (*Cervus unicolor*) and barking deer (*Muntiacus muntjak*) (Sukmasuang and Kutintara, 2001; Sukmasuang, 2004). This agrees with my compositional analysis of second order habitat selection (home range selection), which identified flat to moderate slope and areas close to stream channels as important habitat types for leopards.

The overlapping home range between sexes of leopard was reported in many areas (Le Roux & Skinner, 1989; Bailey, 1993; Stander *et al.*, 1997; Mizutani and Jewell, 1998; Grassman, 1999) and is similar to tigers (Smith *et al.*, 1987). Females established their home range within male home range and males exclude other males. This pattern results in males having access to several females. Male L055 when he shifted his territory to the north had a territory that partially overlapped with 4 females. This pattern of polygamous mating system is common in many cat species (Sunquist 1981, Kitchener, 1991; Mizutani and Jewell, 1998).

For sub-adult female, their home ranges and core areas were highly overlapped (72.47% and 60.01%) with adult females. This was probably because the sub-adults were the offspring of the adults whose range they overlapped (e.g. adult L046 and sub-adult L467). When L046 was collared on January 17, 1996, she had a cub nearby. In June, 1996 a sub-adult female (L467) was captured within is in L046's home range. The locations of L046 and L467 indicate they were associating at least 8 times; 7 times in 1996 and once in 1998. In general, they were often found in close proximity to one another (<500 meters for 29 times over 2 years). In first year, their overlapping home range was 88.61% and 69.08% and their overlapping core area was 81.59% and 52.25% for first and second years, respectively. The results suggest that L046 probably is L467's mother.

A similar, but less clear pattern was that of female L025. A month after L025 was collared, L195 was collared. Based on her pink nipples, she had not had young and her home range was highly overlapped with the home range of female L025. Female L025 subsequent movements back and forth between L195's home range and female's L046 home range (Figure 26). Female L025 also was in close association with L046. Another set of female tracks were observed while tracking L046 and then confirm her association with L025 by radio locating the latter very close to L046. It is unclear who L025 was related to.

A third case of high young female and adult female home range overlap was adult L345 (34.9 kg) and young L035 (24.5 kg). L345 which was the oldest female in this study, had the constant home range through the study. L035 resided in L345's range for 5 months and then moved to a new area that did not overlap her previous home range. This appeared to be another young female shifting to find a breeding home range.

Average daily distance of adult males (2.3 km) was significantly further than adult and sub-adult females (1.67 and 1.71 km), a result in concordance with Bailey (1993) and Mizutani and Jewell (1998) who both reported adult males traveling greater distances than females. In Thailand, Rabinowitz (1989) reported an adult male moved 2.0 km per day (n=35) and Grassman (1997) reported two adult male moved 1.6 (n=30) and 2.8 km per day (n=18) and an adult female moved 1.8 km per day (n=29). Females moved the minimum distances required to obtain prey and rear their young, while the male moved greater distances in order to maximize his reproductive success (Mizutani and Jewell, 1998). Furthermore, others found daily distance influenced by age, physical condition, reproductive status and prey density (Hamilton, 1976; Bothma and le Riche, 1984; Bailey, 1993). An average daily distance and activity radius of L055 in the first capture period was significantly shorter than in the second capture period, which may have due to a change in condition and social status. At the time of the L055's first capture, it was a dominant male in strong physical condition. By the time of it's second capture, it appeared to have lost its home range and dominant male status. However, a different between age classes was not found.

2. Abundance

In this study, 126 photographs of leopards during 2,094 trap-nights (6.02 photographs/100 trap-nights) were obtained. This photo capture rate was higher than obtained in studies in Kaeng Khachan National Park (KKNP), Thailand (3.25 photographs/100 trap-nights, Ngoprasert, 2004) and in Southwest Primorski Krai, Russia (4.69 photographs/100 trap-nights) (Kostyria *et al.*, 2003). In addition, the estimated capture probabilities of this study (0.44, 0.42 and 0.33) were higher than those found in KKNP (0.27, using model M_h) and Southwest Primorski Krai (0.20, using model M_h).

The average maximum distances between capture sites, which varied from 3.19 to 4.65 km, are significantly less than in Southwest Primorski Krai, Russia (9.70 km). Southwest Primorski Krai experiences low temperatures and snow cover in the winter, which are extremal conditions for leopard (Kostyria *et al.*, 2003). These conditions likely result in lower prey densities and higher metabolic requirements, which would cause leopards to hunt over larger areas.

Male leopard photographs were obtained 1.81 times more than female leopard photographs. Ngoprasert (2004) also reported that capture frequency between sexes was different. Male leopards were recaptured more than female leopards (*t*-test, p=0.01). Santiapillai *et al.* (1982) report that male leopards were visually observed more frequently (72%) than female leopards in Ruguna National Park, which parallels the observations of Muckenhirn and Eisenberg (1973) in Wilpattu National Park and Bailey (1993) in Kruger National Park. Bailey (1993) reported that males were captured with less trapping effort than females and were observed more often (63%) than females along tourist roads, although females were observed more often (68%) than males along firebreak roads. Bailey suggested that the females avoided contact with human more than the males. The data support the contention that the females are more reclusive than males (Santiapillai *et al.*, 1982).

Estimated density using capture-recapture averaged 6.0 leopards/100 km^2, which was an average from 3 sampling periods (7.9±5.8, 5.2±3.1 and 4.9±2.3). This average is similar to the mean density of 6.3 leopards/100 km^2, based on 4 years of radio telemetry data (10.1, 6.9, 3.7 and 4.5 leopard/100 km^2 from 1996 to 1999 respectively). Both methods gave similar densities and indicating a decreasing trend of leopard abundance. The average leopard densities in this study were greater than in KKNP (4.78 leopards/100 km^2) (Ngoprasert, 2004) and much greater than in Southwest Primorski Krai, Russia (1.2±0.2 leopards/100 km^2) (Kostryria *et al.*, 2003). Rabinowitz (1989) estimated leopard density to be lower (4 leopards/100 km^2) in Huai Kha Khaeng Wildlife Sanctuary than the results of this study. The average leopard density in this study was lower than that found in Tsavo National Park, Kenya (Hamilton, 1976); Cape Province, South Africa (Norton and Henley; 1987) and Tai National Park, Ivory Coast (Jenny, 1996) but higher than that found in Sri Lanka (Clark, 1901); Wilpattu National Park, Sri Lanka (Eisenberg and Lockhart, 1972); Serengeti National Park, Tanzania (Schaller, 1972; Cavallo, 1993); Kalahari Desert, Southern Africa (Bothma and Le Riche, 1984); Stellenbosch, Cape Province (Norton and Lawson, 1985); Kruger National Park, South Africa (Bailey, 1993); and northeastern Namibia (Stander *et al.*, 1997).

The trend of leopard density decreased throughout the study period, but during the same period the tiger density increased from 1.7±1.0 to 2.9±2.3 tigers/100 km^2. Seidensticker (1976) observed that a tiger may have appropriated a kill from a leopard and believed that social dominance is a major factor in tiger-leopard interaction. He found that leopard was using areas not frequented by tiger to minimize their chance of encounter. Moreover, a female black leopard was killed in the study area. The animal died as a result of a powerful bite to the chest over the heart. Female tiger tracks were found around the carcass.

The leopard density found in this study can be extrapolated to roughly estimate the leopard population size in the 2,780 km^2 Huai Kha Khaeng Wildlife Sanctuary at 166 leopards. If the habitat quality in the Western Forest Complex, which covers an area of 18,727 km^2, were comparable to the HKKWS study area, the estimated leopard population size would be 1,120 leopards. These data indicate that The Western Forest Complex is an important area for leopard conservation. Moreover, data on the abundance and density of leopard will help us to understand their present status in the study area and evaluate habitat quality and success of management.

3. Prey selection

Leopard in Huai Kha Khaeng Wildlife Sanctuary consumed prey of varying size and species, from insects to large mammals. Their principal preys (88.49%) were ungulates, primates and Malayan porcupines (*Hystrix branchyura*). This is in line with other studies undertaken in Africa, India, Sri Lanka, and Thailand (Schaller, 1967; Schaller, 1972; Seidensticker, 1976; Bertram, 1982; Santiapillai *et al.*, 1982; Rabinowitz, 1989; Bailey, 1993; Johnson *et al.*, 1993; Karanth and Sunquist, 1995). The majority of leopard kills were small to medium size.

This study showed that ungulates were the prey that leopards consume in the highest proportion. Pellet density surveys reveal that more than 84% of all pellets were sambar. Pellets of wild boar were found in low density, but leopard scat analysis showed that leopards consumed wild boar in high proportion (12.87%). This discrepency suggests that (a) leopards preferentially hunt wild boar over other more abundant ungulate species or (b) the pellet survey was inaccurate. However, due to the diet of wild boar being earthworm, ground insects and starchy plant roots (Lekagul and Mc Neely, 1977), their pellets contain little fibre and high water content, which leads to more rapid decomposition and may explain the low density of wild boar pellets detected.

Pellet density of banteng and gaur was 7.47% of total pellet occurrence and the frequency of these animals in scats was 7.2%. These results are similar to that reported by Karanth and Sunquist (1995), who reported the percentage of gaur consumed by leopard to be 7.3% in Nagarahole National Park, India. However, Rabinowitz (1989) and Grassman (1997), who studied leopard in Thailand, reported that leopards never consumed banteng and gaur. They reported that the principal prey species of leopard in western Thailand were Artiodactyle ungulates, primates, and Malayan porcupine (*Hystrix branchyura*). The major difference between these studies was the percentage of barking deer and sambar reported in scats. Rabinowitz (1989) reported that leopards consumed 5.4% sambar deer and 43% barking deer. In contrast, this study found sambar deer to be the prey that leopard consumed in the highest proportion, with barking deer at 12.19%. One possible explanation is that prey abundance of these species shifted between the time these studies were made. Leopards in China shifted their primary prey between 1981-1983 and 1984-1987 from tufted deer (85.1%) and virtually no bamboo rat (*Rhizomys sinense*) to 16.1% tufted deer and 41.9-47.6% bamboo rat. This is thought to be because bamboo, *Fargesia robusta* and *Bashania fangiana*, the food preference of bamboo rat, had died. Besides a change in food habitat, mis-identification of prey hair may have been the cause of the differing results. Hair from sub-adult sambar deer, bear, gaur and banteng bear similarities to barking deer hair. The use of light microscopy to identify diagnostic species-specific differences of hair scales and follicles leads to the most accurate scat-based diet analyses.

The weight of southeast Asian ungulates varies dramatically: gaur (650-900 kg), banteng (600-800 kg), sambar deer (185-260 kg), wild boar (75-200 kg), serow (85-140 kg), and barking deer (20-28 kg; Lekagul and McNeely, 1977). Previous research has reported the size of a leopard's prey ranges from 2-175 kg, with an average weight of 37.6 kg (Schaller, 1972; Bertram, 1982; Santiapillai *et al.*, 1982; Karanth and Sunquist, 1995). In the case of large prey species, such as bantang, leopards selectively hunt young individuals (Bertram, 1982). Bertram (1982) agrees observed leopard consuming only 0-4 month old wildebeest *(Connochaetes taurinus*) and topi (*Domalis cus korrigum*) because adults of both species weigh 165-290 kg. There were no studies of banteng and gaur growth rate in Thailand, but Chinchiyanonth and Leangpibule (1998) reported the weight of newborn sambar deer to be around 7-9 kg, 5 months old to be 34-51 kg, and 10 months old to be 52-72 kg.

Weight of a 3-4 month old wild boar was found to be 10 kg, 4-6 months old 15-30 kg, and 1 year old 60-70 kg (Ui-sungnern, 1998; Thongpunchung, 2002; Parker, 1988). This shows that young adult wild boar and young adult sambar deer are of the size suitable for leopard hunting.

The Order Primates, were the second-highest ranked prey of leopard. Primate prey species included *Macac*a spp., *Presbytis* spp., *Hylobates lar* and *Nycticebus coucang*. These species generally remain in the forest canopy, but they are sometimes found on the ground. Ground activities are different among the species. The study area has 4 macaques species: *Macaca arctoides* have a short stumpy tail and spend most of their time on the ground foraging, *M. nemestrina* and *M. mulatta* forage both on the ground and in the canopy, *M. fascicularis* prefer riparian areas and feed on crab and ground animals (Lekagul and McNeely, 1977). Enemy avoidance behavior of macaque is to jump to a lower tree, which sometimes results in their falling to the ground and being hunted by leopard. Macaque kills by leopard were never found during the study period. However macaque kills were found by radio tracking. Langurs have fewer activities on the ground than macaque but they do frequent saltlicks and streams. Bhumpakphan (1988) observed langur alarm behaviour to flee rapidly at the sign of danger, and this jumping and climbing sometime results in their falling to the ground. Bhumpakphan (1988) also observed leopards tug langurs from trees. This study found langurs to comprise 4.97% of leopard's prey, which is less than half that of macaque. The occurrence of slow loris and gibbon was 2-3 time less than macaque or langur, probably because slow loris and gibbon spend almost all of their time in trees (Lekagul and McNeely, 1977). However, in the study period the slow loris was found on the ground twice in the deciduous forest during the dry season. This agrees with Lekagul and McNeely (1977) who reported that slow loris spend most of day in the trees but sometimes forage on the ground. White-handed gibbons are arboreal mammals. They intake water from fruits, water holes in trees or wet leaves. Occasionally they come to drink at a stream (Bhumpakpan, per.comm.), which was observed by a worker at Kapook Kapeing Guard Station, HKKWS, who reported that seeing a gibbon drink water at a stream. The avoidance of the ground probably explains why gibbons comprised the low proportion of leopard prey (1.53%). In summary, the likelihood of a primate becoming leopard prey was related to the frequency of its activities on the ground.

Malayan porcupines were the principal prey of leopard in this study. In a previous study at HKKWS, Rabinowitz (1989) reported that Malayan porcupines were the second most favored prey. In many area, leopard consumed porcupines in different proportion (Schaller, 1967; Bertram, 1982; Bailey, 1993; Johnson *et al.*, 1993). Porcupines are abundant at HKKWS, and frequently seen at night. They use the same jungle trails that leopards use. Although, porcupine hunting by leopard was not directly observed, the spines on the ground indicating a kill were found. Small, soft spines were also found in leopard scats.

Small animals comprised 8.14% of the leopard diet. These included beetle (Cerambyicdae), termites (*Macrotermes* spp.), cloud monitor (*Varanus bengalensis*), butterfly lizard (*Leiolipis belliana*), snake, bamboo rat (*Rhizomys sumatrensis*), bay bamboo rat (*Cannomys badius*), rat (Muridae), Malayan pangolin (*Manis javanica*), hare (*Lepus peguensis*), small Indian civet (*Viverricula malaccensis*) and Asiatic jackal (*Canis aureus*). Bailey (1993) reported that small animals were important prey, consumed in high proportion by leopards in the dry season, especially by female sub-adult leopards. Small animals may be important prey to young adult leopards that are inexperienced in hunting larger prey.

Leopard diet is influenced by seasonality. In the dry season, the forest canopy of the deciduous forest was increased and ground cover densities reduced. After forest fires in December, new grass sprouts in the understory, drawing ungulates to forage, particularly sambar deer. Data showed that leopard consumed ungulate, especially young adult sambar deer, in a higher proportion during the dry season than during the wet season. Limited access to water, new grass growth, and herd size may all lead to greater ungulate consumption during the dry season. This is in agreement with Phetdee (2000) who reported that tigers consumed more ungulate in the dry season than in the wet season. This is in contrast to a study undertaken at Chitwan National Park, Nepal, which reported that tigers consumed less ungulate in the dry season than in the wet season (Seidensticker, 1976). This may be because after the fires the grassland habitat becomes open and unsuitable for a tiger ambush.

Leopard and tiger have a high degree of overlap in Huai Kha Khaeng Wildlife Sanctuary, which is similar to the high overlap of leopards and lions in the Serengeti National Park, Tanzania (Bertram, 1982). Data from radio tracking in Chitwan National Park, Nepal, indicated that leopard and tiger also coexist in riverine forest and savanna (Seidensticker, 1976). However, Seidenstick (1976) and McDougal (pers. comm.) report high avoidance of tigers by leopards. In Huai Kha Khaeng WS, specific data on leopards avoiding tigers were not available. In fact, leopards were observed on numerous occasions scavenging a carcass one or two days after a tiger kill. Although there may be spatial-temporal avoidance, there does not appear to be habitat separation between leopards and tigers at HKKWS. Tigers occurred throughout the study area.

Although they share the same habitat with tigers, the leopard's diet is more diverse than that of tiger or lion and prey size is considerably smaller (Schaller, 1972; Seidensticker, 1976; Bertram, 1982; Phetdee 2000). In this study there was overlap in ungulate species in the diet of leopards and tigers, but leopards preyed on the young of larger ungulates, such as sambar. This is in the line with Karanth and Sunquist (1995) who reported that tiger prefer prey that weigh >176 kg and average size tiger prey size was 91.5 kg. Leopard preferred prey with a weight range of 30 to 175 kg, with an average size of 37.6 kg. Muckenhirn and Eisenberg (1973) reported leopard is the largest carnivore in Sri Lanka then it consumes larger prey than in other parts of its range and is also more active in the day time. This finding suggests that there is ecological release in leopards allowing them to fill some of the tiger niche.

African leopards hide carcasses in trees to avoid theft by other carnivores and scavengers (Bailey, 1993; Bertram, 1982). Rabinowitz (1989), who studied leopard in Huai Kha Khaeng, did not report this behavior. This is possibly due to the population of dholes and vultures being low. In addition, whilst the tiger coexists with the leopard, the tiger prefers to consume large mammals.

4. Habitat selection

Discerning leopard resource requirements by identifying what habitat types individuals are selecting, presumes that animals choose those which will increase survival and reproduction potentials. However, when attempting to characterize selection there may be problems associated with two main underlying assumptions; that recorded observations can be used to infer habitat selection, and that evidence of selection is related to fitness and population growth (Porter and Church, 1987; Alldredge and Ratti, 1992; Garshelis, 2000). Nevertheless, investigating how a species selects different features of its environment is an essential step towards assigning importance to those features, with the acknowledged caveat that subsequent measurements of survival and reproduction parameters will be needed (Garshelis, 2000). In addition, perceived habitat selection was attributed using data collected during the day light hours. Leopards may select habitat differently during the night; an area for further research. A larger sample size would be also be required to determine if there was variation in selection for different demographic groups; in this study male, female, adult and sub-adult leopards were pooled together.

Despite these caveats, many of the results of this study make sense biologically and are supported to some degree by past literature. At the second order level (home range selection), steep slope areas were selected against for all and wet time periods. There was no significant difference between moderate slope (ranked first in both cases) and flat slope (ranked second). Similarly, at the third order level (habitat patch selection), selection decreased as slope gradient increased. This is probably due to the distribution of some important leopard prey items, such as sambar (*Cervus unicolor*) and barking deer (*Muntiacus muntjak*), which have higher relative abundance associated with lower gradient habitat (Sukmasuang and Kutintara, 2001; Sukmasuang, 2004).

For the stream habitat class there was a clear difference between second order selection, where leopards chose a home range with significantly more stream type than available, and third order, where there was no significant selection. This may also be a reflection of prey distribution; drier areas supporting less biomass, and mineral licks adding to prey species' attraction to water courses. At the third order level, possibly leopard may wait for their prey around water course, where it believe that their prey come to use this water course but not look for them at the water course or the leopards are not using these areas as much as they would otherwise choose due to avoidance of tigers (Seidensticker, 1976).

At the second order level of vegetation selection, leopards always selected home ranges containing larger proportions of mixed deciduous forest type than expected, followed by dry evergreen and dry dipterocarp. Mixed deciduous is important habitat for the leopard's main prey species, (sambar), and evergreen forest supports different prey items like primates (Bhumpakphan, 1988), and may also be used as leopard resting areas. Dry dipterocarp does not immediately appear to offer much in the way of resources to leopards and so the second order result of least selected habitat type is not surprising. However, at the third order analysis dry dipterocarp was ranked the highest for wet season locations (the only significant result), so perhaps some important resource becomes available with the increase in precipitation during that time.

The results suggest that leopard populations will benefit from more mixed deciduous and dry evergreen forest types, with flat/moderate gradients and abundant water courses. In Thailand, the protected area system is composed primarily of rugged, higher altitude terrain, with an under representation of lowland forest due to previous conversion into agricultural land (Trisurat, 2006). The continued fragmentation of remaining forests is a serious threat to Thailand's biodiversity (Pattanavibool and Dearden, 2002). Focusing conservation efforts on umbrella species such as tiger, leopard and elephant may be the most effective and immediately available strategy to improve future prospects for Thai wildlife. With regard to leopards, any remaining mixed deciduous, relatively flat forested areas in large watershed areas should be marked as high priority conservation areas. With suitable prey and vegetation assemblage, these areas could help secure a long-term future for leopards, their respective prey and the rich ecosystem on which they depend.

CONCLUSION

The study of ecology of leopard *(Panthera pardus)* covered approximately 180.85 km^2 around Khao Nang Rum Research Station, Huai Kha Khaeng Wildlife Sanctuary.

Sixteen individual leopards were captured using wooden box traps between 1994 to 1999; seven females and nine males. The adult females (n=4) had total body lengths (nose to tail tip along curves) of 179.5-183.0 cm (181.1 ± 1.7), and weights (n=5) of 27.0-34.9 kg (mean 30.3 ± 3.1). Two sub-adult (judging by their teeth) females had total body length of 170.7-178.0 cm (mean 174.4±5.2), and mean weight of 22.5-24.5 kg (mean 23.5±1.4). Adult males had total body lengths of 191.0-220.0 cm (202.9±11.8; n=7), and weights of 36.0-43.5 kg (mean 40.2±3.1; n=6). Two sub-adult males had body lengths of 189.0-202.0 cm (mean 195.5±9.2) and weights of 32.1-34.0 kg (mean 33.1±1.3). Adult male leopards were significantly longer (t=4.799, DF=6.404, p=0.003) and heavier (t=5.316, DF=9, p=0.000) than adult female leopards. Sub-adult males were significantly heavier than sub-adult females (t=6.924, DF=2, p=0.020) but the difference between their length were not significant.

The home range size of radio-collared leopards differed between males and females. The mean accumulative home ranges of 7 adult females was 27.1 (SD=6.5) km^2. The mean accumulative home range of adult males was 48.7 km^2,which was significantly larger (approximately 1.8 times) than female range size (t=-4.576, DF=8, p=0.002). However, the difference in size of their 50% MCP core areas was not significant (t=-1.744, DF=2.174, p=0.213). Home range sizes were not significantly different between seasons for males and females.

95% percent MCP overlap was high between sexes (mean=54.2%, SD=19.1%) and, similarly, their core areas had a high degree of overlap (mean=34.4%, SD=16.9%). Females established their home range within male home ranges, which resulted in a male's home range overlaping two or more female ranges.

The home range of 5 of 7 females was nearly constant throughout the study (L046, L195, L390, L345 and L467); the mean activity radii was 0.81 km. Two females shifted their home range during this study. The first was L025, an older female (based on her tooth wear). The other female, L035, was a sub-adult daughter of L345. She was collared within L345's territory and remained there for 6 months and then shifted to the north to establish a home range with no MCP overlap with L345. Male L055, an adult male, exhibited strong site fidelity for 15 months and then shifted to the north. The northward shift appeared to be in response to other males; subsequently a third male took over the former home range of L055.

Despite a high degree of home range overlap, the average daily distance between each leopards was 4.71 km (SD=2.84, n=3126) among females and 11.30 km (SD=3.72, n=92) among males. The average distance between leopards of opposite sex was 5.33 km (SD=3.79, n=1,197).

The average straight line distance between consecutive daily locations was 2.30 km/day (SD=1.83, n=320) for adult males, 1.67 km/day (SD=1.19, n=1602) for adult females, and 1.71 km (SD=1.27, n=195) for sub-adult females. Adult male daily movement was significantly different from that of adult female ($p<0.001$) or sub-adult female ($p<0.001$).

Camera-trap monitoring of leopard covered an area of 115.9 km^2 around Khao Nang Ram Research Station, Huai Kha Khaeng WS. Eighteen leopards were photographed, including 4 adult females, 3 sub-adult females, 3 adult males, 3 sub-adult males and 5 males that could not be identified by age class. From a total of 27 black leopard photographs, 15 photographs were distinguishable as 4 individual leopards; one leopard had a collar and 3 leopards were identified by their size, sex, and photograph time and location.

Closure tests indicated a closed leopard population in the study. The estimates of population size of leopard using model M_h are 10, 10 and 11 leopards for the sampling periods, respectively. Log-normal based 95% population estimate confidence intervals ranged from 10 to 29 leopards for the first session, from 9 to 17 leopards for the second session, and from 11 to 26 leopards for the third session. Estimated leopard densities were 7.9±5.8 to 5.2±3.1 and 4.9±2.3 leopards/ 100 km^2 during the three sampling periods. The average leopard density in this study was 6.0 leopards/ 100 km^2.

A total of 367 leopard scats were collected, 239 scats in dry season and 128 scats in wet season. The average diameter of the scats was 2.59±0.59 cm. The analysis of 367 scats revealed that leopard consumed at least 26 prey species. The ungulate was the prey that leopard consumed most frequently (58.92%) and the data showed that leopards preferred to consume sub-adults. Primates were found in 15.80% of scats. Diet compositions of wet season and dry season were different. Samber deer were the most frequent prey in dry season, and wild boar were the most frequent prey in the wet season. The relative proportions of ungulates and primates were inversely related: ungulates were detected in 62.91% and primates in 13.07% of scats in dry season, while ungulates were detected in 51.89% and primates in 20.63% of scats in the wet season.

A total of 1,800 circular plots covering 22,628.57 m^2 were used to survey the scats of five principal prey species: barking deer, sambar deer, banteng, gaur and wild boar. The results showed that sambar deer’s scats have the highest occurrence (84.31%) and highest density (304.04 scats/ha).

Leopard and tiger diets were compared by by Phetdee (2000). The leopard consumed a greater variety of prey species than the tiger. 13 prey species were represented in the diets of both leopards and tigers.

The nine leopards that had an adequate number of locations were pooled for compositional analysis. Evaluating second order selection showed that mixed deciduous was selected the most, followed by dry evergreen and dry dipterocarp forest types, for annual, dry and wet seasons. The paired *t*-test between habitat types showed a significant difference between selection for dry evergreen and dry dipterocarp. At third order habitat level, dry dipterocarp was significantly used the most, followed by dry evergreen and mixed deciduous only in wet season.

At the second order level, for full-year and dry season data sets, moderate slope was ranked first, followed by flat and steep slope areas. Steep slope was selected for significantly less than expected. At the third order level, slope class selection was significant for wet season, dry season, and full-year data sets. As slope increased, selection decreased, with flat areas selected significantly more and steep areas significantly less in the full-year data set.

At the second order level, for wet season, dry season, and full-year data sets, leopards selected areas near streams significantly more than areas disant from streams. At the third order level there was no significant difference between proportion of selected and available habitat types.

RECOMMENDATIONS

In this study, the data on prey abundance is not sufficient to estimate prey density. Thus, future designed studies should be emphasized on prey density estimation and the factors influencing prey habitat selection, such as slope, vegetation type, distance to streams, or elevation. These informations are important to understand prey ecology and population dynamics. Moreover, a comparative study on prey species and potential competition between leopard and tiger remain as an important issue for research study in Southeast Asia.

In the future, the use of GPS-collars to study the coexistence of tigers and leopards will be an interesting project. The result can provide a better understanding on habitat use and the interaction between tigers and leopards. Continued monitoring on leopard populations is important for understanding their present status in Huai Kha Khaeng WS and adaptive management for their long-term conservation in the wild.

In the future, genetic analyses may provide answers to many interesting and important questions, such as home range overlapping between mother and daughther and the relationship among individual. DNA extracted from leopard scats can identify an animal's sex, individual identity and diet.

The data from this study shows that leopard conservation should not only protecting animals from poaching but also prevention of lowland forest from conversion to agricultural land, especially mixed deciduous forest near streams. In addition, the long-term conservation of leopard will require the prevention of prey poaching, especially ungulates and primates, which are the main prey of leopard, and it needs a management to maintain suitable habitat for these prey species.

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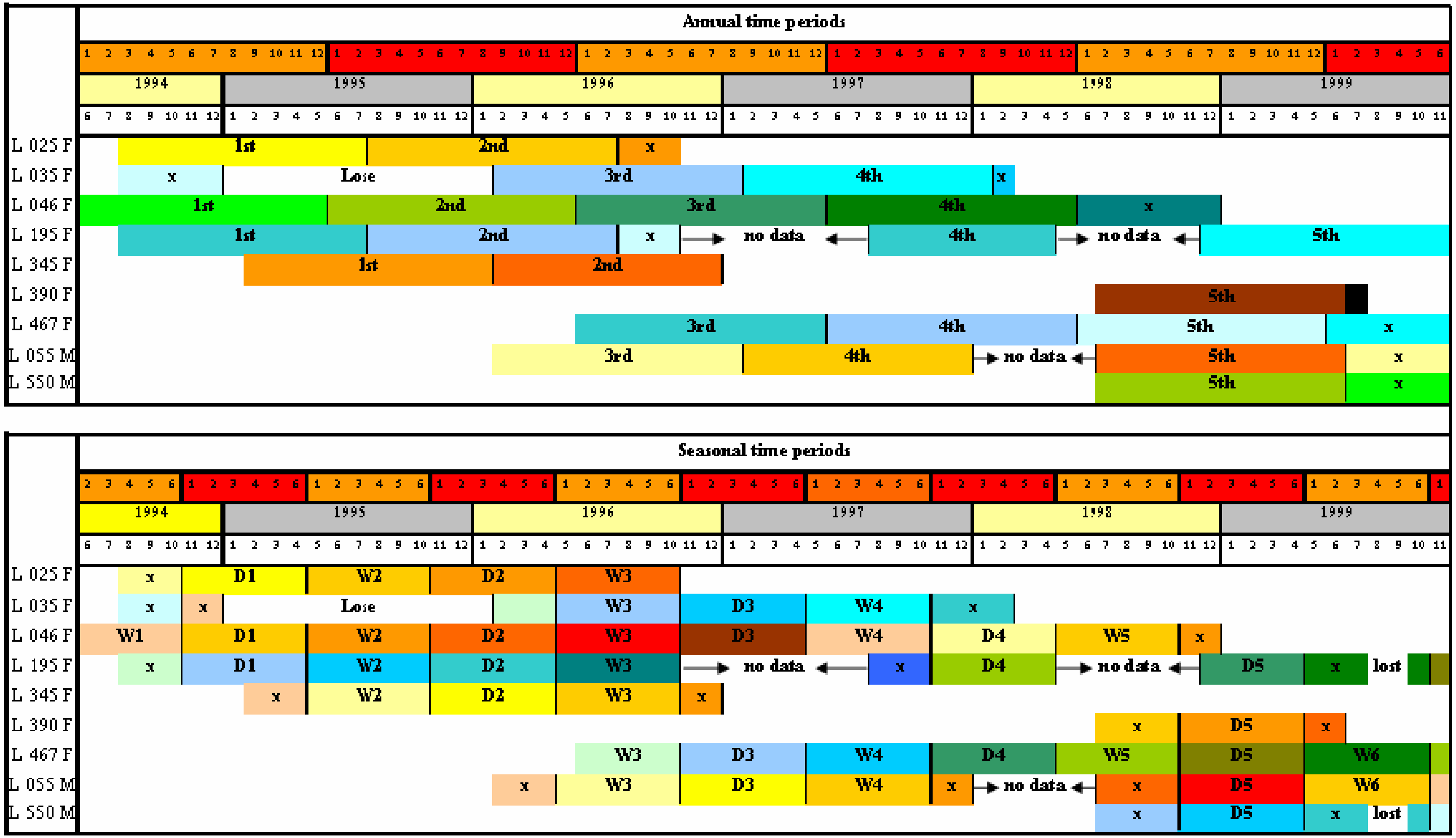
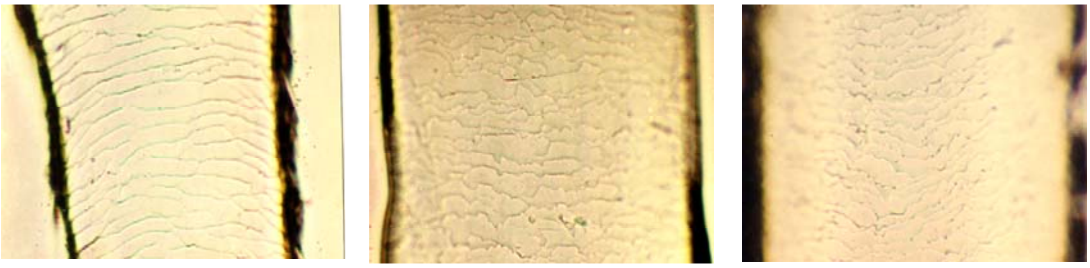
APPENDIX

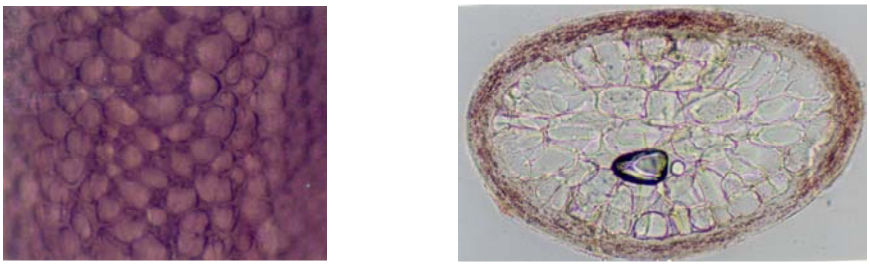


Appendix Figure 1 Annual and seasonal redio tracking time periods.



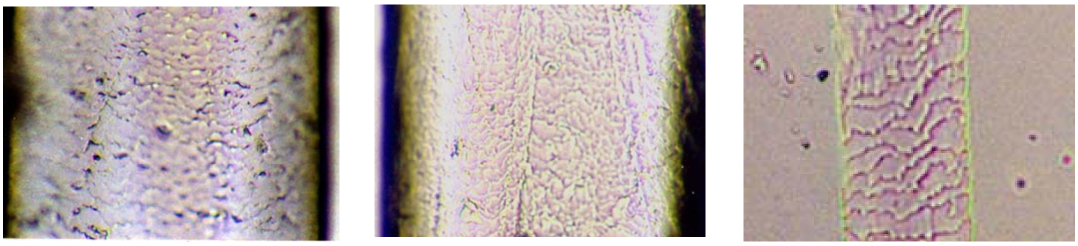
base middle end

Scale pattern



Medulla Cross section

Appendix Figure 2 Hair characteristics of Sambar deer *(Cervus unicolor).*



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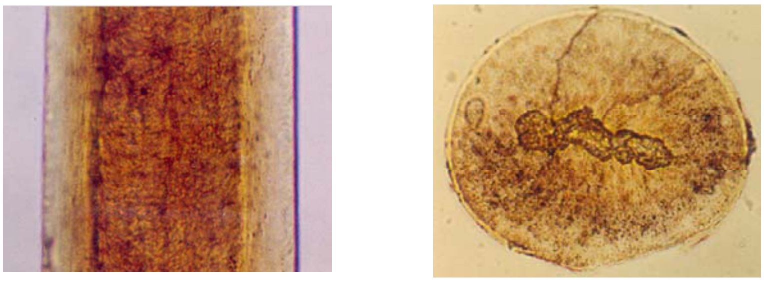
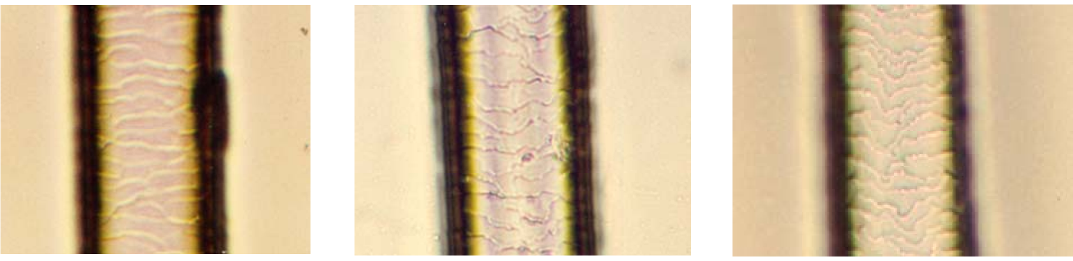
Scale pattern



Medulla Cross section

Appendix Figure 3 Hair characteristics of Wild boar *(Sus scrofa).*



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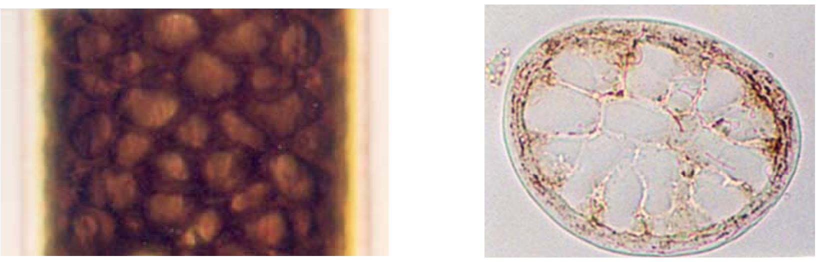
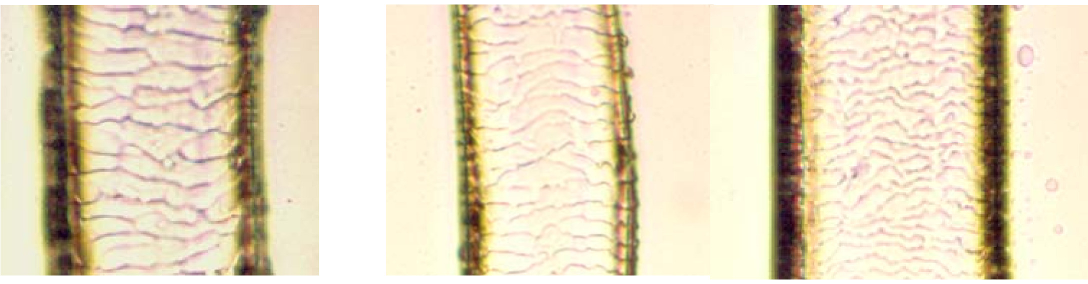
Scale pattern



Medulla Cross section

Appendix Figure 4 Hair characteristics of Barking deer *(Muntiacus muntjack).*



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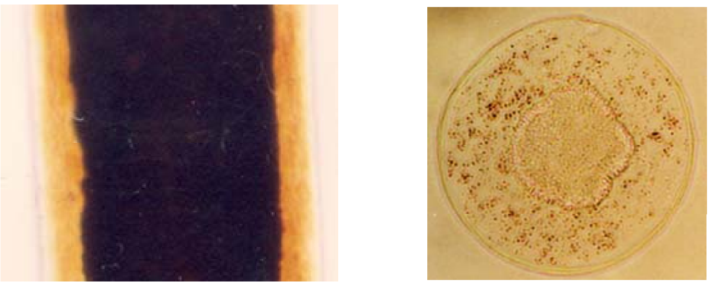
Scale pattern



Medulla Cross section

Appendix Figure 5 Hair characteristics of Banteng *(Bos javanicus).*

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