

CHAPTER 3: SPACE UTILIZATION AND ACTIVITY PATTERNS

INTRODUCTION

An individual's relationship to space reflects it's relationship to resources and other ecological factors. Uneven use of land by an individual and the relative way conspecifics use it, can provide an indication of the importance, distribution, richness and accessibility of an important resource such as food (Henshel 1986).

An individual's range must however satisfy all of it's energetic needs (Gittleman & Harvey 1982). The utilization of other resources, such as mates, water, shelter / hiding sites, depending on the demand for them, may also elicit special behavioural patterns. Depending on the quality and distribution of resources, certain behavioural patterns such as the establishing of territories in fixed areas at a given time, where resident individuals or groups dominate and limit access to resident conspecifics (Kaufmann 1983) may develop. In addition, certain ecological factors such as man-inflicted mortality may influence space utilization patterns in specific areas and of altering the internal characteristics of a population, by removing tenured individuals, creating behavioural instability, and keeping the social organization in a perpetual state of flux (Hornocker & Bailey 1986).

Although radio tracking studies in different regions of the world have revealed information on aspects of leopard spatial utilization (Bertram 1978; Muckenhirn & Eisenburg 1973; Smith

1977; Norton & Lawson 1984; le Roux & Skinner 1989), only the study of Hamilton (1976) and to a lesser extent Hornocker & Bailey (1986) can be regarded as representative in terms of information gained on the association between conspecifics in a specific area which facilitate the interpretation of the social organization of the population.

Hamilton (1976) described the existence of stable recognisable home ranges for leopards in Kenya, which the occupants cover frequently, thoroughly, and more or less evenly, although they do occasionally leave on forays from time to time. These leopards revealed a mosaic arrangement of polygonal male home ranges, which overlap relatively little, while showing that female home ranges do not appear to fit in with the male mosaic but are probably superimposed in a separate overlapping mosaic of female ranges. He confirmed that the leopard is basically solitary, except when females have dependant young. Associates between sexes are not only brief but also infrequent.

OBJECTIVES

By assuming the above mentioned scenario as the intrinsic "norm" of the social system of the species, radio tracking of leopards in the Naboomspruit study area was conducted to gain information on the following aspects of leopard space use and activity.

- a. Extent of movement which includes total and seasonal home range sizes as well as mean distances travelled in a diel tracking period.

- b. Occupancy of range relative to the distribution of cattle- and game farms.
- c. Estimated leopard density.
- d. Diel and seasonal patterns of activity.

METHODS

Radio-telemetry

A male and female leopard were captured as described in Chapter 2, immobilized with Ketamine hydrochloride, Parke Davis, Pty Ltd, RSA; 10 mg/kg and Syclan, Contour Labs Pty Ltd, RSA; 10 mg/kg respectively. The male was darted in the cage with a Varic I dartgun (Telinject R.S.A. Randburg) while the female was captured in the modified steeltrap with mounted darts as described in Chapter 2.

After being weighed and measured (Table 1) the study animals were fitted with radio collars manufactured by the Telonics Telemetry- Electronics Consultants, Mesa Arizona, USA. The complete collars weighed approximately 250 grams and contained 4 B transmitters (150.800 - 150.900 MHz) powered by one Telonics type B - 3H hermetic lithium cell with a theoretical operational life of 15 months. Each collar also contained a S6B motion sensor - inverse mode with a fast pulse rate when active and a reduction in pulse rate after cessation of movement. An LA 12 receiver (AVM Instrument Company, California, USA) was used.

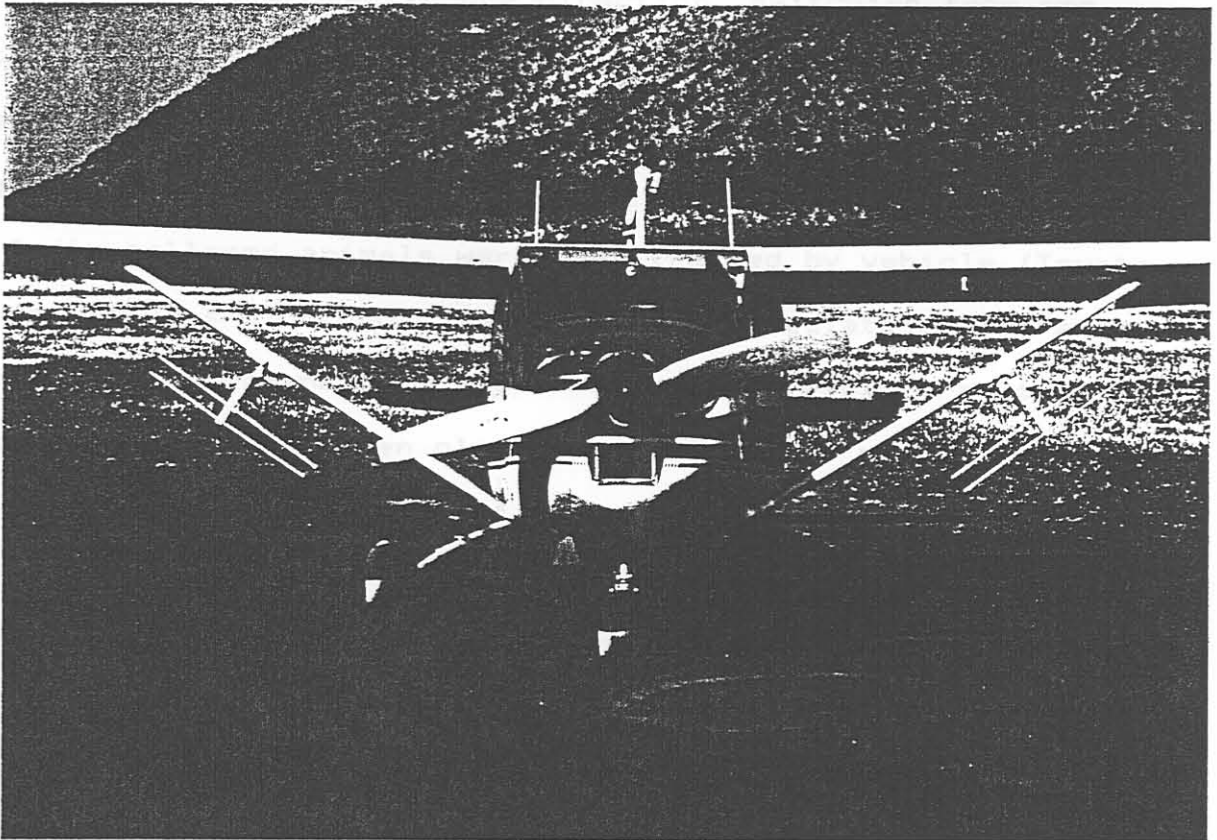


Figure 9 : A Cessna 185 with yagi antennas attached to the wing struts.

Due to the large home ranges of the study animals and broken terrain, initial location had to be done from the air (Cessna 185) with two 2 - element yagi ($\frac{1}{4}$ wave) antennas (CSIR, NEERI, Pretoria, RSA) mounted on the two wing struts (Fig 9). This was based and modified on the methods developed by Inglis (1981) and Whitehouse (1977). The study animals were pin-pointed from the air by flying overhead in one direction, switching from one antenna to the other by means of a switchbox (operated from inside the aircraft). This was checked with another fix at right angles.

Radio-collared animals were then tracked by vehicle (Toyota Landcruiser) and on foot, by means of triangulation with a 4-element yagi antenna from two or more known radio tracking stations, which had been plotted on a 1:50 000 map.

At each point a bearing of antenna direction was taken with a prismatic compass about 8 m from the vehicle. The true bearings were plotted on a 1:50 000 map overlaid by a 1 km x 1 km grid. The point at which two or more lines intersected, represented the leopards plotted position. This was also expressed to the nearest 125 m as a six figure map reference (X and Y coordinates) for computer analyses.

Both study animals were tracked for periods varying from four days to 14 days on a continuous 24 h (diel) basis. Tracking was carried out from November 1986 to July 1987 in the case of Leopard A and from March to September 1987 for leopard B, 759 and 322 radio plots were ascertained respectively. In the male (Leopard A) winter (April - Sept), 451 plots and summer periods (October to March), 308 plots were distinguished.

Extent_of_movement

Home range sizes (including seasonal) were calculated using the minimum area method (Mohr 1947), which measures the area of convex polygon linking the outermost radio-tracking plots. Areas were calculated on the flat plane of a 1:50 000 map, and no allowance was made for the increased area of mountain slopes.

The home range (area covered by normal activities) was separated from the "observed range" (all points included) as described by Hamilton (1981) by excluding plots that were considered to present "forays", away from the main home range.

Observation - area curves (Odum & Kuenzler 1955) indicated for each leopard whether the number of plots was adequate to describe the total area used. Mean distances travelled (MDT) in a diel tracking period from 12h00 to 12h00 were calculated to assess the rate of movement around the home range. This was taken as the total straight line distance between successive points during a diel tracking period.

Occupancy_of_home_range

The intensity of habitat use was measured in terms of the number of locations recorded in each grid for each leopard. This was analysed by the computer programme, ARC/INFO TIN MODULE, (GIS Lab, University of Pretoria), and demonstrated three dimensionally by plotting the frequencies per block (grid).

Peaks represent high values i.e. highly utilized space in the territory. As study animals were basically nocturnal or crepuscular lying up sites (resting sites) at 12h00 were also plotted for each individual. The different farming activities on

each farm is shown as G = Game, S = Stock or M = Mixed.

Activity patterns

Activity patterns were presented as the number of nights active vs the time of the day (hour interval), and compared seasonally. This was done by the continuous monitoring of the study leopards throughout 24 h - periods on a minute basis.

The total number of minutes active in a specific hour interval was classified under the following three categories: Active, i.e. - active for more than 40 min of that hour interval; Intermediate, i.e. active between 20 and 40 min and inactive, i.e. active for less than 20 min of the interval. The intermediate category was not used in the calculations of the data. A total of 52, 24 h periods were observed. The male was monitored for 52 complete 24 h periods while the female's data were obtained from 23 complete 24 h-periods.

RESULTS

Extent of movement

Sufficient data were obtained to calculate the "home ranges" for both leopards. The observation curves for both leopards seemed to level off after 300 radio plots (female) and 675 radio plots (male). (Fig. 10). The first 300 radio plots of the male leopard were obtained during the summer period. After the first 225 radio plots of this period, the graph levelled off but started to increase again in the winter after a total of 375 radio plots. As no forays occurred, the "observed range" sizes

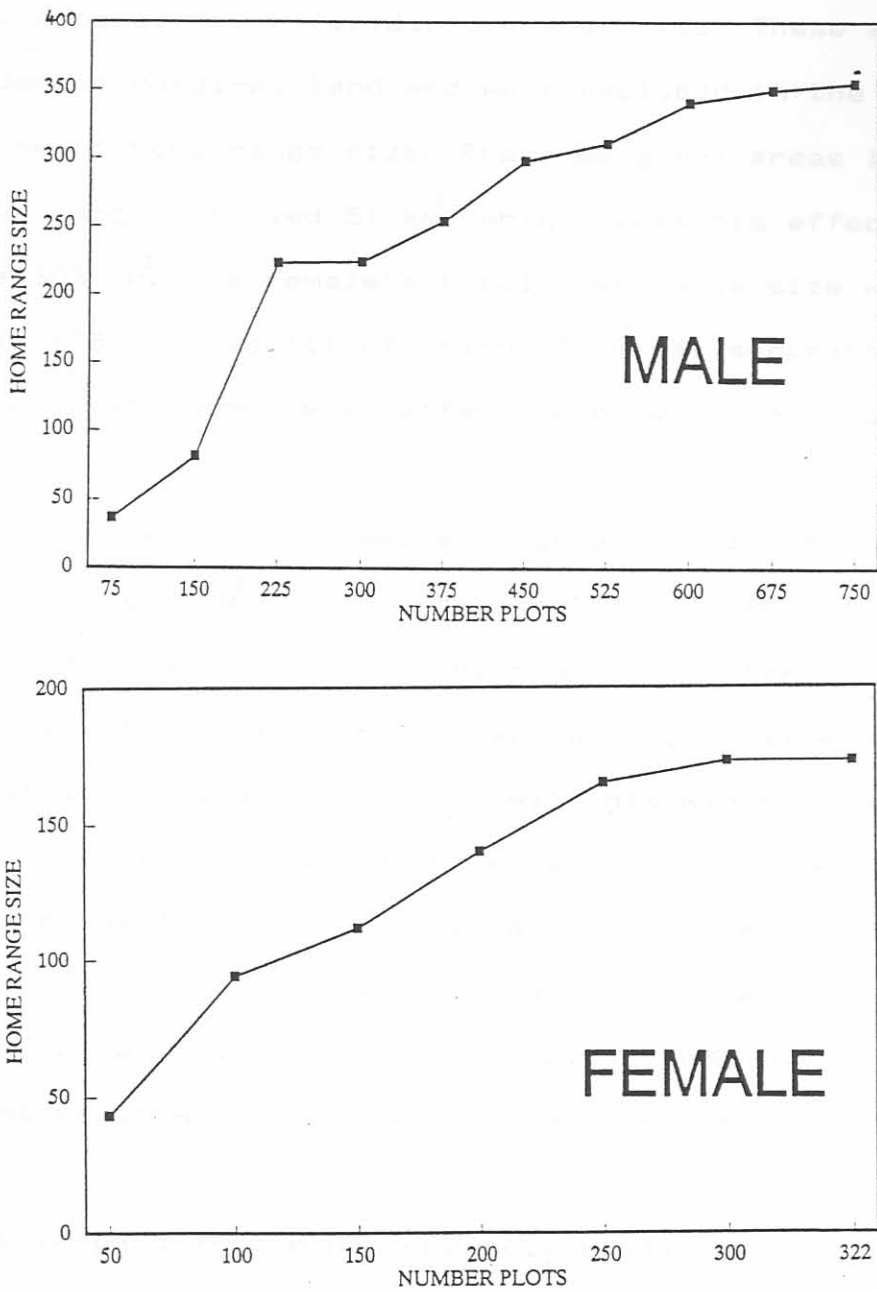


Figure 10 : "Observation - area curves" (Odum & Kuenzler 1955) for the male and female leopard in the Naboomspruit study area.

were taken as representative for the "home range" sizes.

The total home range size of the male leopard was calculated to be 354 km^2 (Fig.11). However, while covering his range he frequently crossed maize fields, orchards, etc. These areas were all regarded as marginal land and were excluded in the calculations of home range size. These marginal areas in the male's home range totalled 51 km^2 , which makes his effective home range size 303 km^2 . The female's total home range size was measured at 173 km^2 (Fig.11) of which 16 km^2 was subtracted as marginal land, which means an effective home range size of 157 km^2 .

The male's home range showed an overlap of 91% of that of the female (excluding 8 km^2 marginal habitat), while 46% of the male's home range was overlapped by that of the female (Fig.11). The male leopard's summer range showed a slight difference in spatial distribution, in comparison with his winter range (Fig. 12). Winter (247 km^2) and summer home range sizes (206 km^2) which excludes marginal land, did not differ significantly. The percentage overlap between the two seasons was calculated to be 43 % (133 km^2). Radio tracking data obtained from the female wasn't being dealt with seasonally, due to insufficient summer data.

The male leopard in the Naboomspruit study area moved a mean distance of 8,6 km per diel tracking period (SD = 5,1), (n = 52). The greatest distance was measured at 21,5 km and the minimum 0,6 km. The female averaged a distance of 6,1 km per diel tracking period (SD = 4,3), (n = 23), with a maximum of 12,2 km and a minimum of 0,2 km. Average seasonal distances of

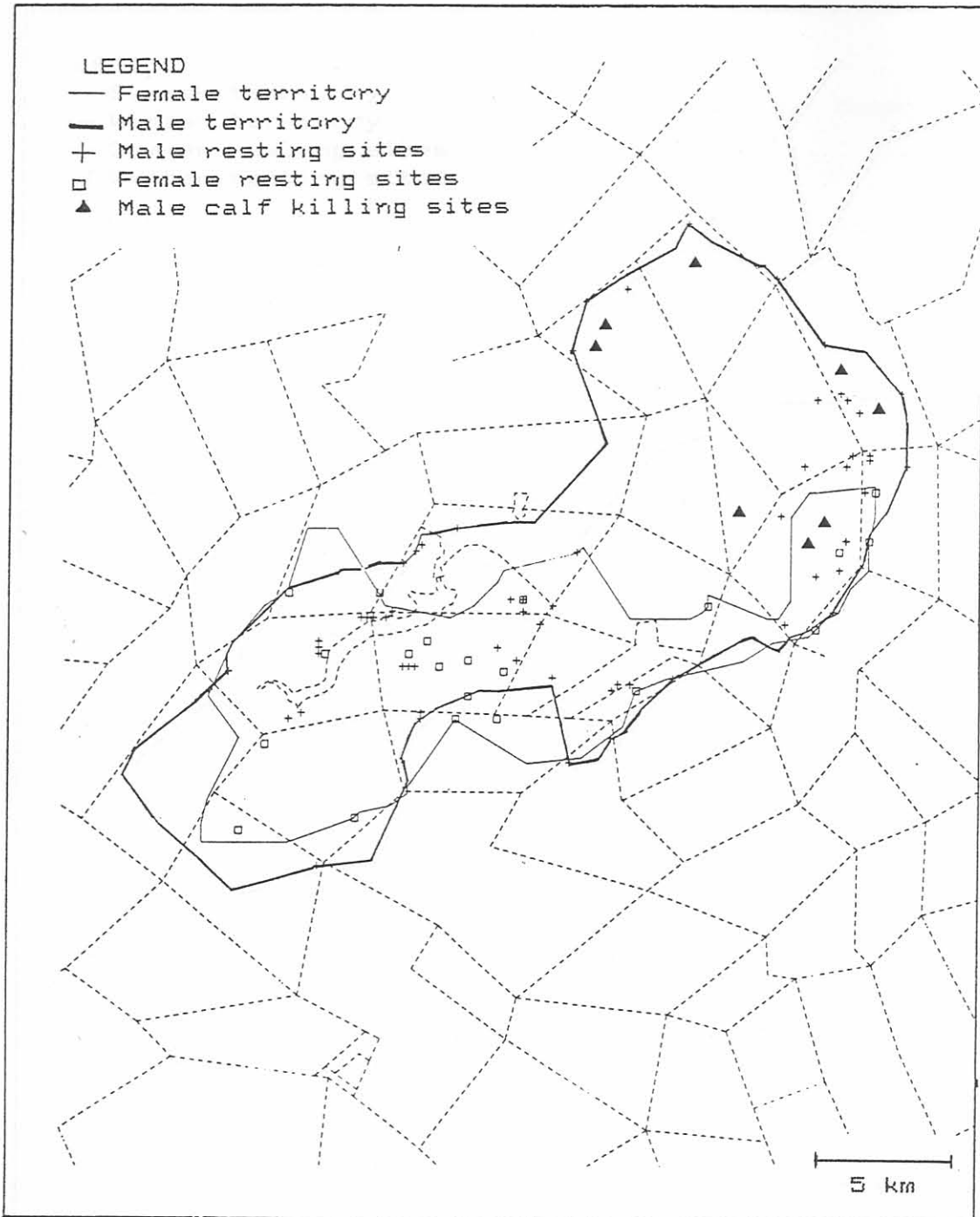


Figure 11 : Spatial distribution of the male and female leopard territories, with 12h00 resting sites and male cattle calf killing sites in the Naboomspruit study area.

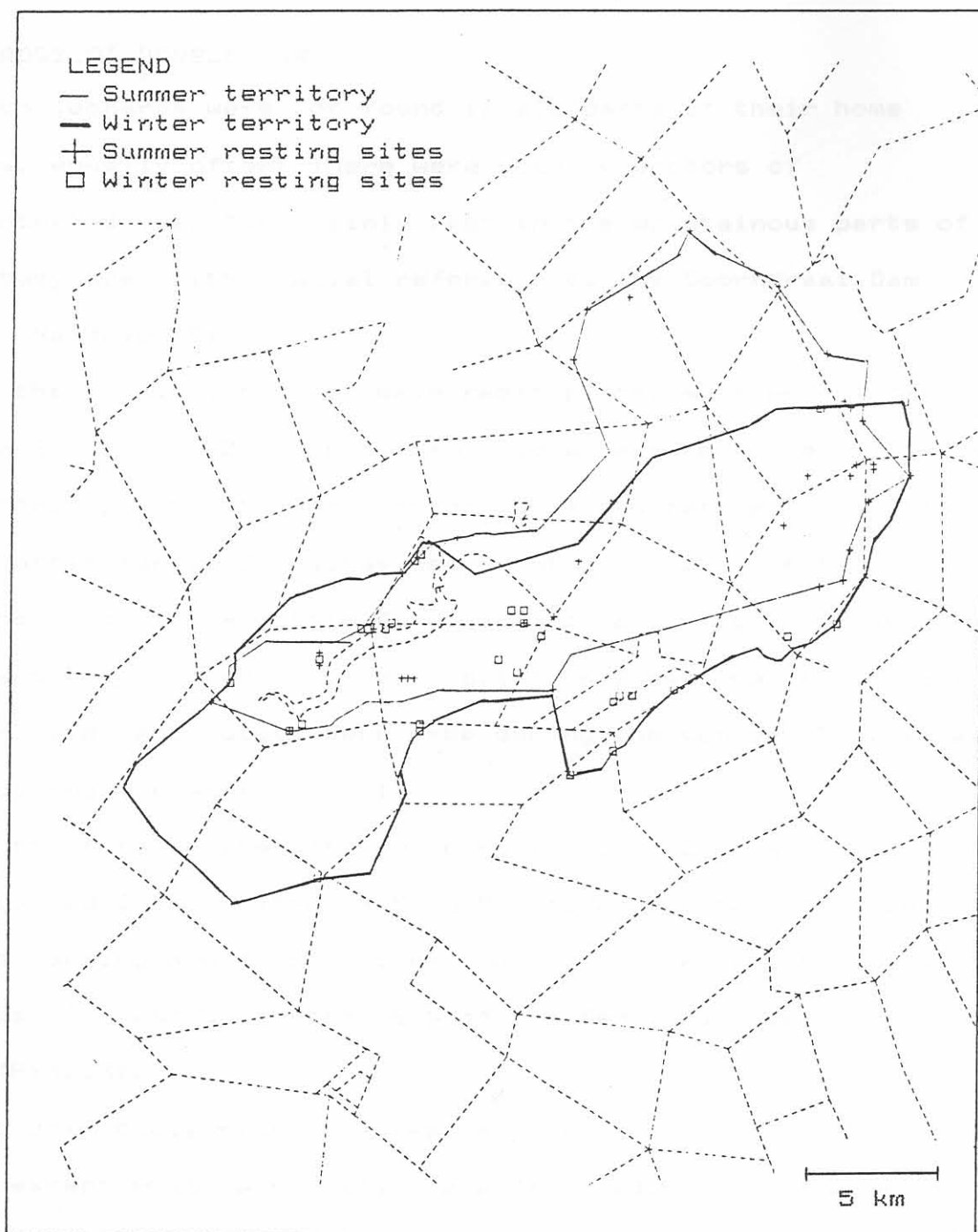


Figure 12 : Spatial distribution of the male leopard's summer and winter territories with 12h00 resting sites.

the male were calculated at 8,9 km during the summer (SD = 5,2), (n = 32) and 8,05 km during the winter (SD = 3,9), (n = 20).

Occupancy_of_home_range

Both leopards were not found in all parts of their home ranges, equally often. There were usually sectors of concentrated use. They mainly kept in the mountainous parts of the study area with special reference to the Doorndraai Dam Nature Reserve (Fig.13).

Of the total numbers of male radio plots, 49 % were located within G - sites (Doorndraai Dam Nature Reserve and exclusively game farms), 3 % within M - sites (Game and cattle farms) and 48 % on cattle farms. G - sites represented 25 %, M - sites 10 % and the remaining - cattle farming 65 % (S - sites) of the male's total home range size. (Fig.13) On a seasonal basis 52 % of G - site radio plots were made during the summer (Fig.14) and 48 % during the winter (Fig.14).

Of the total number of female radio plots 39 % were ascertained in G - sites, 4 % in M - sites and the remainder in cattle farming areas (S - sites). G - sites represented 53 %, M - sites 21 % and S - sites 26 % of the female's total home range size (Fig.13).

The same daily resting sites was not used during consecutive days, except when large kills were involved. They did however, return to the same tree or rock in the course of time and seemed to have favourite resting places, just as they preferred certain game trails and vehicle tracks as travel routes. Resting sites were exclusively on the ridges of mountains which permitted a

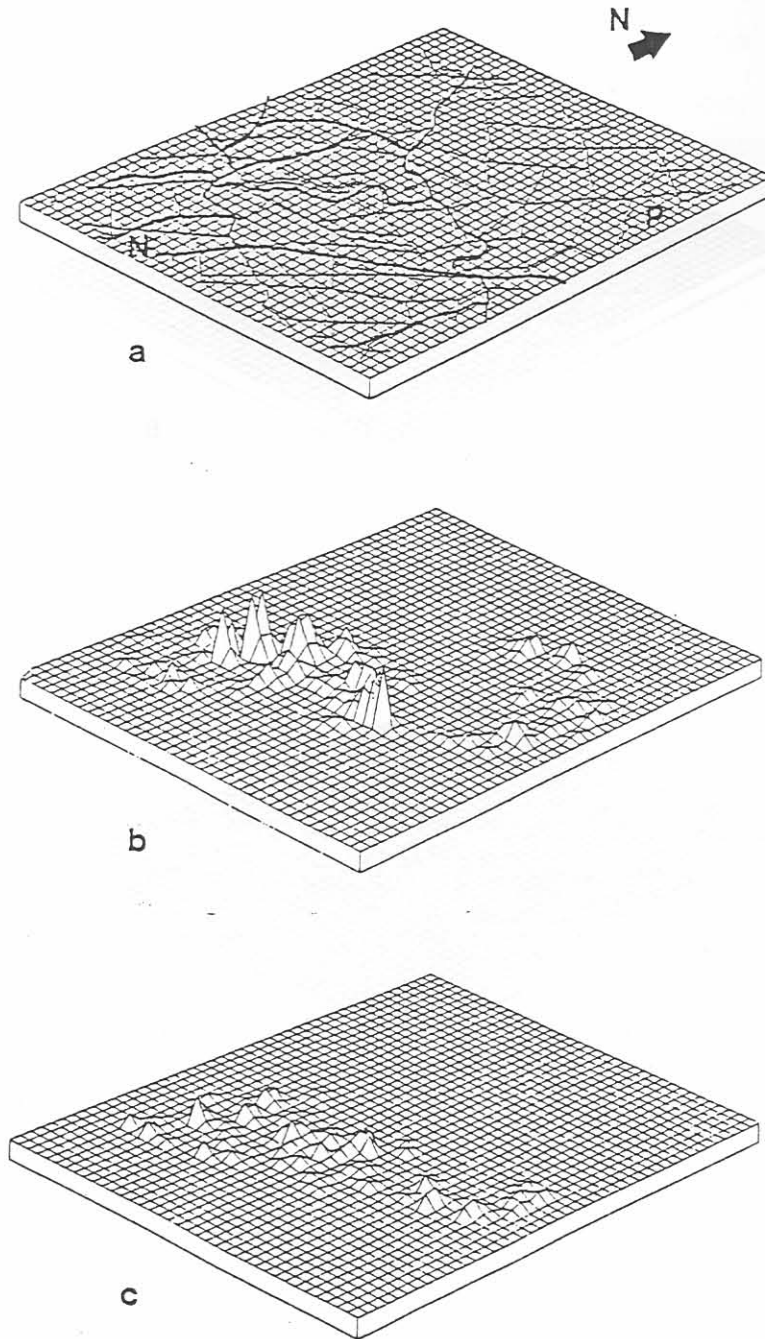


Figure 13 : Three - dimensional, ARC / INFO TIN MODULE - generated map representation of (a) Naboomspruit study area (b) male leopard space use (c) female leopard space use ; based on the number of plots in each grid (N = Naboomspruit ; P = Potgietersrus).

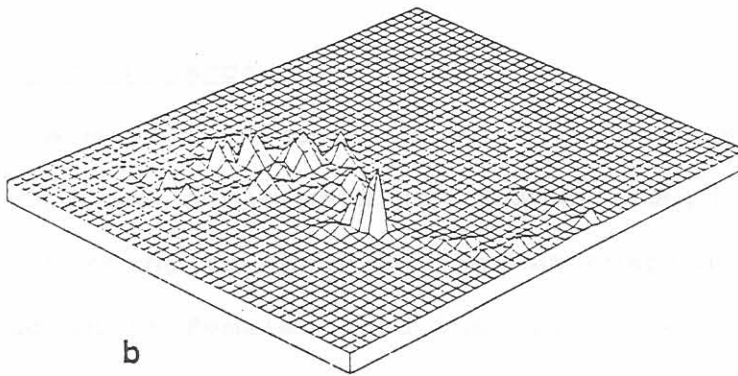
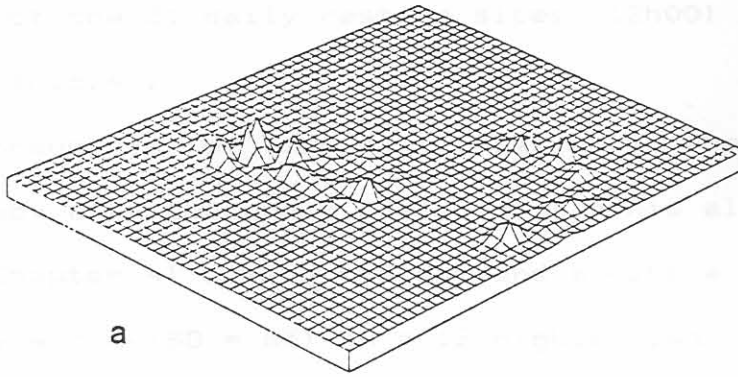


Figure 14 : Three - dimensional, ARC / INFO TIN MODULE - generated map representation of (a) male leopard summer space use (b) male leopard winter space use, based on the number of plots in each grid.

good view of the surrounding area (Fig.11 & 12).

Of the 77 male daily resting sites (12h00), 34 % were recorded in the Doorndraai Dam Nature Reserve. In the case of the female 38 % of the 21 daily resting sites (12h00) were made in this Reserve (Fig.4).

During the consumption of five cattle calves in the Naboomspruit study area the radio collared male hid all carcasses (see Chapter 4) during the day and sought a resting place on average 425 m (SD = 85) (N = 12 nights) away from the carcasses. With each carcass he returned to the same daytime resting site, except for the last night of consumption after which he left the area.

Estimated density of leopards

If one assumes a male overlap of 30 % in the home range of 303 km^2 , a density of one adult male per $303 \text{ km}^2 - 90,9 \text{ km}^2 = 212 \text{ km}^2$ is relevant. According to spoor in the Naboomspruit study area, at least two adult females used the male's home range. This means, one adult leopard per 70 km^2 . The number of subadults can only be a subject for speculation. One subadult was seen during the study period as well as the spoor of two cubs. If one only considers the one subadult, the leopard density for the Naboomspruit study area represents one leopard per 53 km^2 .

Activity patterns

Both individuals were predominantly nocturnal with some crepuscular activity (Fig 15). The female (n = 23) was active in 10 nights between 17h00 and 18h00, with a sharp peak between

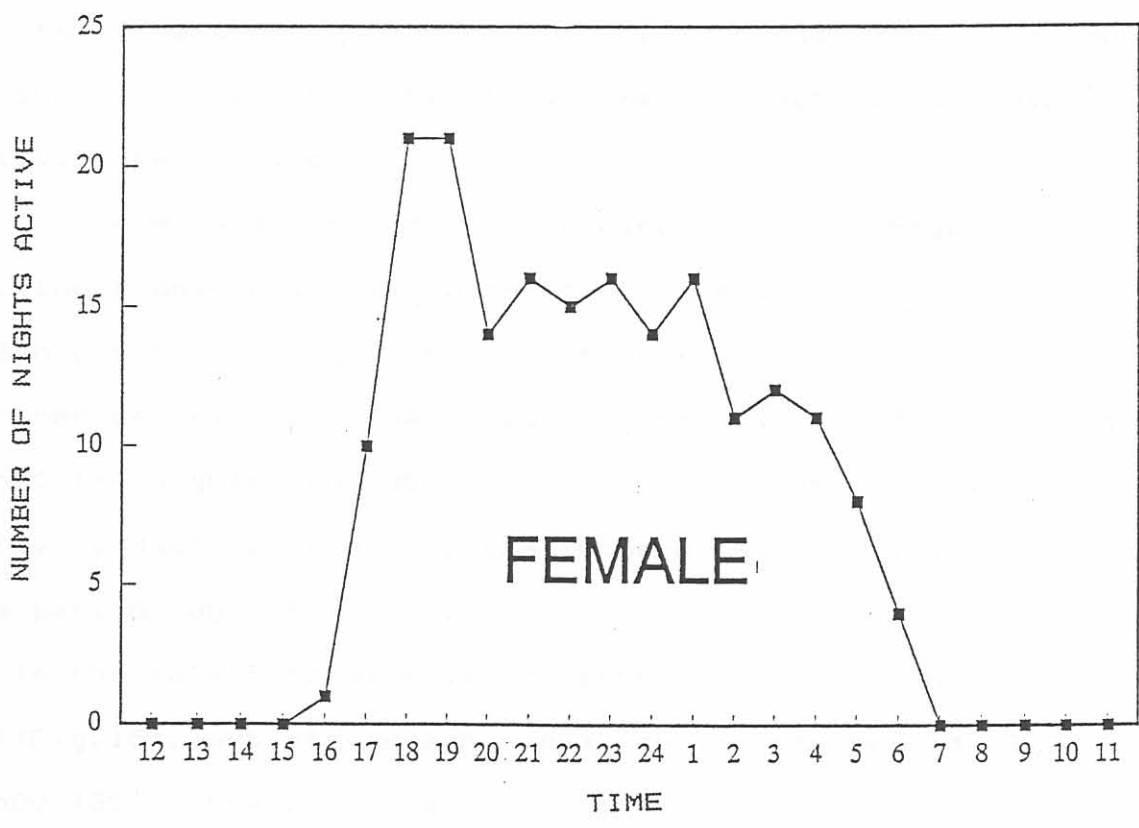
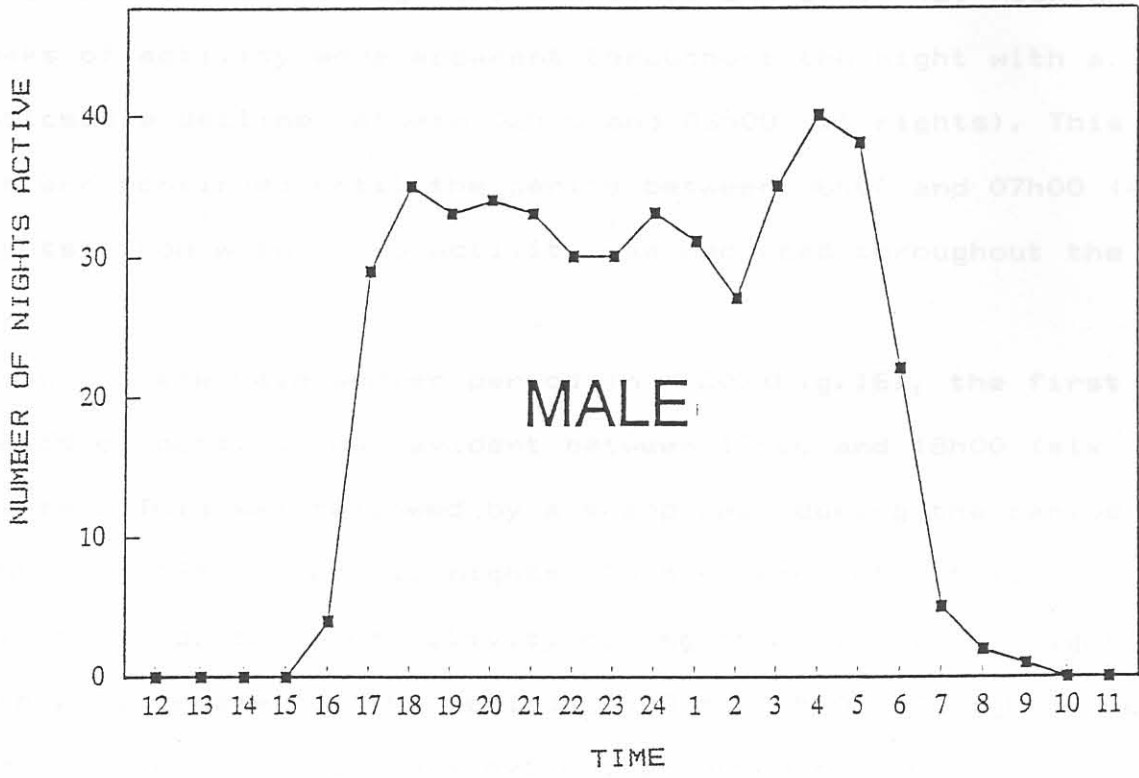


Figure 15 : Diel activity patterns of the male and female leopard in the Naboomspruit study area.

18h00 and 19h00 (21 nights), and 19h00 and 20h00 (21 nights). Peaks of activity were apparent throughout the night with a noticeable decline between 02h00 and 03h00 (11 nights). This pattern continued until the period between 06h00 and 07h00 (4 nights) from when on no activity was recorded throughout the day.

During the male summer period ($n = 20$) (Fig.16), the first period of activity was evident between 17h00 and 18h00 (six nights). This was followed by a sharp peak during the period 18h00 and 19h00 where 15 nights (75 % showed activity). Infrequent patterns of activity during the rest of the night with an increase for the period 24h00 to 01h00 (17 nights) were recorded. Another peak was evident at 04h00 to 05h00 (16 nights). The periods 07h00 to 08h00, 08h00 to 09h00, and 09h00 to 10h00 only showed activity in one day each, after which activity terminated.

In the male winter activity period ($n = 32$) (Fig.16), a prominent peak was also apparent for the period 17h00 to 18h00 (23 nights). Although activity was recorded throughout the night another definite peak was evident during the periods 04h00 to 05h00 (24 nights) and 05h00 to 06h00 (23 nights) from where activity declined sharply, the leopard becoming inactive during the period 08h00 to 09h00.

In the male's total activity pattern scenario ($n = 52$) (Fig.15), activity reach a peak during the period 18h00 to 19h00 (35 nights). This slightly levelled off for a short period between 02h00 to 03h00 (27 nights). A last peak during the period 04h00 to 05h00 (40 nights) was apparent. Low activity

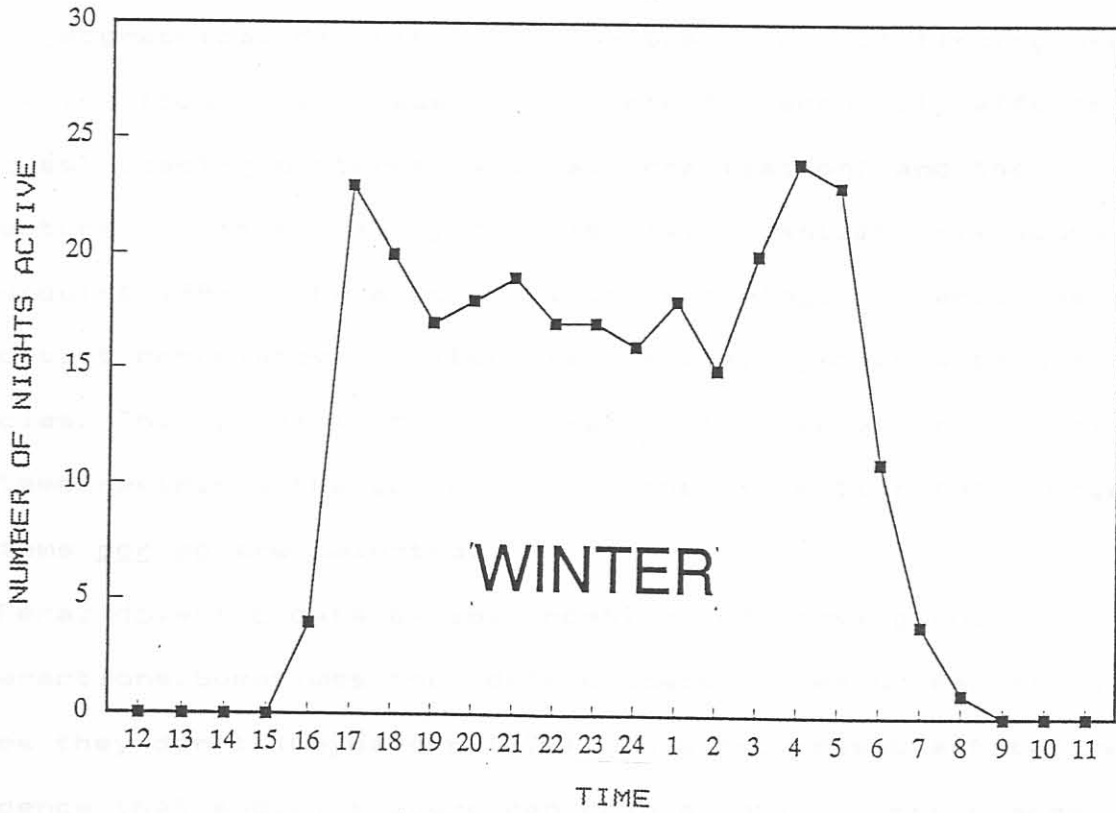
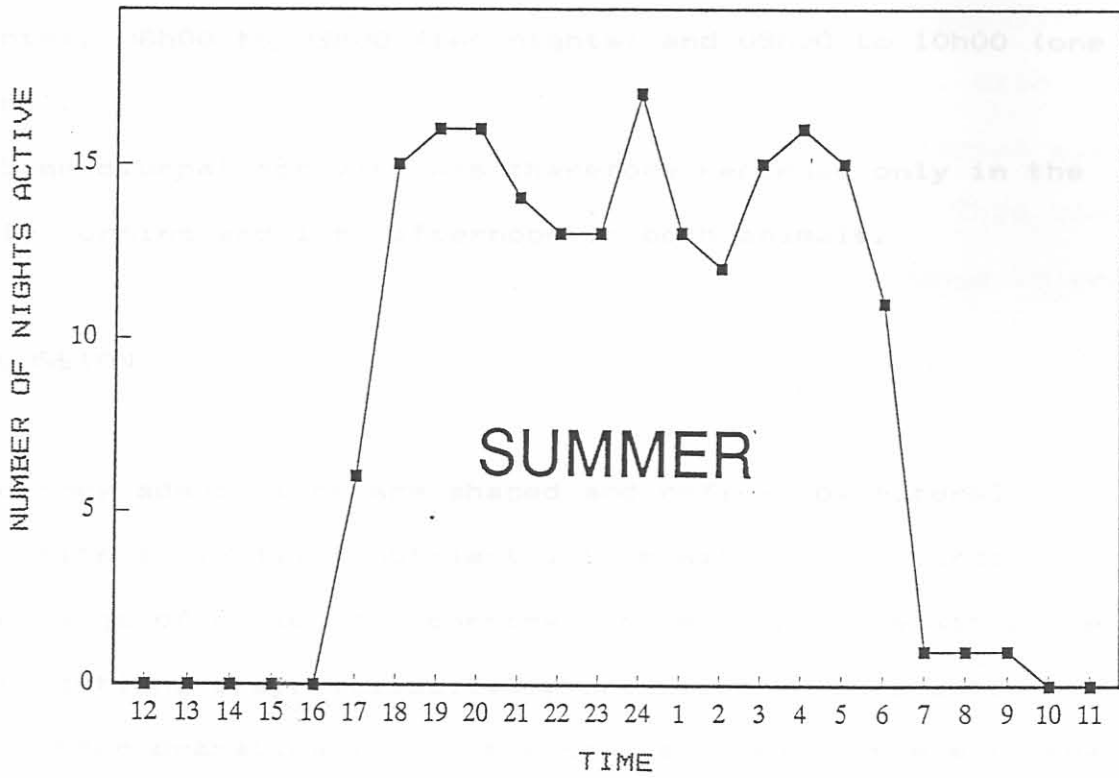


Figure 16 : Diel summer and winter activity patterns of the male leopard in the Naboomspruit study area.

patterns were monitored for the periods 07h00 to 08h00 (five nights), 08h00 to 09h00 (two nights) and 09h00 to 10h00 (one night).

Some diurnal activity was therefore recorded only in the early morning and late afternoon in both animals.

DISCUSSION

Predatory adaptations are shaped and refined by natural selection to maximize nutrient intake within the bounds of a wide range of ecological constraints (e.g. prey density, prey distribution, prey availability, predation or persecution) that may differ dramatically for the same species at the extremes of its geographical distribution. The basic task of finding and gathering food under these constraints fundamentally affects a species' spacing patterns (spacial organization) and the structure of its social systems (social organization) (Sunquist & Sunquist 1989). These constraints or ecological variables are important correlates of alternative social systems within a species. This possibility of intraspecific variation in social systems restricts the generality of the assumption that social systems *per se* are selected.

Feral domestic cats exhibit complex and varying social interactions. Sometimes they defend space or resources, at other times they don't (Leyhausen 1979). This provides quantitative evidence that social systems can have adaptive consequences (Lott 1984) and are not fixed through natural selection. A drastic decline in the bobcat (*Lynx rufus*) food supply, namely

blacktailed jackrabbits (Lepus californicus) led to the complete break down of the territorial system of the bobcat population and the resident adults scattered in all directions. With the recovery of the rabbit population the bobcat territorial system started to operate again (Hornocker & Bailey 1986). This however can be regarded as a sudden and extreme case of change in prey demography.

[The degree to which a territorial system can be achieved and maintained in practice depends on the cost in energy expenditure to the male or female in attempting to exclude possible competitors of the same sex. Because home range size varies depending on for example, prey availability, resident animals may be incapable of defending a territory adequately to exclude possible competitors. This accounts for most of the cases where overlap exists in the home ranges of like sexed adults. Overlap thus occurs when the cost of excluding the neighbour is either too great or, if the home range is large enough, impossible.]

Spotted hyaenas on the Serengeti, get most of their food by scavenging the remains of small, migratory prey. The hyaenas usually are nomadic, living in small, loosely organized social groups. Hyaenas in the Ngorongoro crater get most of their food by killing large bodied sedentary prey. The hyaenas are organized in large cohesive social groups which defend territories year round. The interpretation of this intraspecific variation in social system, is that the food base in the Serengeti is usually too scanty and unpredictable to support large groups of hyaenas or provide the energy required to defend territories. In contrast, most of the food in the crater is only

available to groups large enough to kill it. Moreover, it is predictable and relatively abundant, making territorial defence seem both possible and functional.

[Another ecological factor apart from prey population characteristics that may alter a predator's social system, is the continuous elimination of individual adults in that system through human activity or other mortality agents. This mortality has the capability of altering the internal characteristics of a population by removing tenured individuals creating social instability, and keeping the social organization in a dynamic state (Hornocker, Messick & Melquist 1983).]

[Burt (1943) defined home range as the area that an animal learns thoroughly through habitual patrols. The traditional but controversial definition of territory is an exclusive area maintained through overt defence or advertisement (indirect defence) (Noble, 1939). Although this definition of territory needs a better description for large mammals (Grimbeek 1984), it is used here as a basis in the discussion of the social organization of leopards.]

[In all studies so far conducted on the socio-ecology of leopards, a male arrangement of territories with relatively little overlap and a separate overlapping mosaic of female territories has been described (Hamilton 1981, Hornocker & Bailey 1986, Norton & Henley 1987).]

[Although Hornocker (1969) indicated that solitary predators that depend on their own physical well-being to survive, cannot afford injury through aggressive agonistic behaviour, a number of cases of fighting between leopards have been described in]

defending their territories (Turnbull-Kemp 1967, Hamilton 1981, le Roux & Skinner 1989, pers. observ.)

In addition, indirect means of territory defence may also be present. These include visual, olfactory and auditory (vocal) markings. (Hamilton 1976 ; Bothma & le Riche 1984, this study).

The flexibility of the social systems of solitary felids is becoming more and more apparent as detailed information on this aspect becomes available. Due to the wide distribution of these animals it is reasonable to assume that, along with adaptability, a highly flexible social system has evolved. Striking evidence for such flexibility was obtained in mountain lion and bobcat research (Hornocker & Bailey 1986).

In leopards this phenomenon may also be present as more detailed studies in divergent habitat types become available. Some indications of alternative social systems are present but, as detailed investigation is lacking, this cannot be ascertained. Two scenarios where the manifestation of alternative social systems are possible are to be examined, at this stage.

In ecosystems where the distribution and availability of food necessitates large areas of utilization, the economic cost of defending a territory must be measured against the benefits. Detailed information on the social organization of leopard populations, where home range sizes are in excess of 400 km², e.a. Stellenbosch area in the Cape Province, southern Kalahari and the Judean Desert of southern Israel, would possibly reveal interesting data on the exclusivity of home ranges.

Secondly, in the relatively high density leopard population

in the Kruger National Park (one leopard per 6 km^2) territorial exclusivity by conspecifics was not complete. According to Hornocker & Bailey (1986) this was probably because of the limited habitat available in the southern Kruger National Park. Leopards were largely confined to the Park and nearby private game reserves. Those straying into intensively farmed and grazed areas on the west and south of the Park were probably quickly exterminated.

Most available leopard habitat adjacent to the study area was probably already occupied by resident leopards. Some young leopards didn't disperse from the natal area but remained in the population as non breeding "floaters".

Although some fighting did occur, the effect on the population was minimal. None of the mortality in adults (18% annually) was attributed directly or indirectly to fighting among conspecifics (Hornocker & Bailey 1986).

In a third well studied intermediate scenario where leopard densities are lower such as Kenya, one leopard per 13 km^2 (Hamilton 1976) and Tanzania, one leopard per 29 km^2 (Bertram 1978) and possibly the Waterberg, one leopard per 53 km^2 (present study) and where enough surrounding habitat was available, the maintenance of exclusive territories was evident. However, whenever males made forays into the territories of others, they changed their behaviour outside their own home ranges and tended to withdraw sharply after encountering a resident male.

However Hamilton (1981) is of the opinion that bloody fighting among Kenyan male leopards is more common than has hitherto been believed and that it may even be a significant

cause of mortality.

Home range sizes (territories) of leopards so far described in the literature varied from 8 km² in the Chitawan National Park, Nepal (Seidensticker 1976) to > 400 km² in the southern Kalahari (Bothma & le Riche 1984). However different interpretations exist on exactly what constitutes a home range and the effect of the number of radio plots ascertained (Norton & Lawson 1985). Although not exactly comparable it provides an indication of trends in different regions. In the Naboomspruit study area, the male and female's home ranges can be regarded as representative for the specific period, as both individuals observed area curves (Fig.2, Fig.3) levelled off by the time radio tracking terminated.

[The spacing pattern in a population of solitary carnivores is the result of the behaviour chosen by the individual animal in an attempt to survive and maximize reproductive success. It is believed that female spacing patterns are determined by the availability of food, whereas male spatial organization, at least during the mating season, is determined by the distribution of females (Sandell 1989).

Because a non-cooperative (solitary) species such as the leopard female rears young by themselves, their reproductive success is closely correlated with the amount of energy they can allocate to reproduction. In turn, this amount mainly depends on the food resources available during the rearing period. Thus for females, food is the most important resource, and females should adopt behaviour which maximizes their chances of securing food resources for reproduction and survival. One can therefore

predict that female home range size is correlated with food availability during the critical period of the year (Sandell 1989).

The spatial distribution of the Waterberg (Naboomspruit) female leopard followed the superimposed mosaic arrangement over male territories as described by Hamilton (1981) for Kenyan leopards. As 46% of the males territory has been overlapped by the female, this means that another female (or females) is expected to be present in the northern sector of the males territory (Fig.11). This seemed to be the case as female spoor (different from the radio collared female) were detected in that area. Another male and female's spoor were also encountered on two and three occasions respectively on the south western boundary of the radio collared male's and female's territories. The infrequent presence of these individuals is probably related to the size and spatial distribution of their territories as suboptimal habitat (such as irrigation farming) exists in a south western and north western direction.

[According to Sundell (1989) solitary male spatial organization is influenced by two resources, namely food outside the mating season and receptive females during the mating period. It follows that during a substantial part of the year male and female spacing patterns are determined by different factors, and range size in males should be a function not only of food requirements but also of female distribution. Since food ranges are minimized whereas mating ranges are expected to be maximized, it follows that male ranges should be larger than predicted by energy requirements.]

The interpretation of the spatial distribution of the Naboomspruit radio-collared male leopard in the absence of data on the female(s) reproductive status is however incomplete. Leopards (radio-collared male and female) were known to associate for brief periods (two to three hours) in more or less the same area on four occasions. All of whom were in the Doorndraai Dam Nature Reserve.

The expanding of the male's territory in a northerly direction during the summer period can definitely be attributed to the presence of cattle calves on these farms during the calving season, where he took five individuals (Fig 11). The male's winter movements in the south of his territory can be related to the presence of "winter" cattle calves on the farms. No cattle losses were however recorded in this area during the time, as calves were kraaled every night.

Although Doorndraai Dam Nature Reserve constituted only 20% of the male's total home range size, almost 50% of the total number of radio plots were recorded in the reserve for both winter and summer periods. With the exception of the northern expansion (summer) and southern expansion (winter) as mentioned, the territory of the male was therefore relatively stable over the 11 month period (Fig.12). In the case of the female the Doorndraai Dam Nature Reserve contributed almost 40% of her total territory size in which 53% of the radio-plots were recorded. It seems therefore that the female used her territory more evenly when compared to the male.

It is apparent from Figure 11 that both leopards concentrated in rocky mountainous areas which, on the one hand, are not only

relatively remote from human activities but also facilitates hunting efficiency. All felids rely extensively on physical features in their environment, using almost any type of cover to get as close as possible to prey before making the final attack. (Sunquist & Sunquist 1989). Bothma & le Riche (1989) also recorded optimal positioning in the leopard whereby potential prey were selected from a high vantage point. Thus confirming the concept that cover and sight play an important role in hunting by cats (Kruuk 1986).

Bush density, grass height, ungulate numbers and biomass were uneven over the study area. The mountainous parts are typical sour bushveld with open savannas in the less rocky parts and dense, mixed bushveld in the rugged parts with a high diversity of micro habitats (Acocks 1975).

These mountainous areas supported a whole spectrum of potential prey species especially in the Doorndraai Dam Nature Reserve, where the highest prey numbers and biomass (excluding cattle) were recorded. Open savannas in and surrounding these mountainous ranges in the Reserve, supported small and large ungulates. A high density of small mammals including smaller antelope occurred outside the Reserve. (See Chapter 4) The circadian activity of especially antelope is relevant during the cold winter months, when they seek refuge in the denser mountainous bush away from the water (Doorndraai Dam).

Resting sites were also always on the ridges of mountains to enable proper viewing of the surrounding area. It was thus impossible to approach a leopard without being noticed. No selecting for resting sites in the Doorndraai Dam Nature Reserve

was evident. The male leopard in the present study without exception

returned to the same daily resting places when large prey was captured.

According to Bothma & le Riche (1984) leopards in the southern Kalahari seldom spend two successive nights in the same part of their range. During the hot hours of the day they lay in the shade of a suitable bush or tree or take refuge in the cool underground in an aardvark or porcupine burrow.

Leopards in Kenya (Hamilton 1981) also rested in a different place each day, except when they had large kills or small cubs. They did, however sometimes return to the same tree or rock in the course of time and seemed to have some favoured resting places as been found in the Naboomspruit study area. The leopards in the Cedarberg also appeared to rest in different places each day. There was no clustering of radio plots that would have suggested the use of favourite resting sites (Norton & Henley 1987).

Leopards frequently show maximum activity at night, with activity declining to a minimum at midday (Sunquist 1981). These patterns can however be vastly affected by the amount of human interference. In the southern Kalahari where no human interference exists, leopards rest frequently soon after the onset of their nightly movements, and again when they approach the end of such movements (Bothma & le Riche 1984). Radio collared leopards in Kenya also moved mostly at night and rested during the hotter hours of the day (10h00 to 17h00) (Hamilton 1981). However, in agreement with Bertram (1978) they sometimes

move at any time of day and Hamilton (1981) recorded leopards hunting on two occasions at 09h30 and 15h00 on hot days. Kenya leopards showed a sharp increase in activity between 18h00 and 19h00, with a more or less continuous movement throughout the night.

In the Cape Province leopard activity patterns did not support the popular belief that leopards are mostly nocturnal. Norton & Henley's (1987) results show that the leopards were most active during the day, with peaks in the late morning and late afternoon. Leopards were also usually inactive for most of the early morning from midnight till after sunrise. During the day they were recorded as active under a variety of conditions, and were not apparently by high temperatures. (Norton & Henley 1987)

In the Waterberg, leopards showed almost exclusively nocturnal activity patterns with early evening (18h00 to 19h00) and morning (04h00 to 05h00) peaks (Fig.15). However the later peak in the male is based more on directional movement (travelling). This seems to be patrolling related (territory maintenance or female interactions) and/or to optimize positioning, i.e. to move out of a potential high human activity zone to a more isolated zone. This activity was especially evident when no large kills had been made the previous night or early morning. Early evening and through the night activity peaks, in both sexes, seemed to be more hunting related, although the above-mentioned functions should also be expected to be relevant.

In the female the morning peak (04h00 to 05h00) was less prominent, as her territory didn't expand frequently into human activity zones. The smaller size of her territory also facilitated territorial maintenance.

A possible explanation of winter movement inhibition could be the low winter temperatures (as low as -6°C) experienced in this time interval during the study period. This temperature impact could also be reflected in the movement patterns of larger ungulate prey species, thereby making them more available in the denser rough terrain to leopards.

The incidence of large kills also has an inverse effect on activity, as a leopard would spend most of the night at the carcass feeding at intervals. Rain showers *per se* did not seem to have an influence on activity. The radio collared male in the Naboomspruit study area travelled extensively on two occasions during heavy thunderstorms.

The straight line distance between resting sites of leopards on consecutive days (the daily distance) varied in Kenya from leopard to leopard more or less in direct proportion to the size of the animal's home range. The smallest distance recorded was a subadult male (0,9 km). That of an adult female was calculated to be 2,0 km, while those of five adult males varied from 2,3 to 4,2 km, with a mean distance for all five males of 2,9 km. Maximum daily distances recorded varied from 4,9 for the adult female to 8,4 for the adult male.

The mean daily distances of the study leopards in the Cederberg (Cape Province) were very similar to those found in Kenya, where it varied from 2,3 to 4,2 km (Norton & Henley

1987). In the Stellenbosch area female daily distances of 11,2 km, and daily male distances of 6,7 km were recorded (Norton & Lawson 1985).

In the Waterberg mean distances travelled in a diel tracking period give more detailed information in that different points throughout a night were linked and not only the daily resting sites. Waterberg figures are thus not actually comparable and are expected to be higher. The 8,6 km daily mean distance travelled by the Waterberg male is however much lower than the 14,3 km mean distance recorded by Bothma & le Riche (1984) in the southern Kalahari. A maximum of 33,0 km was travelled by this male in comparison with the maximum of 21,5 km recorded in the Waterberg. Females with cubs moved a mean distance of 13,4 km during a 24 hour period in the southern Kalahari, whilst the female in the Waterberg only covered an overall distance of 6,1 km. These higher distances in the southern Kalahari seemed to correlate with the higher "territories" 400 km^2 in comparison with the 150 km^2 (female) and 300 km^2 (male) in the Waterberg.

The two Waterberg leopards not only showed a tendency to patrol the edges of their territories, but their movements within the territories showed they did cross rapidly backwards and forwards within the area. In the Melk River study area tree-scratching was very common. Only three tree species were utilized namely the water pear (Syzygium guineense), the water berry (Syzygium cordatum) and to a lesser extent (once) the common white pear (Dombeya rotundifolia). High frequencies were encountered for the first two species

especially along watercourses, which probably represented areas of high utilization. In the southern Kalahari tree scratching also occurred frequently, in contrast with the view of Turnbull-Kemp (1976), that tree-scratching is rare in African leopards or Hamilton (1976) who never observed tree scratching in Kenyan leopards.

According to Ewer (1973) tree scratching does not only have a definite communicatory function, but also serves to neat the claws. The selecting of specific tree species for this neatening process indicates that the composition of the bark and/or the woody part of these trees facilitate this function.

Scent marking in the Waterberg followed the same pattern as found by Bothma & le Riche (1984) in the southern Kalahari, Schaller (1972) in the Serengeti and Hamilton (1976) in Kenya, including the fact that faeces does not seem to be used in any special manner. There is also no evidence yet that leopards in the Waterberg (present study) and the southern Kalahari (Bothma & le Riche 1984) use specific trees as scent posts, as leopards do in Sri Lanka (Eisenberg 1970).

Urine-scraping was also relatively common along roads in the Waterberg. In the southern Kalahari these frequent scrapes seem to be associated with squirts of small quantities of urine on low shrubs or grass tufts (Bothma & le Riche 1984) and agrees with the observations of Eisenberg & Lockhart (1972). Although no data could be ascertained in the Waterberg, both sexes of leopards in the Kalahari scent-mark (Bothma & le Riche 1984).

This phenomenon of scentmarking was extended in that leopards

in the Waterberg often rolled in the lavender bush Lippia rehmannii and fever tea bush Lippia javanica which presents a strong aromatic smell when bruised. The leaves and stems of these bushes also possess coarse hair on which leopard hair sticks. It is believed that this is not only functional in marking a territory but the leopard most probably also carried the lavender like smell with him, that would disguise his smell while hunting. This phenomenon was also observed by Bothma & le Riche (1984) who described the frequently rolling in places where other wildlife have urinated or defecated.

The calling of leopards is described by Turnbull-Kemp (1967) as a harsh rasping sound. This rasping is repeated more than fifteen times in unbroken succession. The Waterberg radio-collared male called on six occasions, whereby the rasping sound was repeated for seven to nine times. This happened between 21h00 and 22h00 in all cases, while he was active in the Doorndraai Dam Nature Reserve. Smith (1977) found that vocalisations in the Motobos National Park, Zimbabwe were most common between 21h00 and 24h00 and again between 04h00 and 05h00. Although these callings are possibly primarily territory - maintenance related it can also function as territory independent spacing mechanisms as found with territorial wolf packs (Harrington & Mech 1983). It's role as a communication measure per se is therefore relevant, for example during the mating season.

A knowledge of the density as well as the intrinsic regulatory mechanisms of a population is of critical importance

differ vastly from those that are

where management decisions are to be made. This is even more so where the population is in direct competition with man on the one side, but also may be exploited through trophy hunting. In the high leopard population of the Kruger National Park, one leopard per 6 km^2 (Bailey pers. comm., in Hamilton 1981), the population appear to be regulated by food supply, but the number of breeding adults was regulated by social behaviour.

Due to the lack in exclusivity in home ranges (Hornocker & Bailey 1986; le Roux & Skinner 1989), it seems that conspecifics do tolerate each other as long as the "intruder" shows submissive behaviour.

* (Scars and wounds indicated there was some fighting among adults, but it's effect on the population was minimal as tenured animals remained in the same areas. Further, none of the mortality in adults (18% annually) was attributed directly or indirectly to fighting among conspecifics (Hornocker & Bailey 1986). In this population 18% of the adults, 32% of the subadults and 50% of the cubs-of-the-year died annually; 64% attributed to starvation and 36% to predation or man. In spite of this turnover the population remained constant.

The leopard population in the Naboomspruit area is much lower (one leopard per 53 km^2) but the intensity of territorial maintenance and exclusivity of occupancy seem to be much higher, as described for Kenya leopards (one leopard per 13 km^2) (Hamilton 1981). A high turnover of adult leopards prevails in certain Waterberg areas.

* Mortality factors present in the Kruger National Park also differ vastly from those operating in the Waterberg. In the

Kruger National Park cubs and subadults are particularly vulnerable to predators such as lions and spotted hyaenas while this factor is absent in the Waterberg. Hunting pressure here, is directed more at young and older adults. This population also appear to be controlled by food but social behaviour and hunting pressure plays a greater role in comparison with the southern Kruger Park population.

It is traditionally believed that most stock-raiding is done by either old or immature leopards (transient). Esterhuizen & Norton (1985) showed that most leopards that kill livestock in the Cape Province are prime adult leopards. Twelve leopards that were captured during the study period in different areas of the Waterberg after they had allegedly killed stock, consisted of five adult males, four young males, three adult females and one young female. None of the individuals were old or in bad condition as being found in the Cape Province. Stock preventing measures are therefore to be aimed at the population as a whole.