

THE DENSITY AND BEHAVIOR OF LARGE CATS IN A DRY TROPICAL FOREST MOSAIC IN HUI KHA KHAENG WILDLIFE SANCTUARY, THAILAND

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ABSTRACT

Between June 1987 and March 1989, three leopards were captured and radio-collared at Khao Nang Rum Research Station, Huai Kha Khaeng Wildlife Sanctuary. Two additional leopards and a tiger were followed by their spoor. Male leopards had slightly overlapping home ranges of 27–37 km², while females had ranges of 11–17 km² within the ranges of males. The tiger ranged within a minimum area of 33 km², encompassing the range of a male and female leopard. Marking, in the form of scrapes, was observed most frequently during rainy season, along roads and trails in the area where the ranges of all five big cats overlapped. The major prey of the tiger and leopards was barking deer, although wild boar, sambar deer, porcupine, and hog badger were important secondary prey items for both species. Primates, the second most frequently encountered prey item in leopard feces were not often found in tiger feces. Leopards had a more diverse prey base than tigers, especially in the lower size classes of animals. Leopard behavior was similar to that of the resident tiger who occupied only a third of the study area. Densities were estimated at one tiger per 100 km² and one leopard per 25 km².

INTRODUCTION

Two of the largest extant felids, the leopard (*Panthera pardus*) and the tiger (*Panthera tigris*) have been studied extensively in parts of Africa (BOTHMA & LE RICHE, 1986; HAMILTON, 1976; NORTON & HENLEY, 1987; SCHALLER, 1967, 1972; SMITH, 1978), Sri Lanka (EISENBERG & LOCKHART, 1972), Israel (ILANY, 1986) and Nepal (SUNQUIST, 1981). In Royal Chitawan National Park in Nepal, SEIDENSTICKER (1976) examined the relationship between these two felids where they occur sympatrically. Yet throughout much of Southeast Asia, there has been little research concerning the abundance and behavior of these cats in the wild. In Thailand alone, tigers and leopards were considered endangered over 10 years ago (LEKAGUL & MCNEELY, 1977). This paper presents some observations on ecological and behavioral relations between these two species in one of the largest and most pristine wildlife sanctuaries remaining in Thailand.

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STUDY AREA

Huai Kha Khaeng Wildlife Sanctuary, an area of 2,575 km², encompasses the Huai (= stream or small river) Kha Khaeng and part of Huai Thap Salao (15.00' – 15.45' N, 99.00' – 99.30' E). The main study area included 100 km² around Khao Nang Rum Research Station, in the eastern portion of the sanctuary, which contains parts of two river systems, Huai Chang Tai and Huai Ai Yo. Most of the study area ranged in elevation from 400 – 600 m, but included part of Khao Khieo Mtn. up to 1350 m.

Vegetation in the study area was a mosaic of four forest types: mixed deciduous forest (35%), dry deciduous dipterocarp forest (25%), dry evergreen forest (33%), and hill evergreen forest (7%) (BHUMPAKKAPUN *et al.*, 1985; THITATHAMAKUL, 1985). The dry deciduous dipterocarp forest is maintained by a pattern of annual fires as described by STOTT (1986, 1988). The dry evergreen forest is found primarily at low elevations along the two waterways. Broad transition zones often made it difficult to clearly differentiate between forest types.

Temperature and rainfall records from 1983-1987 (Table 1) indicate April as the hottest month averaging 27.5°C (range: 24.9 – 34.2°C), and December as the coolest month averaging 19.2°C (range: 13.4 – 24.7°C). October was generally the wettest month with an average rainfall of 335 mm (range: 194 – 703 mm), and January the driest month averaging 2.6 mm rainfall (range: 0 – 13 mm). During the 1988 study season, January, November, and December were drier than usual, while February, September, and October had more than average rainfall.

Fire season, usually from December through March/April (STOTT, 1986), was shortened to March through mid-April in 1988 due to unusually heavy rains in February. This resulted in less fire damage to the study area. Heavier than average rainfall during September and October resulted in periodic flooding, inundating some lowland areas for up to two weeks.

METHODS

Two leopards were captured with large box traps baited with live pigs, while a third was captured with a cable snare. Traps were placed along dirt roads where spoor of large cats was found; the cable snare was placed at the site of a sambar deer, *Cervus unicolor*, kill. Captured leopards were anesthetized with 10 mg/kg Telazol (A.H. Robbins Co., Richmond, Va.) before being weighed, measured, and collared with radios (Telonics Inc., Mesa, Arizona). All radios contained activity monitors activated by head movements.

Collared cats were released after full recovery from sedation. Data were not collected for three days after capture to allow full recovery from the trauma of capture and collaring. Thereafter, attempts were made to locate the cats at least three times weekly. Activity was determined by changes in signal strength and

Table 1. Monthly temperature and rainfall at Khao Nang Rum Research Station, Huai Kha Khaeng Wildlife Sanctuary, Thailand, from 1983–1987, and for the study period 1988.

| Month | Temperature (°C) | | Rainfall (mm) | |
|------------------------|------------------|------|---------------|-------|
| | 1983–87 | 1988 | 1983–87 | 1988 |
| January | 20.3 | 20.7 | 2.6 | 0.0 |
| February | 23.8 | 25.3 | 25.2 | 112.0 |
| March ¹ | 25.7 | 26.8 | 45.2 | 36.8 |
| April ¹ | 27.5 | 27.8 | 105.1 | 104.1 |
| May | 26.6 | 27.1 | 229.9 | 294.6 |
| June | 27.1 | 26.7 | 133.1 | 93.2 |
| July | 25.9 | 26.7 | 109.3 | 330.0 |
| August | 25.7 | 26.0 | 114.9 | 227.0 |
| September ² | 25.2 | 25.4 | 302.3 | 603.5 |
| October ² | 24.2 | 24.6 | 335.0 | 402.0 |
| November | 22.2 | 21.2 | 91.6 | 10.7 |
| December | 19.2 | 19.2 | 13.5 | 0.0 |
| Average | 24.4 | 24.8 | 125.7 | 184.5 |

¹ Fire in study area in 1988 season.

² Intermittent flooding in lowlands in 1988 season.

changes in pulse rate of the radio's activity monitor. At least once a month activity was recorded at 30 minute intervals for a 24-hour period.

Roads and trails within the study area were walked regularly to document the presence of feces, scrapes, and tracks. Waterways and salt licks were also visited periodically. Large cat feces were differentiated from other carnivore feces by size, tracks in the area, and/or by the presence of scrapes associated with fecal deposits. Feces and scrapes were measured and their locations were recorded. Prey remains in the feces were identified by comparison with a reference collection of hair and skeletal material from known species. Results are expressed in terms of frequency and percent occurrence (the number of times a particular species is found in relation to all prey items identified). Feces were also collected in other parts of the sanctuary for comparison with those from the study area.

Tiger tracks, feces, and scrapes were differentiated from those of leopard if the paw size was over 11 cm wide (generally 11–18 cm wide). Leopard tracks ranged from 6.4–9 cm wide with feces generally 2–3 cm in diameter. Leopard feces collected from the Dusit Zoo in Bangkok indicated an average fecal diameter of 2.2 cm (range 1.9–3 cm), a size similar to leopard feces observed in S. Africa (NORTON

et al., 1986). Visual sightings and distribution frequencies of track measurements were used to delineate ranges of non-collared big cats in the study area.

Calculations of minimum home range sizes were based on the convex polygon method (MOHR, 1947). Core home range was defined as the area encompassing 75% of the locations from the geometric home range center. The mean activity radius was the average distance from the geometric center of the home range to each animal's recorded location. Daily movements were the straight-line distances measured between consecutive daily locations. Activity level was the percent of time an animal was found to be active. Analysis of these parameters was carried out with the TELEM program (COLEMAN & JONES, 1986).

RESULTS

Between June 1987 and March 1989, two male leopards and one female leopard were captured and radio-collared in the study area. One male died a week after capture. By the end of 1988, spoor and sightings indicated at least two additional leopards (1 black female and 1 spotted male) and one tiger also resident in the study area.

Movements and Activity

L31—This male leopard, weighing 70 kg with a head-body length of 131 cm and a tail of 77 cm, was captured over a sambar deer kill along Huai Chang Tai waterway. He died a week after capture from injuries and trauma sustained while trying to escape the cable snare. Prior to his capture, tracks indicated movements in the eastern portion of the study area, often along Huai Chang Tai waterway. After his death, a second male, *L545*, expanded northward into part of his range.

L760—This female leopard, weighing 21 kg with a head-body length of 109 cm and a tail of 74 cm, was radio-tracked between 31 January 1988 and 13 April 1988. During these two months, she moved within an area of 11.4 km² (N = 45 observations) with a mean activity radius of 1.4 km, and mean daily movements of 1.3 km (N = 17). Her core activity area of 4.1 km² was centered around Huai Ai Yo waterway (Fig. 1).

Overall, *L760* had an activity level of 47% (N = 324 activity readings), with an arrhythmic daily activity pattern (Fig. 2). The lowest activity level (34%) was from 1030-1330 hours.

L545—This male leopard, weighing 60 kg with a head-body length of 119 cm and a tail of 78 cm, was radio-tracked from April 5, 1988 to January 9, 1989. During nine months he used a total area of 27 km² (N = 93 locations), with a mean activity radius of 1.8 km and mean daily movements of 2.1 km. The core home range was 12 km², centered around Huai Ai Yo waterway. His range almost completely overlapped that of the female leopard, *L760* (Fig. 1).

The largest average daily movements for this leopard occurred during May, the end of the dry, fire season and during the onset of rains. During the early rainy

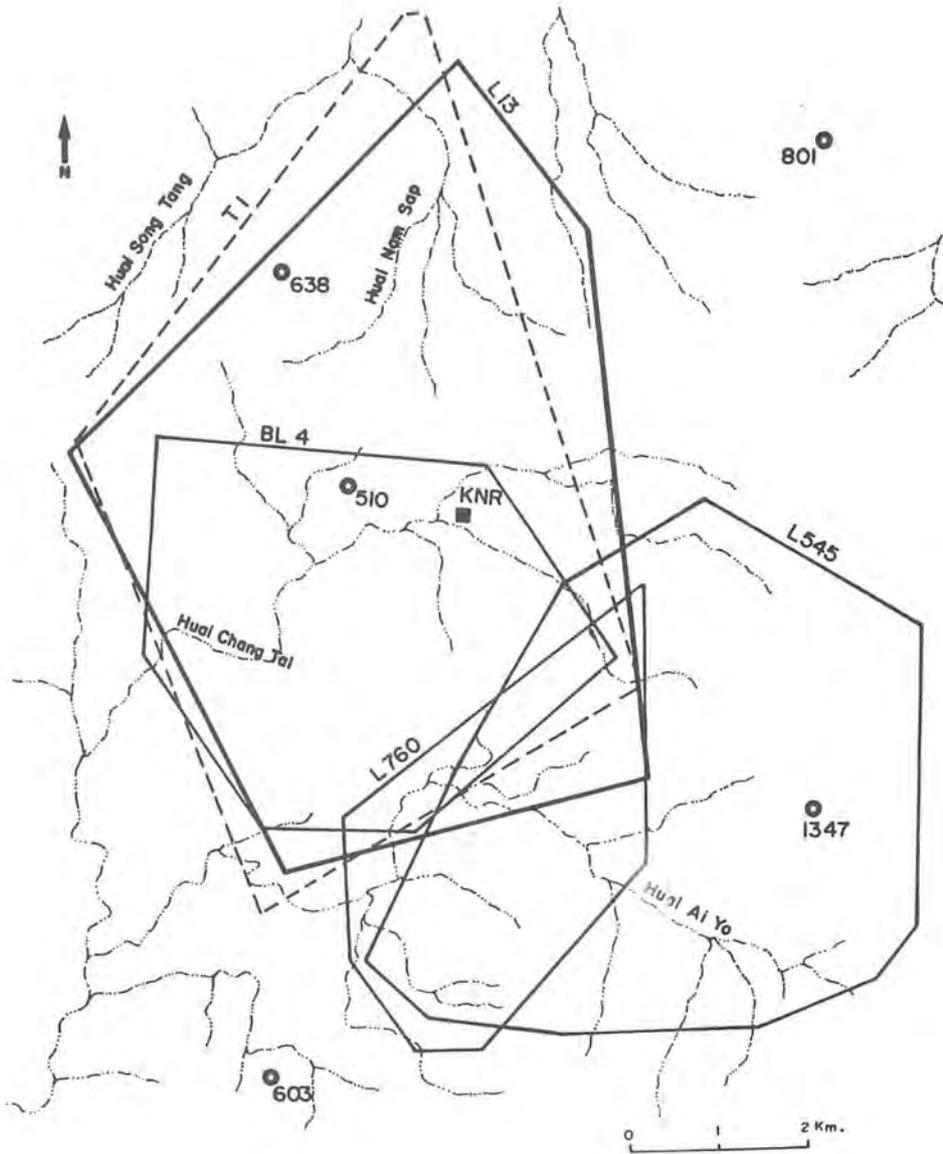


Figure 1. Home range overlap of two male leopards (L545 & L13), two female leopards (BL4 & L760), and a male tiger (T1) resident in the 100 km² study area around Khao Nang Rum Research Station, Huai Kha Khaeng Sanctuary.

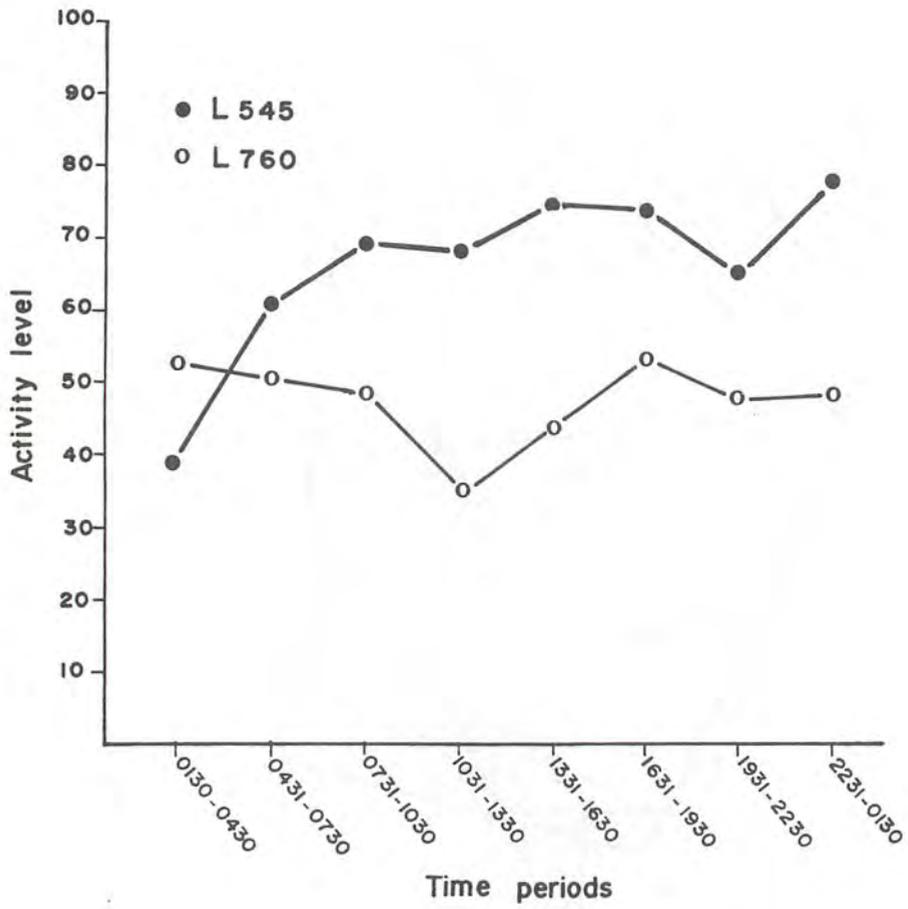


Figure 2. Daily activity levels (% activity) of a radio-collared male (L545) and female (L760) leopard resident in the 100 km² study area around Khao Nang Rum Research Station, Huai Kha Khaeng Sanctuary.

season months of June and July, this leopard had his largest home ranges and range center shifts. The smallest monthly home range and daily movements were during September and October, months of heavy rain and floods (Table 2).

L545 had an overall activity level of 67% (N = 1034 activity readings), with the highest average monthly activity (80%) observed during April. The leopard showed an arrhythmic daily activity pattern (Fig. 2) with the lowest activity level (40%) between 0130-0430 hours.

BL4—This black leopard was sighted in the study area nine times between January 1987 and May 1988. All sightings were of a single individual walking in the dry evergreen or mixed deciduous forest during the morning hours. Based on appearance and track size, this cat was assumed to be female. Sightings and spoor indicated a minimum range of 17.2 km² encompassing much of Huai Chang Tai waterway and part of Huai Ai Yo waterway (Fig. 1).

L13—Spotted leopards were observed six times in the study area in areas where neither of the collared leopards were known to range. All but one sighting was of a single individual walking in the forest during the daytime. On one occasion, two leopards were seen together at a salt lick in dry deciduous dipterocarp forest.

Sightings and spoor indicated one relatively large male leopard, *L13*, with a range of 37 km² that completely encompassed the range of the female, *BL4* (Fig. 1). The sighting of a second spotted leopard with *L13* on one occasion indicated another female. However, spoor of this cat was not observed with enough frequency for it to be considered a regular resident of the area.

T1—Tigers were observed on four occasions in the study area. Three tiger sightings were of a single individual in dry deciduous forest, twice walking along roads, and once over the carcass of a gaur, *Bos gaurus*, killed by hunters. On one occasion,

Table 2. Monthly activity and movement patterns for the male radio-collared leopard, L545.

| Month | Locations (N) | Home range (km ²) | Activity radius (m) | Average daily movement km (N) | Home range center shift (km) | Activity level (N) |
|-------------------|------------------|-------------------------------------|---------------------------|--|---------------------------------------|--------------------------|
| April/May | 15 | 15 | 1789 | 1.7(2)/3.6(5) | -- | 80(115)/68(95) |
| June | 17 | 18 | 1639 | 1.9(9) | 1.4 | 59(405) |
| July | 14 | 17 | 1962 | 2.3(6) | 1.4 | 65(106) |
| August | 15 | 12 | 1857 | 2.2(7) | 0.2 | 63(111) |
| September/October | 18 | 4.4 | 1357 | 0.6(3) | 0.6 | 76 ¹ (105) |
| November/December | 13 | 12 | 1697 | 2.0(3) | 0.7 | 63 ² (97) |
| Average | | 13 | 1717 | 2.0(35) | 0.9 | 66 ³ |

¹ No data for 0130–0430 hours during these months.

² Combined activity data from October-December.

³ Incomplete data for Sept/Oct not used for overall average.

two tigers were seen walking together down Huai Ai Yo waterway in dry evergreen forest. Spoor of one tiger, T1, was found regularly throughout an area of 33 km² within the study area. Most of the spoor was concentrated in the northwest corner of the study area overlapping the range of only one other leopard, L13. The total range, however, completely overlapped those of L13 and BL4, and partially overlapped the ranges of the two radio-collared cats (Fig. 1). Spoor indicated that this cat also ranged outside the 100 km² study area.

Food Habits

A total of 237 leopard feces and 38 tiger feces collected in the study area showed the cats feeding on at least 22 prey species, from sambar deer to small lizards and rodents (Table 3). Eighty-eight percent of the feces contained only a single prey item, 11% contained two prey items, and 1% contained three prey items. Fifty percent of the feces contained grass.

Barking deer, *Muntiacus muntjak*, was the major prey item identified in both tiger and leopard feces in the study area, occurring in 43% of leopard feces and 46% of tiger feces (Table 3). Both species had overlapping prey preferences but the leopards fed upon a greater prey diversity, primarily in the lower size classes of animals. Primates, specifically *Macaca* spp. and *Presbytis* spp., were the second most frequently encountered prey items in leopard feces but were not often found in tiger feces. Wild boar, *Sus scrofa*, sambar deer, the crestless himalayan porcupine, *Hystrix hodgsoni*, and hog badger, *Arctonyx collaris*, were important secondary prey items for both species. Large ungulates such as sambar deer and wild boar might have been preyed upon with greater frequency than their presence in feces suggests. The difficulty of analyzing feces produced after meaty meals of larger ungulates may have contributed to the relatively large "unknown" category (Table 3), which comprised feces with no hair or skeletal remains.

Large cat feces (N = 141) collected in different areas of the sanctuary comprising mixed deciduous and dry evergreen forest, indicated similar prey preferences as those observed in the study area but with a lower overall prey diversity (Table 4).

Marking Behavior

Between March 1987 and December 1988, more than 350 scrapes from large cats were documented in the study area. Although recorded throughout the year, scraping behavior occurred most frequently during the rainy season months. The largest proportion of recorded scrapes (44%) were in the area where the ranges of all five resident large cats overlapped (Fig. 1). Most scrapes were found along roads and trails either in grass, if present, or in dirt near the edge of the road. Scrapes were also frequently observed at large salt licks, and alongside big cat kills.

Table 3. Frequency of occurrence of prey items in leopard feces (N = 237) and tiger feces (N = 38) from around Khao Nang Rum Research Station in Huai Kha Khaeng Wildlife Sanctuary.

| Species | Frequency of occurrence | |
|-------------------------------------|-------------------------|------------|
| | Leopard | Tiger |
| Cervidae | | |
| <i>Muntiacus muntjak</i> | 118 (43.0%) | 18 (42.0%) |
| <i>Cervus unicolor</i> | 15 (5.4%) | 3 (7.0%) |
| Suidae | | |
| <i>Sus scrofa</i> | 13 (5.0%) | 4 (9.0%) |
| Cercopithecidae | | |
| <i>Macaca nemestrina</i> | 3 (1.0%) | |
| <i>Macaca</i> spp. | 18 (7.0%) | |
| <i>Presbytis phayrei</i> | 8 (3.0%) | 2 (5.0%) |
| <i>P. cristata</i> | 1 (0.4%) | |
| Hylobatidae | | |
| <i>Hylobates lar</i> | 2 (0.8%) | |
| Hystricidae | | |
| <i>Hystrix hodgsoni</i> | 23 (8.0%) | 5 (12.0%) |
| <i>Atherurus macrourus</i> | 6 (2.0%) | |
| Mustelidae | | |
| <i>Arctonyx collaris</i> | 10 (4.0%) | 4 (9.0%) |
| Viverridae | | |
| <i>Paguma larvata</i> | 1 (0.4%) | |
| <i>Arctictis binturong</i> | 1 (0.4%) | |
| Manidae | | |
| <i>Manis javanica</i> | 4 (1.4%) | |
| Rhizomyidae | | |
| <i>Rhizomys sumatrensis</i> | 4 (1.4%) | |
| Sciuridae | | |
| <i>Ratufa bicolor</i> | 2 (0.8%) | 1 (2.0%) |
| <i>Callosciurus</i> spp. | 1 (0.4%) | |
| Muridae | | |
| <i>Maxomys surifer</i> | 4 (1.4%) | |
| <i>Maxomy</i> or <i>Rattus</i> spp. | 4 (1.4%) | |
| Bird | 4 (1.4%) | |
| Lizard | 2 (0.8%) | 1 (2.0%) |
| Crab | 1 (0.4%) | |
| Medium-large mamal | 2 (0.8%) | |
| Unknown | 25 (9.0%) | 5 (12.0%) |
| Total | 272 | 43 |

Table 4. Frequency occurrence of prey items in large cat feces (leopard and tiger, N = 141) from various areas of mixed deciduous/dry evergreen forest outside the study area in Huai Kha Khaeng Wildlife Sanctuary.

| Species | Frequency of occurrence | |
|--------------------------------------|-------------------------|-------|
| Cervidae | | |
| <i>Muntiacus muntjak</i> | 99 | (66%) |
| <i>Cervus unicolor</i> | 1 | (1%) |
| Suidae | | |
| <i>Sus scrofa</i> | 8 | (5%) |
| Cercopithecidae | | |
| <i>Macaca nemestrina</i> | 2 | (2%) |
| <i>Macaca</i> spp. | 8 | (5%) |
| <i>Presbytis phayrei</i> | 6 | (4%) |
| Hystriidae | | |
| <i>Hystrix hodgsoni</i> | 6 | (4%) |
| <i>Atherurus macrourus</i> | 1 | (1%) |
| Mustelidae | | |
| <i>Arctonyx collaris</i> | 4 | (3%) |
| Viverridae | | |
| <i>Paguma larvata</i> | 1 | (1%) |
| Sciuridae | | |
| <i>Ratufa bicolor</i> | 1 | (1%) |
| Muridae | | |
| <i>Maxomys surifer</i> | 1 | (1%) |
| <i>Maxomys</i> or <i>Rattus</i> spp. | 2 | (2%) |
| Bird | 1 | (1%) |
| Snake | 1 | (1%) |
| Medium-large mammal | 2 | (2%) |
| Unknown | 5 | (3%) |
| Total | 149 | |

Feces were found uncovered in or next to scrapes on 270 occasions; urine was present in scrapes on 14 occasions; a dark musky secretion, assumed to be from the anal gland (SMITH et al., 1989), was found in scrapes on 10 occasions. Urine and anal secretions could only be documented when scrapes were still fresh.

Density

The data indicated the presence of four resident leopards and one resident tiger in the 100 km² study area. Although evidence of other big cats was occasionally found, their spoor was sparse enough to indicate transient or only partial use of the area. Overall, the area was estimated to contain one leopard per 25 km², and one male tiger per 100 km².

DISCUSSION

Evidence that tigers and leopards do not usually coexist harmoniously has been reported from previous studies (SCHALLER, 1967, 1972). Where they share the same area, they often partition the habitat spatially, temporally, and by prey size (SEIDENSTICKER, 1976). Since tigers are capable of both stealing leopards' prey and of killing leopards, leopards generally frequent areas where tigers are not currently present (SEIDENSTICKER, 1976). When both large cats are present in an area, leopards tend to be more nocturnal and less terrestrial than tigers (EISENBERG & LOCKHART, 1972; MUCKENHIRN & EISENBERG, 1973), and avoid roads and major pathways used by tigers (SEIDENSTICKER, 1976).

In the study area, sightings and radiotelemetry data showed leopards often active during daytime hours, with an arrhythmic daily activity pattern. The overall activity level of the radio-collared male (67%) was greater than that of the radio-collared female (49%) yet both were lower than the 75% activity level observed for an overlapping tiger and leopard by SEIDENSTICKER (1976) in Chitawan. In addition, spoor indicated that leopards frequently walked roads and trails also used by the tiger in the study area.

The fact that resident leopards in the study area did not show some of the subordinate behavior patterns documented for leopards occurring sympatrically with tigers in Chitawan (SEIDENSTICKER, 1976, SUNQUIST, 1981), is probably due to the low use of the study area by tigers, making social dominance unnecessary in the relatively infrequent leopard-tiger coactions. Not only was less than one-third of the study area used by the resident tiger, but the estimated tiger density of one per 100 km² in the area is 3 – 4 times less than that estimated for some other tropical areas (MCDUGAL, 1977; SCHALLER, 1967; SMITH, 1978; SUNQUIST, 1981). The remaining two-thirds of the study area had sporadic evidence of tiger presence indicating more transient use of this area by tigers. However, the ruggedness, relative inaccessibility, and lack of extensive trails made it difficult to accurately determine the status of non-collared

large cats in some areas. In Chitawan, where social dominance was clearly documented in tiger-leopard interactions, SEIDENSTICKER (1976) estimated that three leopards and four tigers used an area approximately one-fourth the size of this study area.

The low density of tigers in this study area may have been due to a variety of factors. A third of the area is comprised of dry deciduous dipterocarp forest which, during the driest parts of the year, experiences fire and drought. In Chitawan, tigers clearly did not prefer sal forest (SUNQUIST, 1981), which is ecologically similar to the dry deciduous dipterocarp forest in Thailand and also undergoes periodic burning. Tigers did not re-use burnt areas as quickly as leopards, and preferred shaded areas of dense vegetation, often near permanent water sources (SEIDENSTICKER, 1976; SUNQUIST, 1981). The availability and distribution of permanent water sources is potentially an important factor in allowing tigers to fully utilize an area (SUNQUIST, 1981). During this study, surveys done along the Huai Kha Khaeng, a large permanent waterway at the center of the sanctuary, indicated a greater abundance of tigers relative to leopards than at the Khao Nang Rum study site.

Leopards not only adapt well to drier areas with low cover (SEIDENSTICKER, 1976) but they have been shown to be independent of free water, using it when it is available (BOTHMA & LE RICHE, 1983; HAMILTON, 1976). There is speculation that leopards have evolved to exploit dry environments to a much greater extent than tigers (KLEIMAN & EISENBERG, 1973). Estimated leopard density for the study area was one leopard per 25 km² while home ranges varied from 11 to 17 km² for females and 27 to 37 km² for males. The female leopards, which ranged within the central, low elevation portions of the study area, maintained home ranges similar in size to those observed in Chitawan (SEIDENSTICKER, 1976) and in the dry open woodland and grassland habitat of Tsavo National Park in Africa (HAMILTON, 1976). The males home ranges however, incorporating more of the hilly, rugged perimeter of the study area, were larger than those observed in Tsavo, though much smaller than in the mountainous areas of South Africa which had higher leopard densities (NORTON & HENLEY, 1987).

Another major factor influencing the structure of the large cat community is the abundance and availability of prey, particularly prey within different size classes (SEIDENSTICKER, 1976). Although both tigers and leopards are known to prey upon a wide variety of similar prey items (NORTON *et al.*, 1986; SUNQUIST, 1981), leopards generally concentrate on prey items less than 50 kg, while tigers generally take larger prey from 50 to 100 kg (SCHALLER, 1967; SUNQUIST, 1981). This permits some degree of resource partitioning in areas of overlap (SEIDENSTICKER, 1976).

Around Khao Nang Rum, the most frequently encountered prey species in the feces of both tigers and leopards was barking deer, a species weighing 20 to 28 kg. Second to this prey item was the crestless himalayan porcupine (10–30 kg weight) in tiger feces and macaques (5–12 kg weight) in leopard feces. Predation on *Macaca* and *Presbytis* by big cats has been shown to be directly correlated with availability and abundance of alternative prey (SEIDENSTICKER, 1983). In this study, relatively



Figure 3. The author and field assistant, Suwat Kaeosrisut, setting a big cat trap baited with a live pig, along a road often travelled by leopards.



Figure 4. Testing the level of sedation of a leopard captured in a trap.



Figure 5. Field assistant, Ms. Susan Walker, attaching a radio-collar to a sedated male leopard.

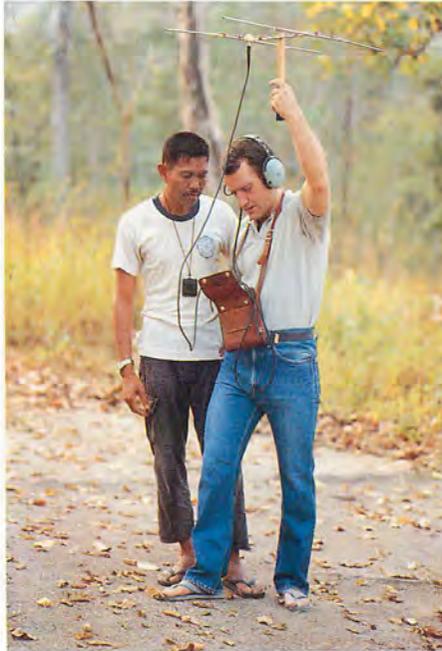


Figure 6. The author and a field assistant radio-tracking one of the radiocollared leopards.

heavy predation by leopards on these primate species might have also been influenced by competitive pressure from the tiger for the major ungulate food source, barking deer, and by the structure and composition of the forest community. A more open canopy in this dry tropical forest may necessitate more frequent movements by primates on the ground as compared to closed canopy rainforests elsewhere (Warren Brockelman, personal observations). The presence in leopard feces of the white-handed gibbon, *Hylobates lar*, a totally arboreal species, has never before been reported.

Competition between the big cats might have also influenced the diverse food habits of the leopards in the study area. Opportunistic feeding including everything down to lizards and rodents has been observed in areas where leopards have a limited diversity and abundance of medium to larger prey items (NORTON *et al.*, 1986). Although tigers are known to prefer large ungulate prey, their availability in the study area was limited. While initial surveys indicated a relatively large ungulate biomass for the study area (SRIKOSAMATARA, 1990), the crude ungulate biomass utilized by large cats was only 400-700 kg/km², one-third of that estimated for Chitawan, which comprised several ungulate species greater than 50 kg such as chital, *Axis axis* hog deer, *Axis porcinus* and domestic livestock (SUNQUIST, 1981). The ungulates utilized most by large cats within this study area basically comprised only two species, barking deer and sambar deer (SRIKOSAMATARA, 1990; personal observations). Other ungulate species such as gaur, *Bos gaurus*, and banteng, *Bos javanicus*, apparently are not easily taken by big cats, and wild boar was not common in the area (RABINOWITZ & WALKER, in preparation). Such a relatively low available ungulate biomass, particularly in the large size classes, probably contributed a great deal to a low tiger density in the study area. On the island of Java, SEIDENSTICKER & SUYONO (1980) correlated a reduction in tiger density to a reduction in the ungulate prey base.

Previous research indicates that leopards can thrive in areas of disturbed or even marginal habitat as long as a relatively broad prey base is present. Tigers prefer areas that provide water, shade, and dense vegetation such as riverine forest and show preference for medium to large sized ungulate prey. In Thailand, rapid and large scale loss of forest, as well as hunting pressures, have restricted large cat populations to a limited number of forest pockets. The future of even these populations is uncertain as long as comprehensive planning and forest management is lacking. The situation is particularly precarious for the tiger, since forested riverine habitat is often the first area to be encroached upon, or inundated by reservoirs, and large ungulates are often the first species to be hunted out of an area. Of the six species of deer that have occurred in Thailand in recent times, four are extinct or very rare, including Fea's barking deer (*Muntiacus feae*), hog deer, Eld's deer (*Cervus eldi*), and Schomburgk's deer (*Cervus schomburgki*) (LEKAGUL & MCNEELY, 1977). If Thailand wishes to conserve its remaining large cat populations, comprehensive forest management and protection must be implemented to maintain the integrity of wild riverine areas and complete mammalian assemblages.

ACKNOWLEDGEMENTS

I would like to thank Dr. Warren Brockelman and Dr. Sompoad Srikosamatara for critical review of this manuscript. Excellent field assistance on this project was provided by Ms. Susan Walker, Saksit Simchareon, Suwat Kaeosrisuk, and Ramesh Boonratana. This project was conducted with the permission of The Royal Thai Forestry Department (RTFD). Special assistance was given by Mr. Phairot Suvannakorn, Director-General of RTFD. Additional assistance and resources were provided by The National Research Council of Thailand, The Center for Wildlife Research, Department of Biology, Mahidol University, and Wildlife Fund Thailand.

REFERENCES

- BOTHMA, J. DU P. and E.A.N. LE RICHE. 1986. Prey preference and hunting efficiency of Kalahari Desert Leopard. Pages 389-415 in S.D. Miller and D. Everett, eds. *Cats of the World: Biology, Conservation, and Management*. National Wildlife Federation, Washington, D.C.
- BHUMPAKKAPUN, N., KUTINTARA, U., and N. NAKSATIT. 1985. *The Wild Fauna of Huai Kha Khaeng Wildlife Sanctuary*. Dept. of Forest Biology, Kesetsart Univ. Report, Thailand. 19 pp.
- COLEMAN, J.S. and JONES, A.B. III. 1986. *User's guide to TELEM: Computer Analysis System for Radio-telemetry Data*. Dept. of Fisheries and Wildlife, VPI and SU, Blacksburg, VA. 44 pp.
- HAMILTON, P.H. 1976. *The Movements of Leopards in Tsavo National Park, Kenya, as Determined by Radio-tracking*. MS Thesis, University of Nairobi, Nairobi, Kenya.
- EISENBERG, J.F. and M.C. LOCKHART. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian Contributions to Zoology*, 101: 1-118.
- ILANY, G. 1986. Preliminary observations on the ecology of the leopard (*Panthera pardus*) in the Judean Desert. Pages 389-415 in S.D. Miller and D. Everett, eds. *Cats of the World: Biology, Conservation, and Management*. National Wildlife Federation, Washington, D.C.
- KLEIMAN, D.G. and J.F. EISENBERG. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* 21:637-659.
- LEKAGUL, B. and J.A. MCNEELY. 1977. *Mammals of Thailand*. Assoc. for the Conservation of Wildlife, Bangkok. 758 pp.
- MCDUGAL, C. 1977. *The Face of the Tiger*. Rivington Books, London.
- MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. *Amer. Midl. Nat.* 37:223-249.
- MUCKENHIRN, N.A. and J.F. EISENBERG. 1973. Home ranges and predation of the Ceylon leopard. Pages 142-175 in R.L. Eaton, ed. *The World's Cats*, Vol. 1. World Wildlife Safari, Winston, Oregon.
- NORTON, P.M. and S.R. HENLEY. 1987. Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *S. Afr. J. Wildl. Res.* 17(2): 41-48.
- NORTON, P.M., A.B. LAWSON, S.R. HENLEY and G. AVERY. 1986. Prey of leopards in four mountainous areas of the South-western Cape Province. *S. Afr. J. Wildl. Res.* 16(2): 47-52.
- SCHALLER, G.B. 1967. *The Deer and the Tiger: A Study of Wildlife in India*. University of Chicago Press, Chicago.
- SCHALLER, G.B. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago Press, Chicago.
- SEIDENSTICKER, J.M. 1976. On the ecological separation between tigers and leopards. *Biotropica* 8: 225-234.

- SEIDENSTICKER, J.M. 1983. Predation by *Panthera* cats and measures of human influence in habitats of South Asian monkeys. *Inter. J. Primatol.* 4(3): 323 – 326.
- SEIDENSTICKER, J.M. and I. SUYONO. 1980. *The Javan Tiger and the Meru-Betiri Reserve: A Plan for Management*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- SMITH, J.L.D., C. MCDUGAL, and D. MIQUELLE. 1989. Scent marking in free-ranging tigers, *Panthera tigris*. *Anim. Behav.* 37: 1 – 10.
- SMITH, R.M. 1978. Movement patterns and feeding behavior of the leopard in the Rhodes Matopos National Park, Rhodesia. *Carnivore* 1: 58 – 69.
- SRIKOSAMATARA, S. 1990. Density and biomass of mammals in a mixed forest dominated by dry dipterocarp forest or savanna forest of western Thailand. *Thai J. of Forestry* (in press).
- STOTT, P. 1986. The spatial pattern of dry season fires in the savanna forests of Thailand. *J. Biogeography* 13: 345 – 358.
- STOTT, P. 1988. The forest as phoenix: Towards a biogeography of fire in mainland south east Asia. *The Geographical Jour.* 154(3): 337 – 360.
- SUNQUIST, M.E. 1981. The social organization of tigers (*Panthera pardus*) in Royal Chitawan National Park, Nepal. *Smithsonian Contributions to Zool.*, No. 336. 98 pp.
- THITATHAMAKUL, Prayat. 1985. *Vegetation Change along the Altitudinal Gradient in Huay Kha Khaeng Wildlife Sanctuary*. M.S. Thesis, Univ. of Kasetsart, Bangkok. 157 pp.

