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THE ETHOLOGY, SOCIOLOGY AND INTERSPECIFIC INTERACTIONS OF THE YELLOW MONGOOSE, *CYNICTIS PENICILLATA*, IN THE KAROO

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THE ETHOLOGY, SOCIOLOGY AND INTERSPECIFIC INTERACTIONS OF THE YELLOW MONGOOSE, *CYNICTIS PENICILLATA*, IN THE KAROO

by

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CHAPTER 1

1 GENERAL INTRODUCTION

Cynictis penicillata is widespread throughout both Namibia and Botswana, being absent only in the extreme north and in the Namib Desert (Smithers 1983). In South Africa, they occur in a central belt in the Transvaal. They are also widespread in the Cape Province and Orange Free State, but occur only in the north western parts of Natal.

Cynictis penicillata is widely distributed throughout the Karoo and lives together with *Suricata suricatta* and *Galerella pulverulenta*. These three species occupy different home range sizes which overlap with one another, and their relative densities differ.

The social system of *Cynictis penicillata* apparently varies from being social in some regions of its geographical range (eg, Southern transvaal, Wenhold pers.comm.; Kalahari and Etosha National Park, Rasa pers.comm.) to solitary or pair-living in other area. This difference in sociality poses many questions on the selective pressures resulting in its evolution.

The social system of a species is clearly one of its most important biological characteristics and why animals live in groups is a fundamental problem of biology (Wrangham 1986). If we make the reasonable assumption that even complex animal behaviour reflects at least some component of genotype, then we must expect social systems to have evolved, just as structure and physiology have evolved. As the products of evolution, social systems should thus be adaptive; that is they should be adjusted to each environment in which they occur so as to confer maximum reproductive success upon individuals of the species adopting them. From this point of view, the diversity of animal social systems takes on a new order and significance when considered as part of the adaptive mechanisms of an individual species.

Social structure comprises and is influenced by population composition and individual - and group - ranging patterns (Hinde 1988). A species' social structure, therefore, cannot be fully described or explained without reference to these parameters or to the overall ecological and species biological variables that control the distribution and movement of individuals within a population (Hinde 1988). Hinde (1988) further points out that the basic framework of sociality is dependent on interactions between individuals and where these are very infrequent it is doubtful whether a real social relationship can even exist. This brings to mind only extreme cases: the inter- and intra-specific interactions in *Cynictis penicillata* will be investigated in this thesis.

Sociality is defined as the state of group formation when members of a population of differing sex and age structure share the same space; i.e. have markedly overlapping home ranges, communicate with one another, and whose social interactions include cohesive behaviours (Armitage 1981). Social relationships differ between species and because they have widespread effects on individual fitness they demand explanation in terms of their adaptiveness. As mentioned above, intraspecific variations occur in many vertebrate species, including *Crocuta, Panthera leo, Canis mesomelas*, and many bird species (Smithers 1983). A case in point is that of a population of Acorn woodpeckers (Wrangham 1986): on one occasion, more than half the adult population at a particular site switched to breeding in male-female pairs rather than in communal groups and did not maintain the stable long-term bonds typical of their species. In this species, a temporary shortage of food appeared responsible for the change (Stacey & Bock 1978; Wrangham 1986). Other examples may be found in primates, where the most extreme variation in social relationships concerns the number of individuals per group rather than whether groups are temporary or permanent (Yoshiba 1968).

The interspecific differences in sociality between closely related taxa are generally attributable to differences in habitats, foraging ecology, predation and resource distribution (Rubenstein & Wrangham 1986). The social organisation of mongooses can be placed along a continuum ranging from solitary individuals (e.g. *Galerella pulverulenta* (*Galeralla*) (pers. obs.), *Attilax paludinosis* (*Attilax*) and *Herpestes sanguineus* (Baker 1989)), through moderately social female/male kin clusters and familial groups (e.g. *Cynictis penicillata* (Wenhold 1990), to highly social groups (e.g. *Helogale rufula* (Rasa 1977), *Suricata* (MacDonald 1985). The most social of the mongooses tend to be the smaller diurnal species. Rasa (1976) has noted that diurnal viverrid species (*Helogale*, *Suricata*, *Mungos*, *Crossarchus*) inhabiting areas with little or no cover have almost all evolved a relatively high degree of sociality whilst larger, nocturnal and arboreal species occupying denser habitats have a tendency to solitary or pair living (*Ichneumon spp.*, *Herpestes spp.*, *Attilax paludinosis*). The major factor involved in the evolution of sociality in the smaller species appears to be predation pressure in an exposed environment and the subsequent necessity for effective anti-predation mechanisms (Rasa 1989, 1990).

Sociality amongst larger carnivores is generally related to cooperative hunting (Kruuk 1972; Schaller 1972; Kleiman & Eisenberg 1973; Kruuk & MacDonald 1985; Lamprecht 1990) and group defence against predators (Rasa 1986). Group size in many species of carnivores may be determined by the food resource size and availability (Bekoff & Wells 1980; Caraco & Wolf 1975). However, as Waser (1981) points out, the apparent success of models relating the degree of sociality to resource dispersal falls short when considering viverrids. As an alternative, Waser suggests that the renewal rate of a prey resource, rather than its actual distribution, is instrumental in the selection for sociality in viverrids.

The evolution of sociality is determined and influenced by a number of complex and diverse factors. Sociality in carnivores has generally been discussed in terms of the advantages to cooperative hunting and predator defense (Kruuk & MacDonald 1985). In addition, group size in social species has been suggested to reflect food "patch size" where a patch is a prey individual, but may also be a local concentration of small prey (Kruuk 1985). That group size should ultimately be determined (or at least limited) by food patch size is a hypothesis that has been proposed in several forms for a variety of animals (Bekoff 1972). This may be applied not only to the spatial dispersion of food, but also its temporal characteristics ie, the renewal rate. The average rate of resource renewal and the details of its time course should influence the likelihood that sociality may evolve, and, more specifically the benefits of maintaining and defending a territory.

Armitage (1981) carried out an extensive study on sociality in ground squirrels, and questioned the presence of varying social systems in different populations of the same species. He proposed that sociality in ground squirrels is associated with delayed maturity, and that a system has evolved where a male retains female kin within his territory to form a harem and hence a social group. Further, he suggested that group formation is associated with resource availability (food in particular), the defense of females as a resource, and the prolonged association of young with adults in the winter (as suggested in prairie dog sociality - although females remain essentially individualistic (Emlen & Oring 1979)).

In this study, a model will be proposed in which the defense of a territory becomes significantly relevant in the evolution of a social system. In small carnivore species the defense of territories or home ranges may be achieved by sociality. Consider the costs of living in a group: whatever the advantages of foraging with conspecifics, tolerating them in a social group will be costly to the individual to the extent that their presence decreases the amount of food available. One type of resource characterized by a low cost to social tolerance is food occurring in patches larger that can be immediately exploited by a single individual (such as the food source selected by *Cynictis penicillata* - insects, small mammals, reptiles) (Kruuk 1985). If foraging areas are regularly revisited, these costs should also depend on how soon an area just exploited by a conspecific replenishes itself. Resource depression and renewal characteristics should determine how much exploitation competition results from a given degree of home range overlap (see Carpenter 1987; Mares 1987). However, in cases, such as found in *Cynictis penicillata*, where the food sources are perennial and widely dispersed, it is advantageous to be essentially solitary. A further example of an extreme case is that of the orangutan which forage for specialised food resources and is solitary. This is highly atypical of primates (Galdikas 1979; McKinnon 1974; Rodman 1973, 1977) and except for mothers and their most recent offspring, individuals meet rarely and these interactions are invariably agonistic, if at all acknowledged (Hinde 1988).

By studying a local geographical variants of the yellow mongoose, where a tendency is found or variations in group size, the adaptive nature of the social behaviour will be established. *Cynictis penicillata* is a particularly appropriate subject or studies of comparative socioecology: they are diurnal, large enough to be seen easily and vary in their group size through their geographical range. Because they are a burrow dwelling species they are also relatively easy to locate for daily observations. A detailed analysis of predator-prey related behaviour, and the various inter- and intraspecific interactions occurring within a study group of *Cynictis penicillata* will, therefore, be undertaken.

The aim of the thesis is thus to document the degree of sociality of *Cynictis Penicillata* in the Karoo and to correlate this to ecological parameters pertaining to the Karoo. By comparison of these data and examination of published data relating to other areas of its geographic range, suggestion will be made about the complex of parameters influencing the social structure of this species.

CHAPTER 2

MATERIAL AND STUDY AREA

2 STUDY AREA

2.1 **Locality**

The Karoo-Namib Region comprises the extensive arid and semi-arid areas of the south western part of southern Africa (Werger 1978; White 1983). The region encompasses a high diversity of climates, landforms, soils and vegetation. Recently Rutherford and Westfall (1986) have divided the region into three biomes on the basis of the Summer Aridity Index, percentage of winter-half rainfall, and life-form mix. These biomes are: Nama-Karoo Biome, Succulent-Karoo Biome and the Desert Biome (Figure 1.1). The study site is found in the Nama-Karoo. Here the vegetation is dwarf scrubland.

The fieldwork for this project took place from July, 1987 to August, 1988 on the farm Biesjiesfontein, in the Hutchinson district of the Central Upper Karoo. The population density and distribution of the mongooses on the farm was established using various incidental and dedicated census records collected throughout the study period.

The farm is situated near Victoria West at 31° 30' S and 23° 15' W witha mean elevation of 1280 meters (Geoloical Survey, 1979)

2.2 **Ecological Characteristics of the Karoo Biome**

2.2.1 Geology, Physiography and Soils

The geology and physiography of the Karoo vary greatly from one region to the next. The Great Escarpment formed by the mountains of the Roggeveld, Nuweveld and Sneeuberg lies at approximately 3 050 meters and encompasses the vast peneplains of the Upper Karoo. To the south lie the lower regions of the Great Karoo, Little Karoo and Robertson Karoo, with the Tanqua and Namaqualand Karoo regions lying to the west.

The geology of the area is predominated by the rocks of the Karoo Sequence where the soils are weakly developed, shallow and alkaline (pH 7.0 to 8.3) (White 1983). These are formed from underlying sedimentary rocks of the Permian age which have been extensively intruded by dolerite of Jurassic age, resulting in the characteristic presence of koppies or inselbergs (Werger 1978).

1. **Topography**

The region is characterised by a flat expansive topography resting on a bedrock of shale. Soils are characteristically shallow and under severe erosion as a result of denudation of the vegetation (Booysen and Rowswell, 1983).

The farm occupies a total area of 13 983 ha of which 12 625 ha is actively used. This latter area is divided into 49 paddocks or "camps" of mean area 258 ha (range 20 to 564 ha) by 1.3 m high fencing. These fences have proved adequate for the enclosure of livestock.

2.2.3 Vegetation

Karoo shrubs comprised the major component of the vegetation in the camp, while grasses and ephemerals were the minor components with traces of geophytes occurring.

The vegetation of the area can be distinguished into "rand" veld and "pan" veld by consulting aerial photographs. The constitution of these veld types was different. Geophytes together with plant species such as *Pentzia spp., Eriocephalus sp., Ericoides, and Pteronia spp.* predominated the "rand veld, while grasses and species such as *Sasola spp, Psilanlon absinle* and *Zygophyllum incrustatum* predominated the "pan" veld.

According to Cowling (1986), the plants of the Karoo show a high degree of population instability, even in the relatively short term, as species respond differentially to particular sequences and combinations of climatic conditions. The ability of species to endure droughts as long-lived seeds imparts a resilience on their populations which is broken only by depletion of the seed banks.

Biesjiesfontein is particularly flat and is comprised primarily of "plains" vegetation (Viljoen & Immelman 1989) which is predominated by Karoo scrub such as *Pentzia spp*. and *Eriocephalus spp.* One third of the farm, however, is classified as a floodplain which has a higher plant cover and a lower species diversity (Acocks 1975). Grasses, especially *Erogrostis* spp, dominate the flood plain which is believed to have a higher carrying capacity (Davies 1987).

Vegetation on the farm is typically very short and is maintained this way by the effects of aridity and herbivory.

2.2.4 Climate

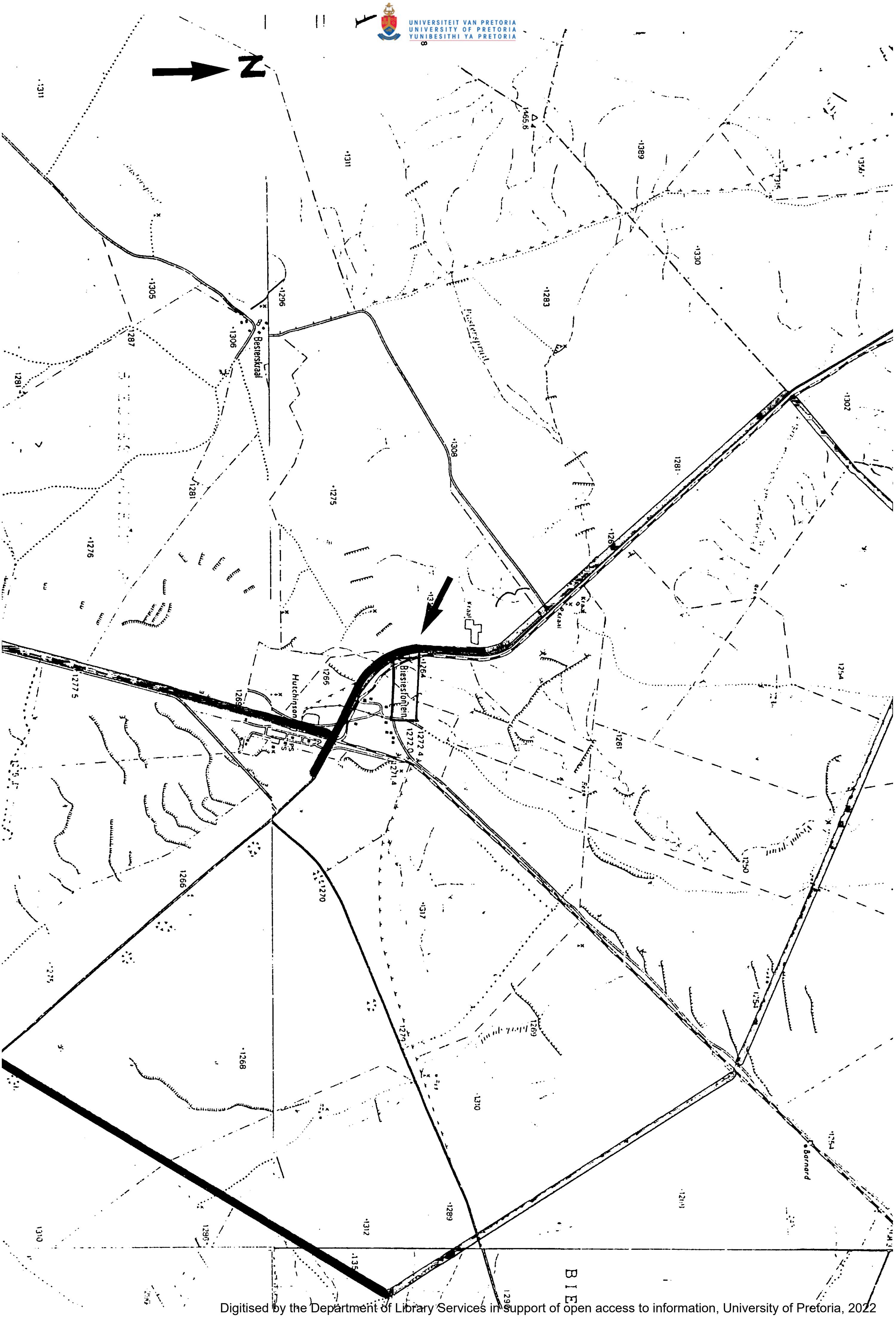
Rainfall

Arid and semi-arid regions have characteristic climates showing extremes in temperature and annual rainfall. In this respect the climate of the Karoo is no exception owing to its unfavourable geographic location relative to the rain-bearing atmospheric circulation of South Africa (Booysen & Rosswell 1983). The mean annual rainfall is 262 mm (Davies 1987) of which approximately 75% falls during the summer months. Rainfall has been well below average (1978 - 1986, South African Weather Bureau) and the drought had considerable impact on the vegetation and geohydrology in the area.

Temperature

The semi-arid climate shows extremes of ambient temperature ranging from -14 °C to 40 °C, with a mean annual temperature varying from 22.5 °C in the north to 15 °C on the Great Escarpment (Schultz 1965). The greatest diel and annual temperature ranges occurs in the Upper Karoo where the incidence of frost is extremely high (*ca* 180 days a year).

The driving variable in arid and semi-arid ecosystems is rainfall, whose timing, abundance and spatial patterns are not only discontinuous but also highly stochastic (Noy-Meir 1973). Consequently the unpredictable variation in soil moisture exerts a profound effect on biological activity and hence ecosystem functioning.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3 METHODS

3.1 GENERAL METHODOLOGY

3.1.1 Preparatory Fieldwork

The initial phase of the study (July 1987 - April 1988) involved establishing the distribution and density of colonies of *Cynictis penicillata*, and their immediate suitability for field observation. The movement patterns and home range size were then investigated for a chosen colony, to establish the foraging requirements and social structure away from the home burrow system. The population density and distribution of the mongooses on the farm was established using various incidental and dedicated census records collected throughout the study period.

Daily recordings of any sightings made of *Cynictis penicillata, suricata suricatta,* and *Galerella pulverulenta* were taken during trips between the house and the study site. Information noted included :

- species
- time of observation
- camp and site of observation
- activity
- direction of movement

3.1.2 Observation Methods

Dawn to dusk observations were made from a vehicle positioned at a predefined site established during the previous day's observations. The vehicle was in position before sunrise, on a daily basis, to prevent disturbance of the animals in the vicinity.

Average observation distance was estimated at being around 15m, and actual observations were made with the aid of binoculars (10x50). In addition, a 40x50 telescope was used for detailed behavioural observations. The mongooses were left as undisturbed as possible to prevent false interactions, and followed as seldom as possible during foraging trips to minimise disturbance. The vehicle was removed only after the mongoose colony had moved into a home burrow system for the night i.e. approximately half hour after sunset. Such daily observations took place during a period of 8 months, which included the initial 5 months of fieldwork and the breeding season.

Subsequent observations (ie, May 1988 - August 1988, after the initial 8-month study period) took place daily from sunrise to 1.5 hrs after the mongooses had left the Home Burrow System (HBS), and again 1.5 hrs before sunset to after the mongooses had returned to the burrow. This proved to be adequate observation time for the purposes of this study: results of data collected during the initial phase of showed that the animals do not return to the HBS during the day - and return only around sunset when they enter the HBS. The animals were not seen out of their burrows during the night.

3.1.3 Equipment

A portable 5 metre high metal-framed observation tower and platform was constructed and was positioned 15 metres from the burrow system studied. The observation platform was enclosed in hessian sheeting, thus forming a hide which concealed the observer from the animals. The advantage of height for observations gave the observer increased field of vision and thus enabled a larger area of the animal territories to be covered without the disturbance caused by a moving vehicle. This prevented disturbing the animals.

Two home burrow system sites (see 3.4) were chosen for observation: the first home burrow system was 15 meters from the observation tower which enabled detailed behaviour studies; whilst a second Home burrow system at 100 meters from the tower enabled observations of general behaviour and interactions. Thus it was possible to gather data from two home burrow systems, with their respective mongoose inhabitants, concurrently.

3.1.4 Study Animals

The *Cynictis penicillata* individuals and home burrow system (HBS) studied were chosen for accessibility, the proximity to a road, and the flatness of the topography which enabled easier observations and allowed me to effectively observe the animals on their foraging routes with little disturbance. Each animal could be individually recognised, using facial and/or ear scars, and was given a name. As the vegetation in the area was short and sparse, the animals were easily observed. Unfortunately fences transecting animals' territories prevented the following of animals in either the vehicle or on foot. This factor proved instrumental in the site-choice as it was necessary to choose a site where most of the territory was within a single camp, and where the entire home range could be easily seen from the observation point despite the presence of fencing. Habituation of the animals to allow data collection on foot was not considered due to the limited period available for fieldwork.

The group observed for the first eight months of the field work comprised one sedentary adult male, one semi-nomadic adult female, and their offspring. The number of offspring produced to maturity was only one, although a total of eight young were born to this pair during the three breeding cycles observed over one breeding season.

The animals occupied a HBS built into the end of a man-made erosion dyke which ran east-west along the northern side of a camp (KooiKamp) (Figure 1). A retaining wall formed the western side of the HBS, whilst the compacted sand and clay of the dyke formed the foundations into which the burrows were dug. Bush provided 40% cover over the surface of the HBS, and rock approximately 10% cover. Thirty seven burrow entrances, most of which inter-connected with one another, gave access to the burrow system, .

3.1.5 Sampling Methods

A combination of continuous focal animal sampling, interval scan sampling and random data collection was used during observations.

Two minute scan sampling was taken of the animals during each observation period and the animals' position on the HBS and behaviour pattern it was performing at the time recorded. Concurrent focal sampling was conducted on the *Cynictis penicillata* individuals at the HBS, where continuous records were taken of the behaviour patterns occurring between each 2 minute time point. Such data were entered onto a data sheet in the sequence with which it occurred.

Behavioural data were recorded on a predesigned data-sheet, on which time, species, individual identity of the subject animal/s, behaviours, and inter- and intra-specific interactions were documented. Any additional information was noted on a second standard data collection sheet consisting of columns for environmental parameters, time parameters, which were recorded with a stopwatch, species, and individual identity. Columns were available for general comments and other data where either predominant behaviour and occurrences were noted. Notable aberrancies in the observations were documented in detail in separate notes.

Social interactions between individuals were recorded on a dictaphone and later transcribed onto similar pre-prepared data sheets. This method of data recording during such complex behaviour patterns enabled detailed observation and gave the observer the necessary time to record the events.

These methods of recording allowed for accurate recording of the animals' spatial distribution, the behaviour pattern complexes they performed and their sequences, the social actions they initiated and received and also the frequency and duration of the behaviour pattern, or behaviour pattern sequences.

Observation periods of about one month of uninterrupted study, with breaks of *ca* one week in between for data consolidation, were conducted throughout. There was, however, a period of continuous fieldwork during the breeding season (September 1987 - December 1987) which lasted for 3.5 months. Other periods of intensive observations took place during "male recruitment" and field experiments (March 1988 - July 1987).

3.2 POPULATION ESTIMATES - DENSITY AND DISTRIBUTION

Previous population density estimates of *Cynictis penicillata* have not been published although Earle (1984) and Smithers (1983) recorded average group size per colony of the populations of *Cynictis penicillata* in the Southern Transvaal (Vaal Dam Area) ($X = 8$, $n = 5$) and Botswana ($X = 10$, $n = 10$) respectively.

Borders of home ranges were drawn from census data: recognised individuals and repeated sightings of animals in areas over an extensive census period showed that certain individuals were found in the same area repeatedly. A home range refers to the area in which the animal was seen. The extent of the home range is an estimate only. This permitted the allocation of estimated boundaries. The size of the home range is only an estimated calculation of the area.

Home ranges were then constructed to enclose the area in which individual animals were sighted regularly and at different times. The home ranges indicated in this figure are for male *Cynictis*, although they are estimates only.

Due to the error factors inherent in the sampling methods used, where the same animal or group of animals may been seen twice during one census period, the population figures are approximations only. In addition, estimated home range or territory size are subject to error due to the small study area. Those home ranges overlapping with land outside the farm Biesjiesfontein did not form part of the study.

Methods routinely used in population estimates e.g. mark- recapture, are not readily applicable to mongoose species due to difficulties of trapping, and the fairly elusive behaviour of the species. However, the following census techniques were used :

(a) censusing, during which I drove around the farm on a specific route at specific times of the day. All sightings of carnivore species, their site, activity and the direction in which they were moving were noted.

(b) incidental sightings were also recorded, noting the same information recorded above.

Information collected was plotted on a map of the farm, and the population numbers calculated from sighting occurrences in the different areas, noting the fact that on average two individuals occupied a single home range. The time of the observation was important in order to (a) prevent duplicate recordings of a single animal on the same day, and (b) to assist in the recognition of the individuals in an area on different days (it was later determined that the mongooses followed similar routes when marking their home ranges and when foraging).

This method of population estimation proved to be adequate for the purpose of this study. The census continued throughout the year, and the data were accumulated for many areas of the farm.

From these data, population densities, population distributions and home range utilization were monitored :

$$\text{population density} = \frac{\text{No. in population}}{\text{area surveyed}}$$

home range utilization = time spent in different areas of the territory

3.3 ACTIVITY PATTERNS

Differences in the basic behaviours of animals were observed during different environmental conditions. The objective of this section is to establish whether there is a relationship between specific environmental factors and certain behaviour patterns in *Cynictis penicillata.* This will highlight the ecological parameters which may influence the social behaviour of these animals.

The times of sun rise and set, and temperature, rainfall and wind conditions were recorded and the corresponding behaviour patterns, such as emergence from the burrow, foraging activity and sunbathing, were noted.

3.4 HOME BURROW SYSTEMS AND MIDDEN STUDY

The home burrow system (HBS) may be defined as the area within a home range where the mongooses have a number of burrow systems in which they sleep, breed, and which forms the focal point from which other daily activities begin. The HBS provides the mongooses with the following major functions (Rasa 1977; Simpson 1964; Smithers 1983):

- Protection from predators (raptors in particular): shelter for raising young, resident burrow i.e. the shelter where the animals sleep every night;

- Shelters from weather (rain, cold, heat and wind).

- A base from which a territory is defended: the daily marking behaviour of the mongoose begins at the HBS. Intruders are challenged from the HBS when entering the territory.

Extensive surveys were made of 75% (ie, *ca* 10 000 ha) of the farm to map the distribution and numbers of HBS's.

The entire study area was surveyed on foot and the home burrow systems located. The HBS were plotted on a 1: 10 000 map of the farm (Figure 1).

The approximate density and distributions are calculated for two different conditions:

(i) the entire area, which was not comprehensively surveyed due to logistic problems;

(ii) the camps/home ranges which could be comprehensively surveyed. The latter is a more accurate calculation as all HBS's could be located and mapped.

Fourteen study sites were randomly selected and each was mapped. Each site was measured and divided into one square meter grids which enabled the following data to be accurately plotted on each map:

- site dimensions
- the number and location of middens,
- the prevalence of bush and rock cover,
- the height of the home burrow system above the surrounding ground,
- the aspect of the mound.

In addition it was noted whether the home burrow system was built in:

- a made-made/artificial mound or
- a natural or self-constructed site.

The data were then transcribed onto data sheets and entered onto Lotus 123 on a computer for analysis. These factors were considered relevant to choice of site for the location of the home burrow systems, and for the siting of middens.

Once the mapping was completed, each midden was inspected. The number of faeces found at each midden was recorded, and each was designated a status according to the number of faeces found (where most faeces were found = primary defecation site etc...).

At seven of the home burrow systems, plastic markers were used to record the site of the middens following which all faeces were removed from the area. The site was then left for a period of 14 days after which I returned to the HBS to record any new middens. Again the sites were mapped and the primary middens noted according to the number of faeces present. Number of faeces was recorded.

In a further phase of this experimental work, 4 HBSs were chosen at which the middens were relocated and an inch of sand was carefully laid over the original site in an attempt to erase any both visual and olfactory evidence of the previous midden. Both the new and original midden sites were marked with different coloured plastic tags. The site was left for 10 days, after which I returned to re-map the HBS, to count the faeces, and to designate status to the middens.

The data were then transcribed onto data sheets and entered onto Lotus 123 on a computer for analysis.

3.5 DIET

Cynictis penicillata is primarily a solitary forager, occasionally being accompanied for short periods by the mate throughout the year; and, in the case of the male, by the subadults during the post-weaning period prior to their dispersal from the natal territory. The solitary foraging seems to be dictated, in part, by the availability of food resources. When food is abundant a higher percentage of time is spent accompanied by the mate on foraging expeditions, whereas in times of poor food availability they forage alone. In addition to the season availability of food, social structure whilst foraging is dependent on the richness of the habitat or territory.

Faeces were collected at various home burrow systems, and were categorized into two ages groups according to the appearance of the faeces: (a) new (b) old. The criteria for this was the colour and moisture content of the faeces e.g. dry and white = old. Note was made of the site at which the faeces were found and the species to which it belonged. Because *S. Suricatta*, *Cynictis penicillata* and *Galerella* share HBS at various times, the division into species was made difficult.

The faeces were dried in an oven (conventional) at 80 °C and broken up in order to identify the constituents. Contents of the faeces was divided into: a vegetation component, arthropod component, mammal component, and "others".

The principal method of faecal analysis used was frequency analysis (Arden-Clarke 1983) :

(a) Percentage frequency - the number of faeces in which a prey species is identified - given as a percentage of the total number of faeces in that sample (van der Zee 1981).

(b) Relative frequency - the number of records of a prey species in a sample of faeces given as a percentage of the total number of records of all categories of prey in the sample (van der Zee 1981).

Conversion indices were used to estimate the live-weight of the prey species found in the faeces, and these were then analyzed comparatively with similar work done by other authors (Earle 1981).

In addition to the faecal analyses, the gut contents of four animals were examined, and the composition determined. These gut samples were taken from animals found dead within the study area. The date of death was recorded so that the gut contents could be related to season and availability of various food resources.

3.6 VIGILANCE

The vigilance behaviour of *Cynictis penicillata* was studied for four different kinds, or occurrences, of social structures. The study was conducted in order to establish whether or not there is a significant difference in the vigilance behaviour of the dominant adult male of a territory when he is solitary as opposed to being in the company of other individuals.

The data collected were from natural situations occurring during the routine observations at a single burrow system. This enabled continuity of results by observing a single male individual throughout the duration of the study. The following examples of social structure were observed:

(a) alone at the HBS
(b) with the adult female at the HBS
(c) with the adult female and a subordinate, and
(d) when present with a group of *Suricata suricatta* (and the female)

Continuous focal animal sampling was performed on the individuals present at the HBS. Data collection included the position and posture of the animal, and the frequency and duration of vigilance behaviour. Thus by continuously mapping the position of each individual it was possible to measure distance from cover, distance from vantage points, and inter-individual distances. In addition to data related to the vigilant individuals, continuous recording of the behaviour of others was noted. This enabled comparison of behavioural activity under different conditions.

As far as possible, an attempt was made to record the source or motivation of any vigilant behaviour so that the occurrence of the behaviour could be correlated to the presence of certain external factors eg. the presence of raptors, sounds, interspecific warning mechanisms such as vocalisations and mobbing.

3.7 MALE RECRUITMENT

In order to investigate the occurrence of male recruitment by females in *Cynictis penicillata*, it would be necessary to manipulate the population in an area by removing a male individual for a period of time.

Standard carnivore traps (100cm x 30cm x 30cm) were used, having been proved effective by Taylor (pers. comm.). The traps had single doors and treadle-activated door-release mechanisms. Three traps were baited with chicken eggs, placed under bushes and covered with Karoo brush to camouflage them. These were then placed within a radius of 50 m of the home burrow system frequented by the male. The traps were set after sunset and checked by 09h00 the next morning. This ensured that the animals had sufficient time to leave the HBS and begin foraging, during which time they were likely to find the baited trap.

The territory from which the male was to be removed was chosen on the basis of various criteria which enabled unobstructed observation of the HBS and territory, and was also occupied by an adult female. In preparation for the removal of the male, the selected home burrow system was observed for a period of 10 days during which time a set of "control" behavioural data were collected.

On the 11th day, the traps were set. On the third night, the male took the bait and was caught, after which the traps were removed from the area. The male was removed from the area for a period of 10 days during which time it was placed in a (2 m x 2 m) housing cage in Victoria West. The female was not captured.

The selected home burrow system was again closely observed and the behaviour patterns and social structure of the resident female recorded. Intraspecific interactions were particularly important during this phase of the observations.

After the second 10 day period was over, the original male from the territory was removed from the housing cage/enclosure and was released back into the territory. The behaviour of the male was observed closely, as were the behaviours of the other individuals in the territory. It was noted that the original male was only present in the territory for a short period of time (1.5 hrs) after which he left the area and was not seen again.

CHAPTER 4

RESULTS

4 POPULATION DENSITY AND DISTRIBUTION

4.1 DISTRIBUTION AND DENSITY OF *CYNICTIS PENICILLATA, G.PULVERULENTA AND S. SURICATTA*

The density figures presented below were calculated from daily census information taken over the entire fieldwork duration. Although field data were taken daily in the same areas, and areas studied were of relatively uniform habitat and topography, it is possible that ecological restraints, such as vegetation and geological factors, may have limited *Cynictis penicillata* distribution, and hence density. Therefore, the RELATIVE and not the ACTUAL densities are given.

4.1.1 *Cynictis*

Fifty one individual *Cynictis penicillata* were sited over a period of twelve months in a total area of 12 625 hectares.

$$\text{Population density} = \frac{\text{Area of farm}}{\text{No. in population}}$$

$$= \frac{12\ 625}{51}$$

$$= 247.5$$

i.e. An average of 1 *Cynictis penicillata* per 247.5 ha, or a relative density of 0.004 animals ha^{-1}.

The number of individuals occupying each home range is fairly constant ($\bar{x}$ = 1.8 individuals; s.d. = 0.2; n = 16,)

The home ranges vary in size ($\bar{x}$ = 250 hectares - *ca* 500 hectares, n = 16). However, there is no correlation between the number of sightings, number of individuals and territory size.

Sixteen home ranges were defined for *Cynictis penicillata* in a total area of 10 000 hectares.

4.1.2 *Suricata suricatta*

Results for *S. suricatta* indicate a total of 110 individuals recorded present in a total area of 12 625 ha. Thus, an average of 1 *S. suricatta* present per 114.7 hectares, or a density of 0.008 animals ha^{-1}.

Home ranges were constructed to incorporate the home ranges of *S. suricatta* groups. The comparative difference between home range sizes of *Cynictis penicillata* and *S. suricatta* can be noted. Based on the number of individual animals observed, seven home ranges were estimated for *S. suricatta* in a total area of 10 000 hectares. The average size of the home ranges = 1 500 ha, s.d. = 200 ha, n = 7.

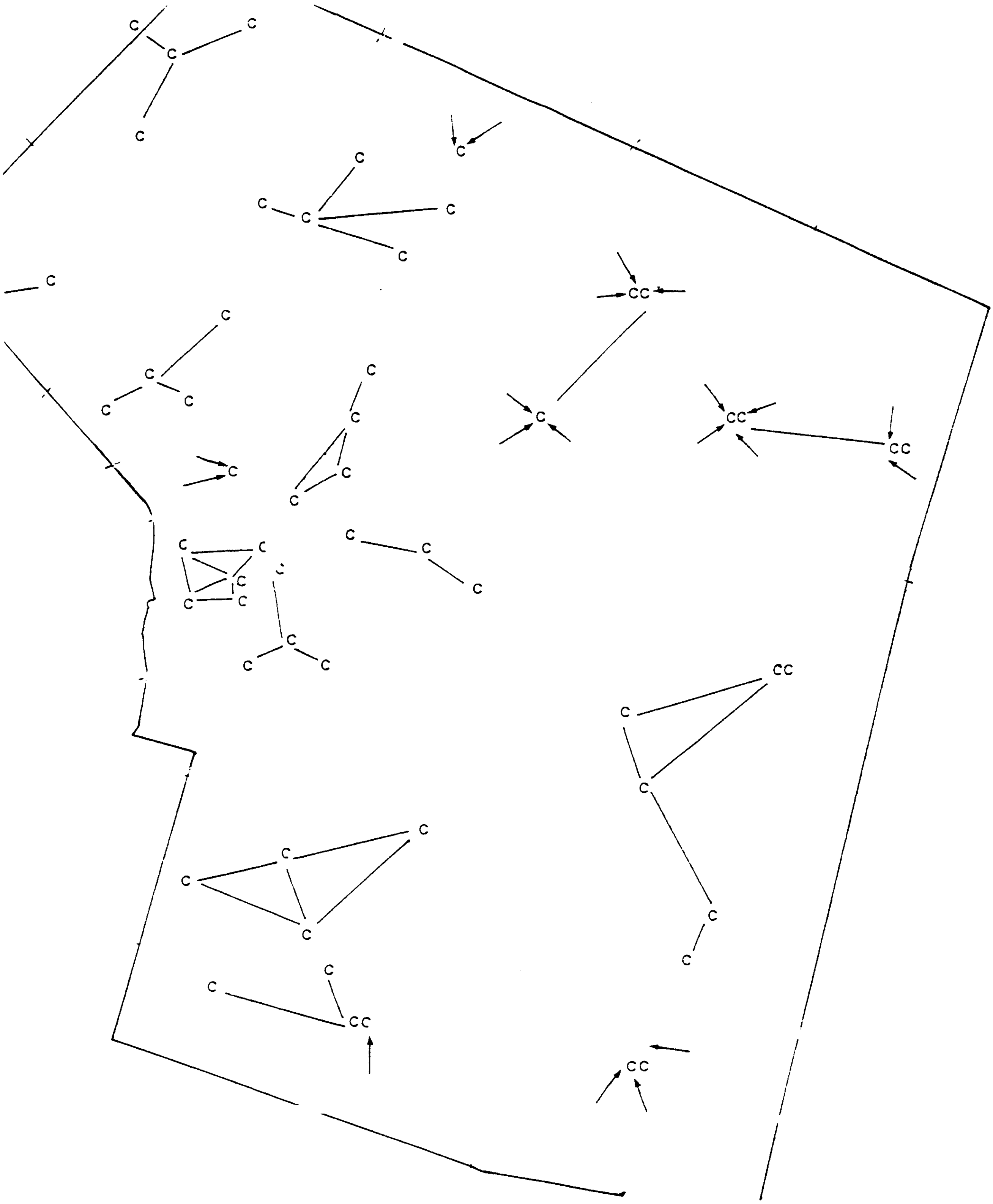
4.1.3 *Galerella pulverulenta*

Six individual *Galerella pulverulenta* were sighted during the study period in a total area of 12 625 ha. Thus, an average of 1 *Galerella pulverulenta* is present per 2104.2 ha, or they are present at a density of 0.00047 animals ha^{-1}.

Home ranges were large and the population density small. The comparative difference in home range sizes between the three different species can be noted in the figures below.

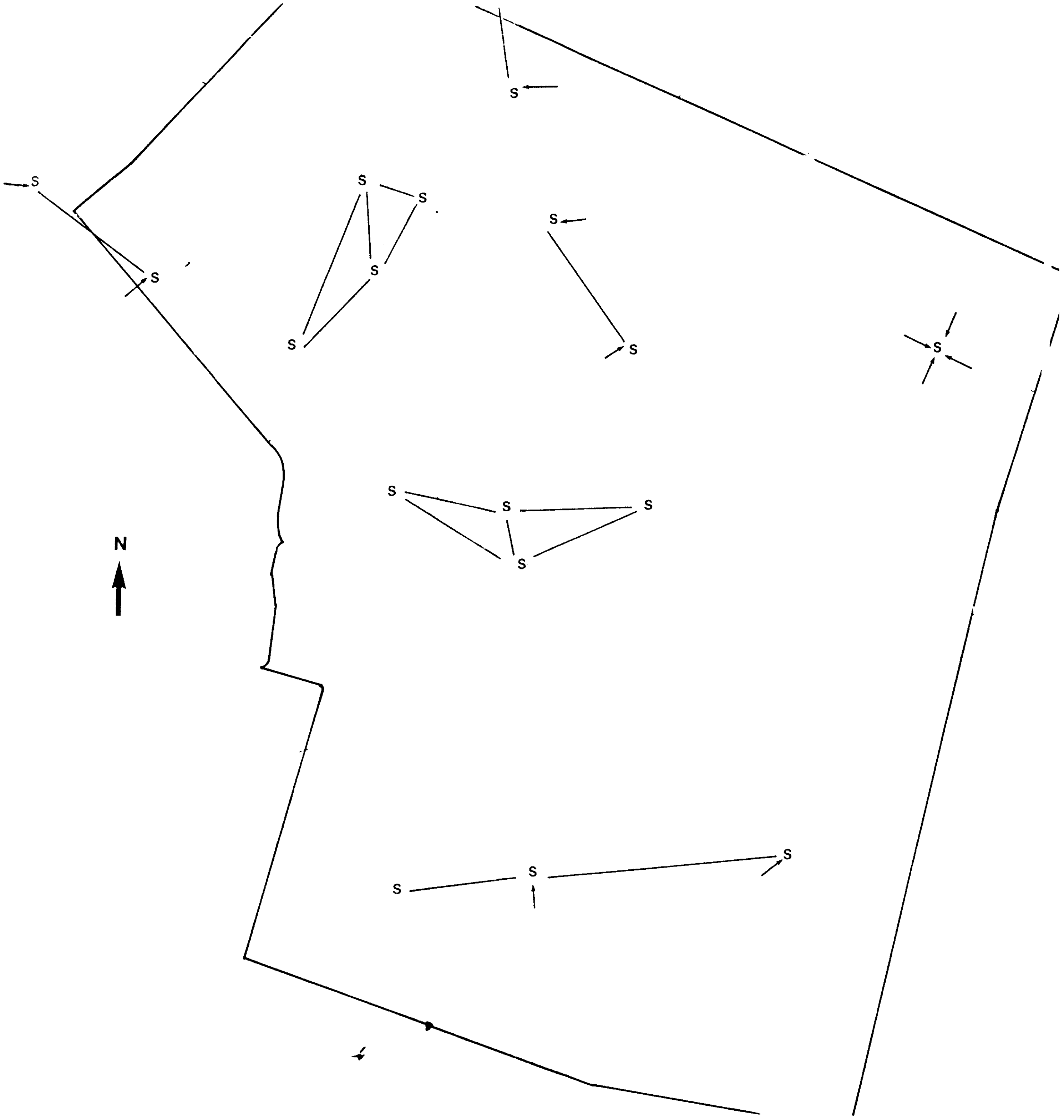
Three *Galerella pulverulenta* were seen in a total area of 10 000 hectares. The mean territory size could not be estimated, although it should be larger than that of *Cynictis penicillata,* and smaller than that of *Suricata suricatta*. These figures are estimates only, as it is possible that individual animals were not recorded due to the elusive nature of the species.

Figure 4.1 Map of the farm Biesjesfontein showing distribution of *Cynictis penicillata*. Points "C" designate repeated sightings of *Cynictis penicillata* at various times during the day : recorded from dedicated censuses and incidental sightings. Arrows indicate direction of movement of the individual sighted.



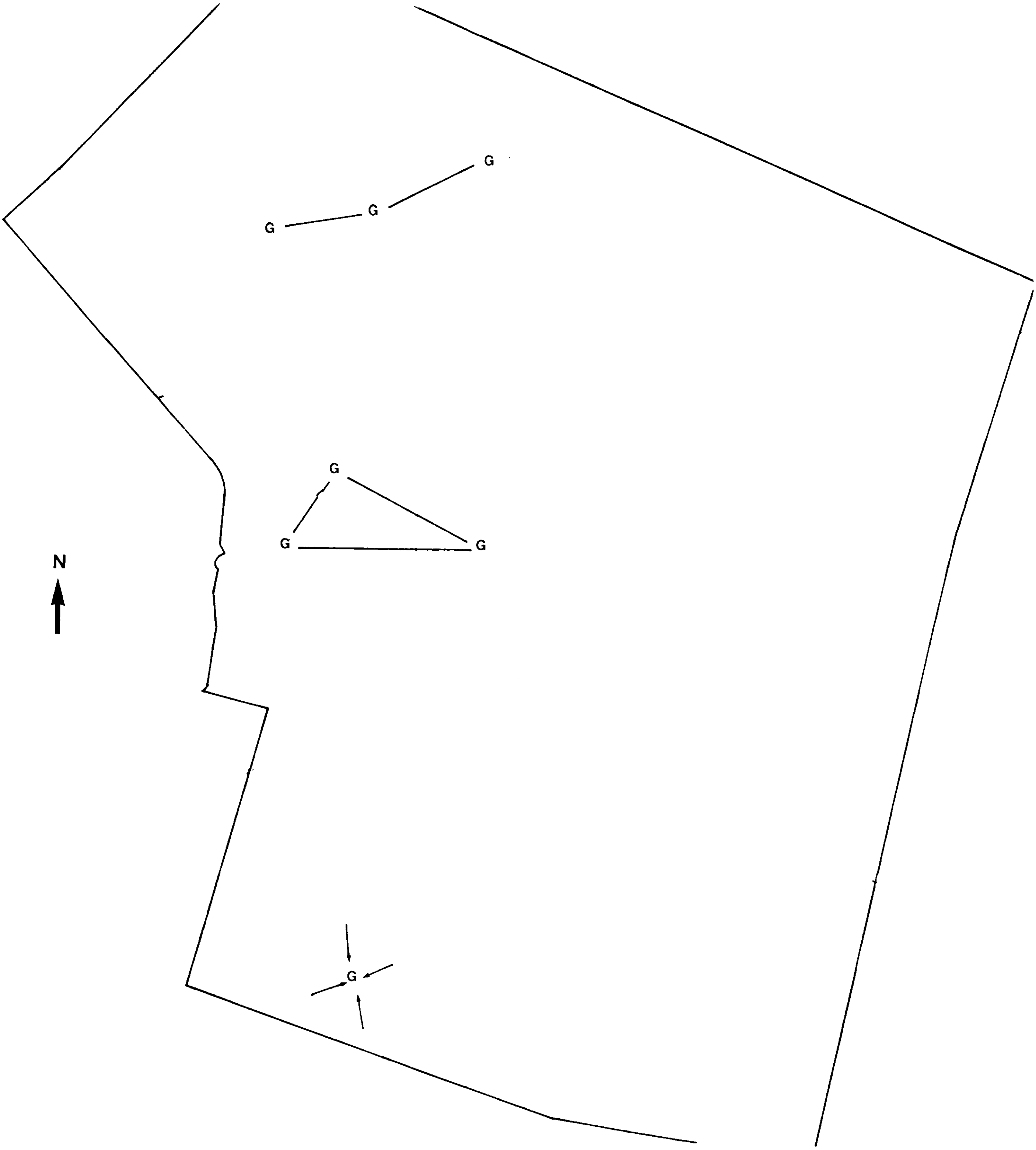
P Howard 1993

Figure 4.2 Map of the farm Biesjesfontein showing the distribution of *S. suricatta*. Points "S" indicate repeated sightings of *S. suricatta* recorded during dedicated censuses and recorded incidental sightings. Arrows indicate the direction in which the individual sighted was moving



P Howard 1993

Figure 4.3 Map of the farm Biesjiesfontein showing the distribution of *Galerella pulverulenta*. Points "G" indicate repeated sightings of *Galerella pulverulenta* recorded during dedicated censuses and recorded incidental sightings. Arrows indicate the direction in which the individual sighted was moving



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4.2 HOME BURROW SYSTEMS AND MIDDENS

4.2.1 Home Burrow Systems

Results show that an individual *Cynictis penicillata* uses more than one HBS in its territory. The spacing and distribution of the burrow systems are important for the success of the group in providing easily accessible cover from predators at regular intervals. The mean distance between burrow systems is 530 +- 41 meters. Thus the maximum distance *Cynictis penicillata* must travel to avoid predators is 265 meters (see table (4.1)).

Table 4.1 Number of Home Burrow Systems found in the study area and number per territory, as recorded on surveys of the study area. "Complete" home ranges include all those home ranges falling within the boundaries of the study area, while "incomplete" denotes those home ranges found to overlap into areas outside the study area.

No. of HBS	No. of home ranges	HBS/Territory
86	15 (incomplete)	5,73 (incomplete)
64	8 (complete)	8 (complete)

Of the 130 HBS's identified on the Farm Biesjiesfontein, 93 were found to have more than 1 midden at the site, whilst the remaining sites had 1 or no middens. These sites were deemed unoccupied and categorised as burrows used for cover from predators.

Figure 4.5 Map of a typical home burrow system (selected at random from the study area). Bushes and rocks (cover/shelter) are shown in relation to burrow entrances and midden (m) sites. The diversity of burrow systems is noted, with particular reference to the number of burrow entrances, the number of bushes and the total area utilized. The number of each map correlates with the data in tables (4.3 and 4.5).

Table 4.2 Nearest neighbour distance between the HBS's, recorded on dedicated surveys.

Mean Distance	Standard Deviation	n	Range	Distance to nearest HBS
530 m	± 41 m	96	20 - 2 000	265 m

Table 4.3 Characteristic site parameters of Home Burrow Systems measured (n = 14). L = length, B = breadth, A2 = area, H = height (above ground) of the HBS"s - all in meters.

No.	No. of Middens	L	B	A^2 LxB	V^3 AxH	H	No of Burrows	aspect	No.of Rocks	No.of Bushes
1	2	17	3	51	2	102	24	E	26	0
2	3	12	3	36	1,5	54	20	E	7	1
3	10	17	2,5	42,4	0,3	14,2	22	E	37	0
4	6	20	3	60	0,4	24	16	E	34	34
5	7	12	10	120	1,2	144	16	NE	19	11
6	5	14	10	140	1,2	168	19	ENE	19	0
7	4	17	3	51	0,5	25,5	14	E	11	1
8	5	16	10	160	0,2	32	20	NE	16	1
9	3	12	10	120	1	120	20	W	8	0
10	2	10	4	40	0,1	4	10	NNE	14	10
11	3	15	4,5	67,5	0,5	32	25	E	27	16
12	14	18	10	180	0,5	90	25	SE	20	8
13	6	25	3	75	1	75	43	S	36	3
14	7	15	12	180	1	180	37	NE	37	7

The size of the HBSs vary within a territory. The numbers of burrow entrances at a HBS ranges from 3 - 45,(n = 38, x = 24 +- 8 (see Table (4.3)), and the area 36 m2 - 180 m2 (n = 38, x = 94.8 +- 53.2 (see Table (4.3)). The HBS may only be occupied temporarily during the day, or regularly during the night (or both). The average height of the burrow entrances is 0.8m above ground level. No burrow entrances were found at ground level. The general aspect of the entire HBS is given (as opposed to the aspect of individual burrow entrances).

Table 4.4 Statistical data for characteristic site parameters. X = mean value, s = standard deviation.

Parameter	X	s
No. of middens	5,40	3,24
length (m)	15,70	3,71
breadth (m)	6,28	3,56
area (m^2)	95,21	52,14
No. of burrows	22,78	8,23

The above statistical data summarizes Table (4.4). Of interest at HBS's, is the predominance of easterly facing burrows (93 %) and the relationship between the area of the HBS and the number of burrows present ($r = 0.69$, $p = 0.90$). The number of burrows also correlated positively ($r = 0.67$, $p = 0.90$) with amount of cover available (rocks + bushes). This suggests that there is higher utilization of a burrow system when there is more available cover.

A representative sample of 14 HBS's is given in Table 4.5. The preferred substrate chosen for an HBS is sand (66.6 %, n = 48), whilst 22.6 % are found on rocky outcrops and 10.4 % in gravel. Of the 48 burrow systems studied in detail, 63.2 % were found on man- made or man-modified topography such as erosion dykes, dam walls and soil dumps near dams. These sites provide elevation and a soft substrate in which to excavate burrows. In addition, the erosion dykes are often spaced regularly over the terrain, thus providing an excellent distribution aid in the siting of the HBSs (see table (4.5)).

Table 4.5 Features of Home Burrow Systems which may influence site choice. Where Sur = *S. suricatta*, Cyn = *C. penicillata*, Gal = *Galerella pulverulenta*, y = yes, man = man-made substrate, natural = natural substrate. Shapes described as long (= length > 3 times width), oval, rectangle (length < 3 times width), bean (kidney). The structures in which the HBS are found were man-made dykes (water diversion), man-made dumps made of rubble and soil, and other natural topographical features.

No	Man/Natural	Occupied	Species	Substrate	Shape	Structure
1	man	Y	*Sur/Cyn*	sand	long	dyke
2	man	Y	*Cynictis*	sand	long	dyke
3	man	Y	*Cynictis*	gravel	long	dyke
4	natural	Y	*Cyn/Gal*	rock/sand	rectangle	natural
5	man	Y	*Cynictis*	sand	oval	dump
6	man	Y	*Gal*	sand	long	dyke
7	man	Y	*Sur/Cyn*	gravel	long	dyke
8	natural	Y	*Cynictis*	sand	oval	natural
9	natural	Y	*Sur/Cyn*	sand	oval	natural
10	natural	Y	*Cynictis*	sand	bean	natural
11	natural	Y	*Cynictis*	sand	rectangle	natural
12	natural	Y	*Cynictis*	gravel	rectangle	natural
13	man	Y	*Cynictis*	sand	long	dyke
14	man	Y	*Cynictis*	sand	long	dyke
TOTAL	8 man 6 natural	14 yes	13 *Cynictis* 1 *Gal* 4 *Sur*	8 sand 3 gravel 3 rock	7 long 3 oval 3 rect. 1 bean	7 dyke 1 dump 6 natural

4.2.2 Middens

Home burrows are also sites of extensive faecal deposits and marking by individuals residing, or visiting, them. Table (4.6) shows results taken from a survey of 14 HBS's to investigate the placement of faecal deposits or middens at different sites. A mean of 189.9 +-96.2 faeces were found at each HBS. An average of 40.9 faeces were found per midden, with X = 5.42 +- 3.24 middens were present at each site.

Table 4.6 Middens and faeces found at each of the 14 HBS in the study.

No	No. of Middens	Total No. of faeces	Ave No. of Faeces
1	2	250	125
2	3	170	57
3	10	231	23,1
4	6	132	22
5	7	95	13,4
6	5	130	26
7	3	90	30
8	5	228	45,3
9	3	220	73,3
10	2	35	17,5
11	3	95	32,5
12	14	546	42
13	6	137	22,8
14	7	330	48,8
Mean	5,42	189,9	40,9
Total	76	2689	572,7

Table 4.8 Matrix grid of the home burrow system (no. 1). Each grid represents a one metre square area in which Marking posts were situated. 1, 2, 3, 4 & 5 indicate number of marking posts in each square meter.

No.	A	B	C	D	E	F	G	H	I	J	K	L	M
1	/	/	/	/	/	/	/	/	/	/	/	/	/
2	/	/	/	/	/	/	/	/	/	/	/	/	/
3	1	/	/	/	1	/	/	/	/	/	/	/	/
4	2	/	/	/	1	/	1	/	/	/	/	/	/
5	/	1	/	/	/	/	/	/	/	/	/	/	/
6	2	1	/	1	/	/	/	/	/	/	/	/	/
7	/	1	/	/	/	1	/	/	/	/	/	/	/
8	/	/	1	2	/	/	/	/	/	/	/	/	/
9	1	/	1	3	1	/	2	/	1	/	/	/	/
10	/	2	1	5	3	1	/	1	1	/	1	/	/
11	/	/	1	/	/	/	1	/	/	/	/	/	/
12	/	/	1	/	/	/	3	/	/	2	1	2	1
13	/	/	1	/	/	/	1	2	/	2	3	/	4
14	/	/	/	/	/	/	/	/	/	/	2	3	/
15	/	/	/	/	/	/	/	/	1	/	/	2	/

Statistics

Burrow = 11 (12.7 %)
bush = 48 (55.8 %)
rock = 13 (15.1 %)
sand = 14 (16.3 %)

Total = 86 (100 %)

Cynictis penicillata utilised four substrates for marking purposes at the home burrow system: bushes, burrow entrances, rocks and sandy mounds. Bushes comprise the primary substrate (55,8 %), while sand, rock and burrow entrances comprise 16,3 %, 15,1 % and 12,7 % respectively.

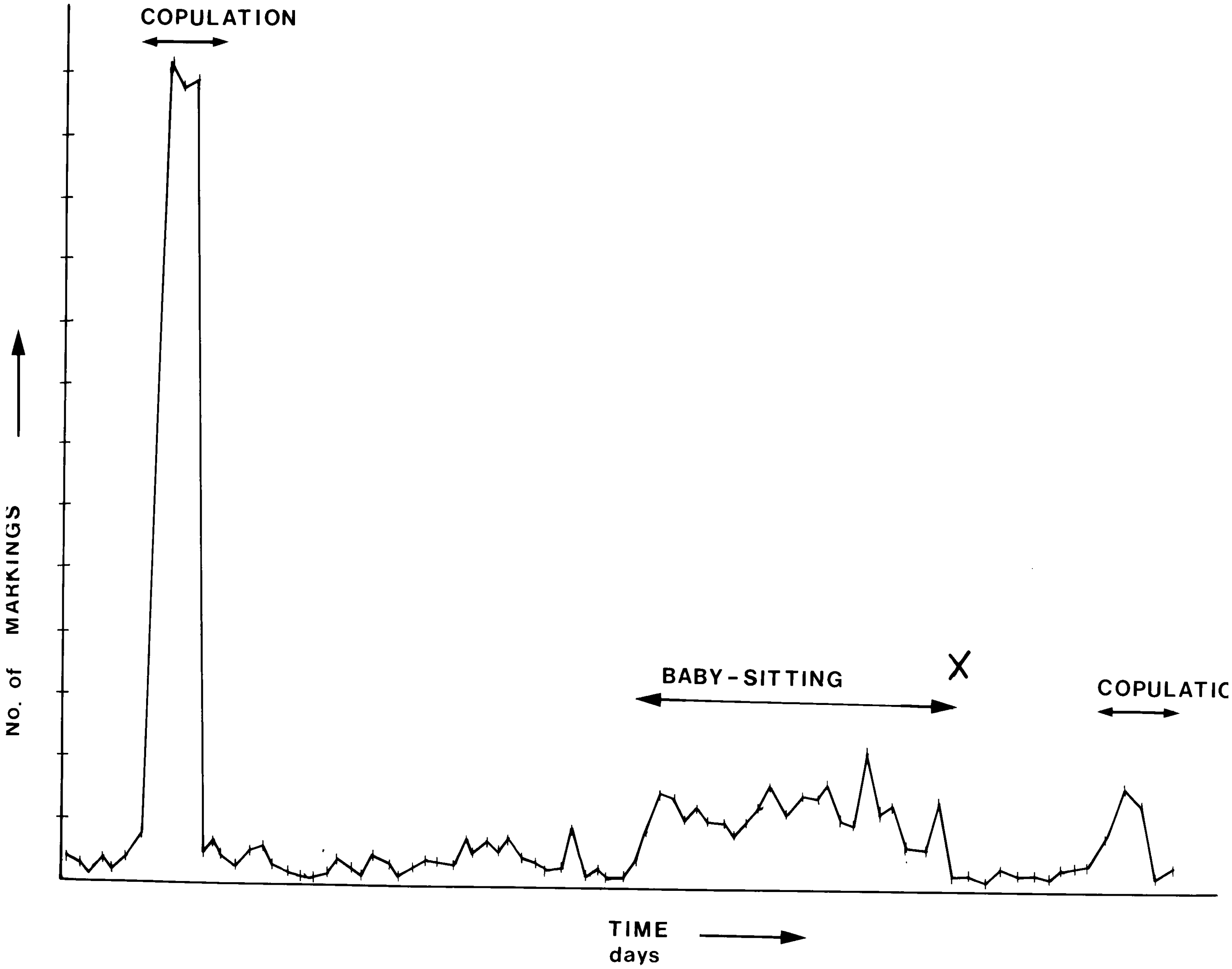
1. Marking Behaviour and Pheromones

Cynictis penicillata exhibits a variety of marking behaviours. During a 40 day observation period, *Cynictus penicillata* spent 5.05 % of its time marking, and marked on 37 out of 40 of the days (see Appendix B for detailed description of the marking behaviour). Bushes were marked most frequently, accounting for 67% of marking posts around the HBS (both cheek and anal marking) (see Figure 4.9) while earth and rocks were marked 11 % and 22 % respectively. The following data on amrking

Figure 4.6 Map of the Home Burrow System and immediate home range of the *Cynictis penicillata* group observed over an eight (8) month period. Daily marking posts in the area are shown : "v" denotes marking performed during the non-breeding period, whilst "o" denotes marking posts utilized during the breeding season. The latter were distributed over a far greater area and were utilized extensively at the time.

Figure 4.7 The number of markings performed by the resident dominant male *Cynictis penicillata* over the breeding season. Data shows marking behaviour 4 days prior to the onset of oestrus and copulation and continues until 2 days after a second breeding cycle began. Each point (/) represents one day.

"X" designates the death of the litter of offspring produced during the first cycle.



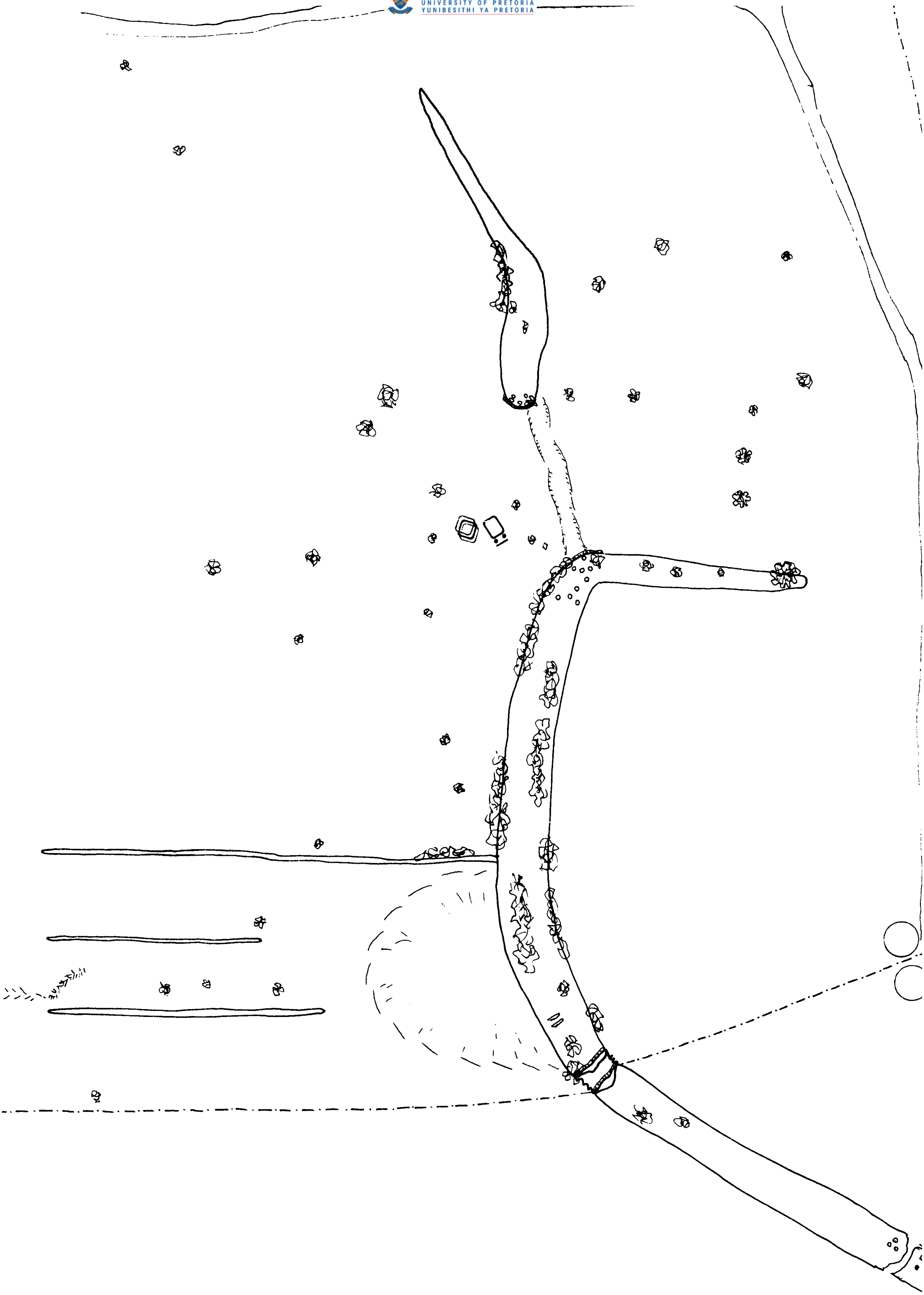
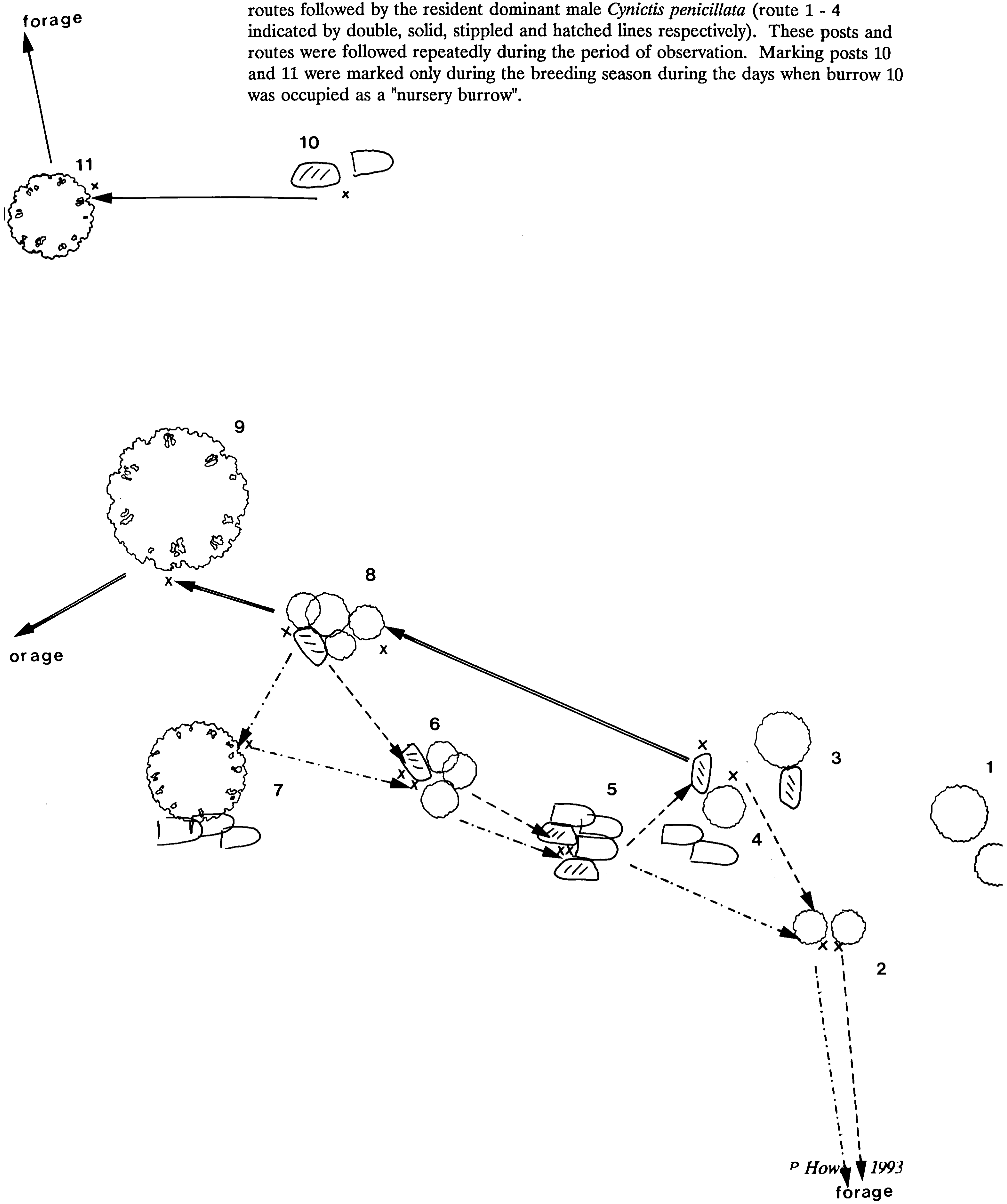


Figure 4.9 Map of the Home Burrow System showing eleven marking posts and four marking routes followed by the resident dominant male *Cynictis penicillata* (route 1 - 4 indicated by double, solid, stippled and hatched lines respectively). These posts and routes were followed repeatedly during the period of observation. Marking posts 10 and 11 were marked only during the breeding season during the days when burrow 10 was occupied as a "nursery burrow".



4.3 ENVIRONMENTAL FACTORS INFLUENCING *CYNICTIS PENICILLATA* ACTIVITY PATTERNS

Figures (4.10) to (4.17) and Table (4.8) give result of environmental data collected during the study period.

Figure 4.10 Daily times of sunrise (hrs) measured as the time the sun was fully over the eastern horizon, and sun's rays reached the burrow entrances.

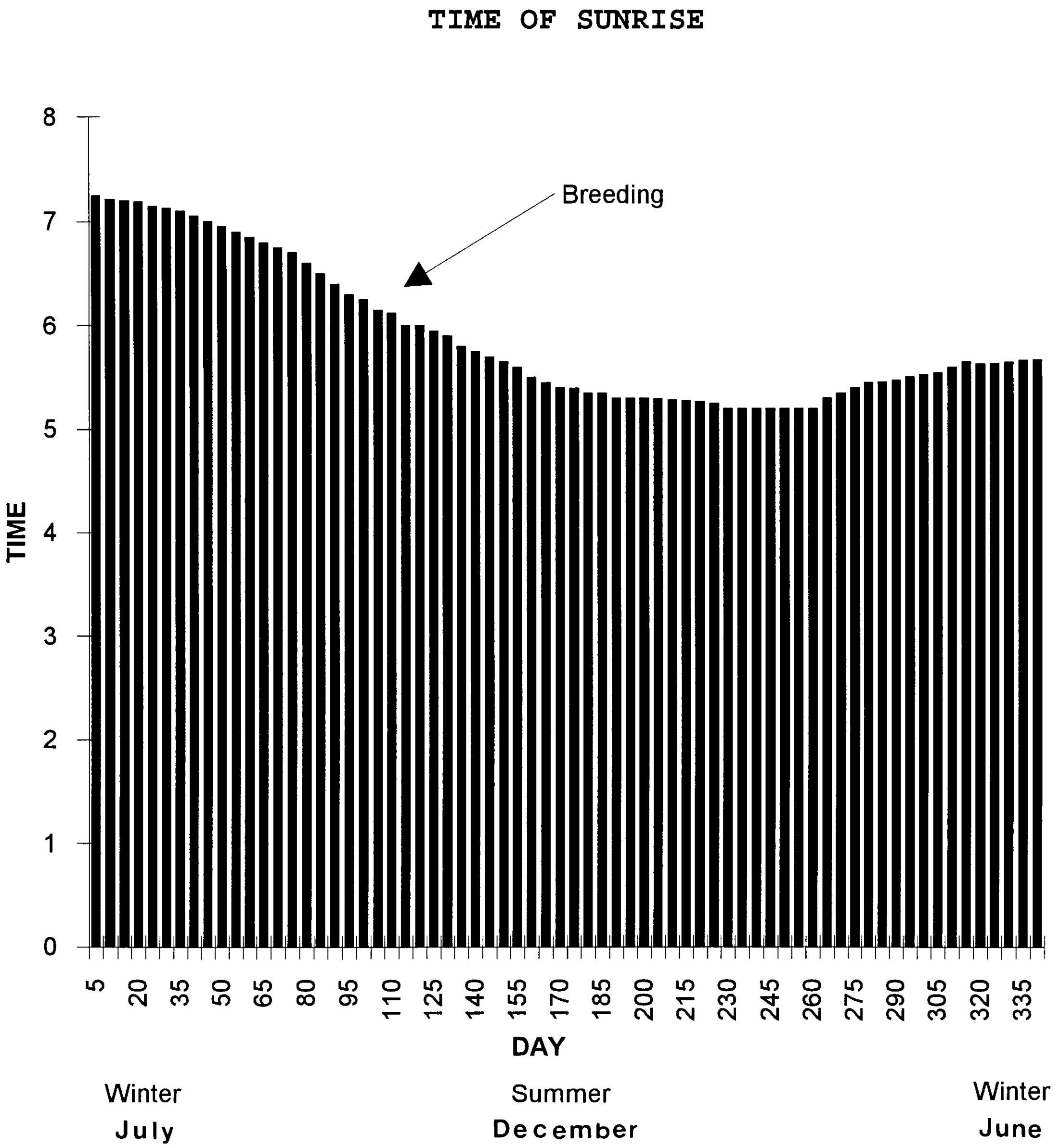


Figure 4.11 Mean time in hours (hrs) at which *Cynictis penicillata* emerged from the burrow in the mornings.

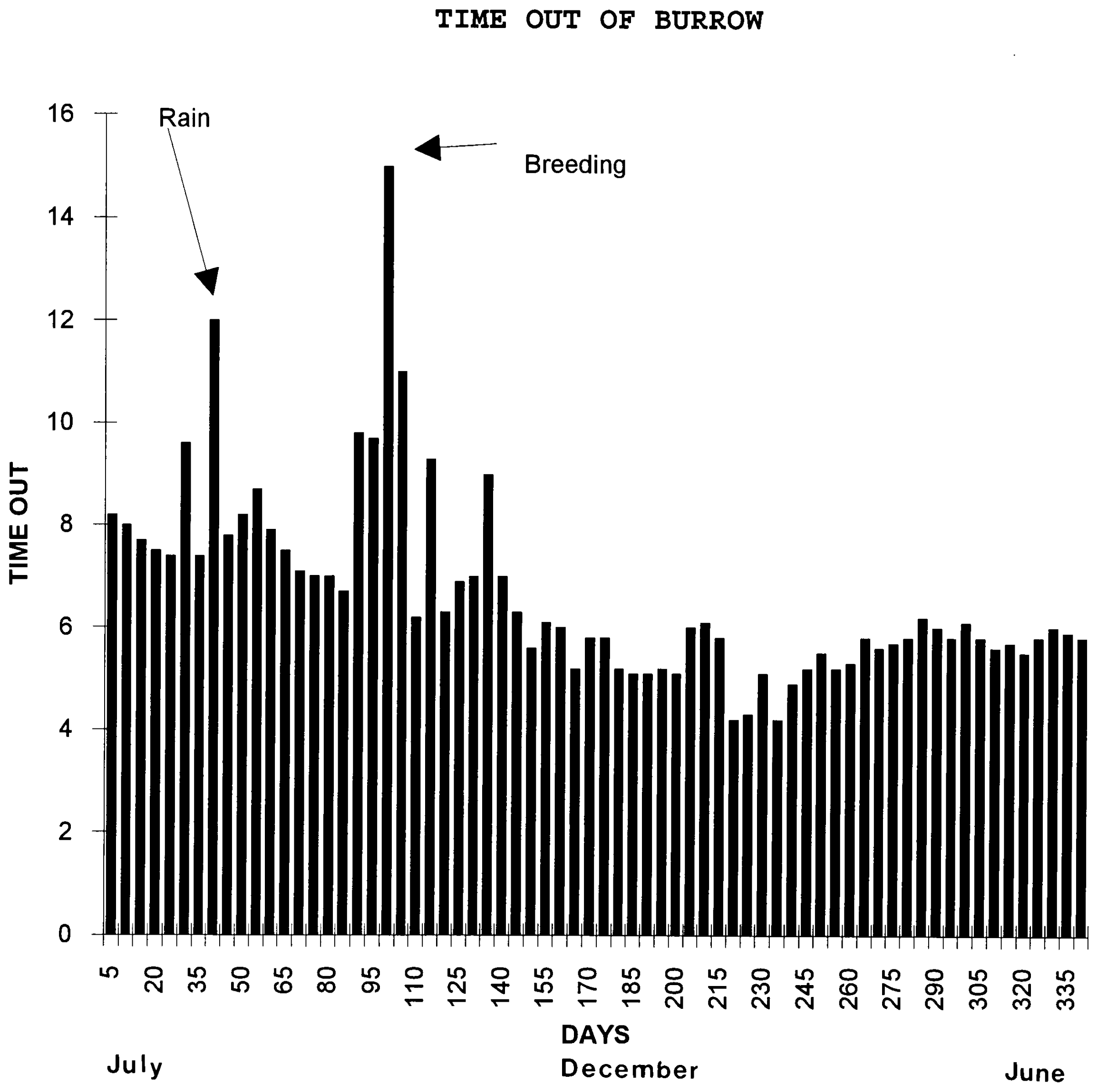


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Figure 4.12 Time in minutes spent by adult *Cynictis penicillata* at the home burrow system (predominantly overnight). Peaks in the graph occur (x, y and z) when the adults remained for longest periods. X and y mark the time spent babysitting offspring during the summer months. Y marks the winter months during which *Cynictis penicillata* remained at the burrow sunning and grooming for longer periods before foraging (see "Breeding" later).

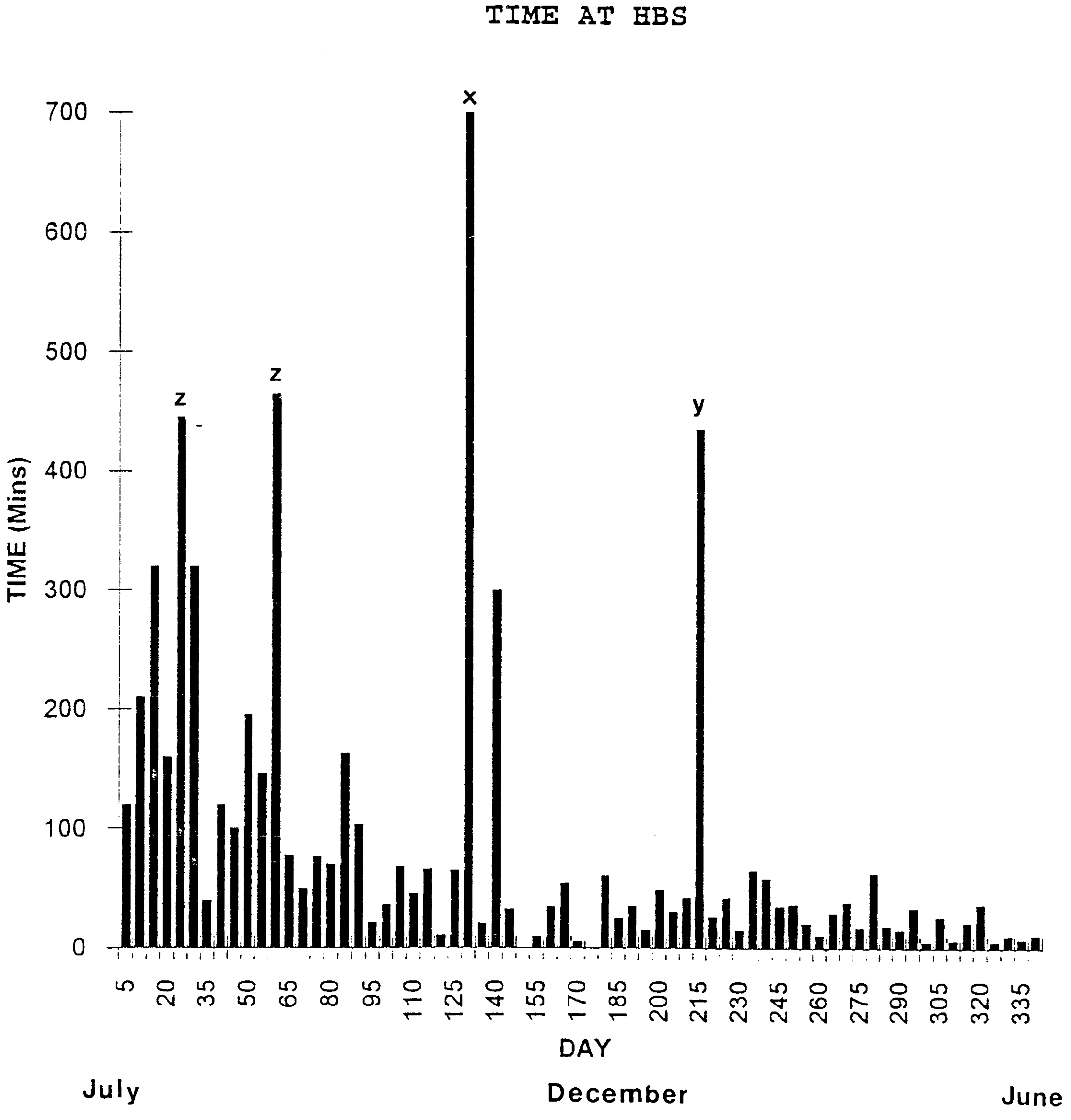
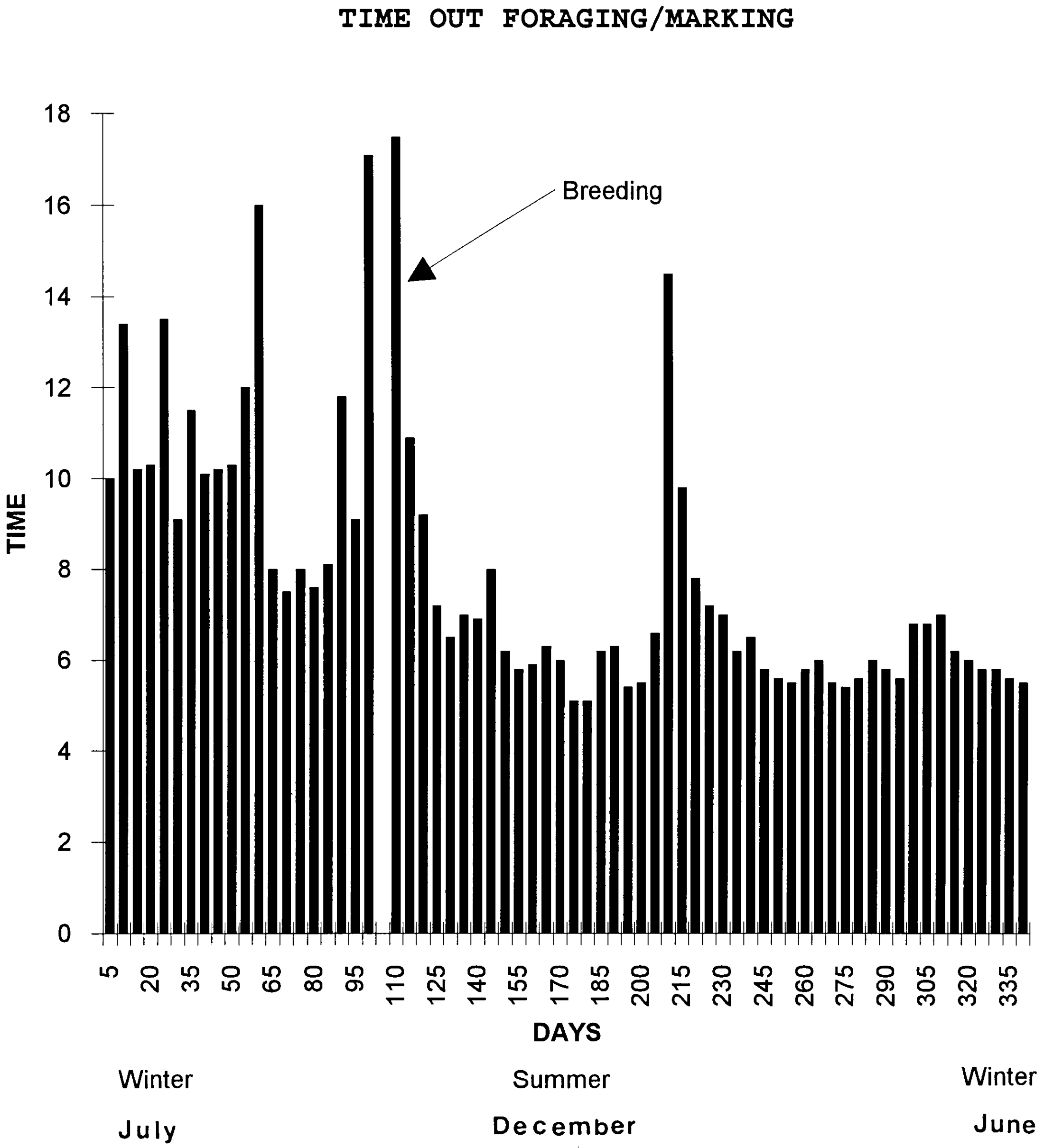


Figure 4.13 Time at which *Cynictis penicillata* left the home burrow system to go foraging.



P Howard 1993

Figure 4.14 Daily wind speed taken over an eight month period.

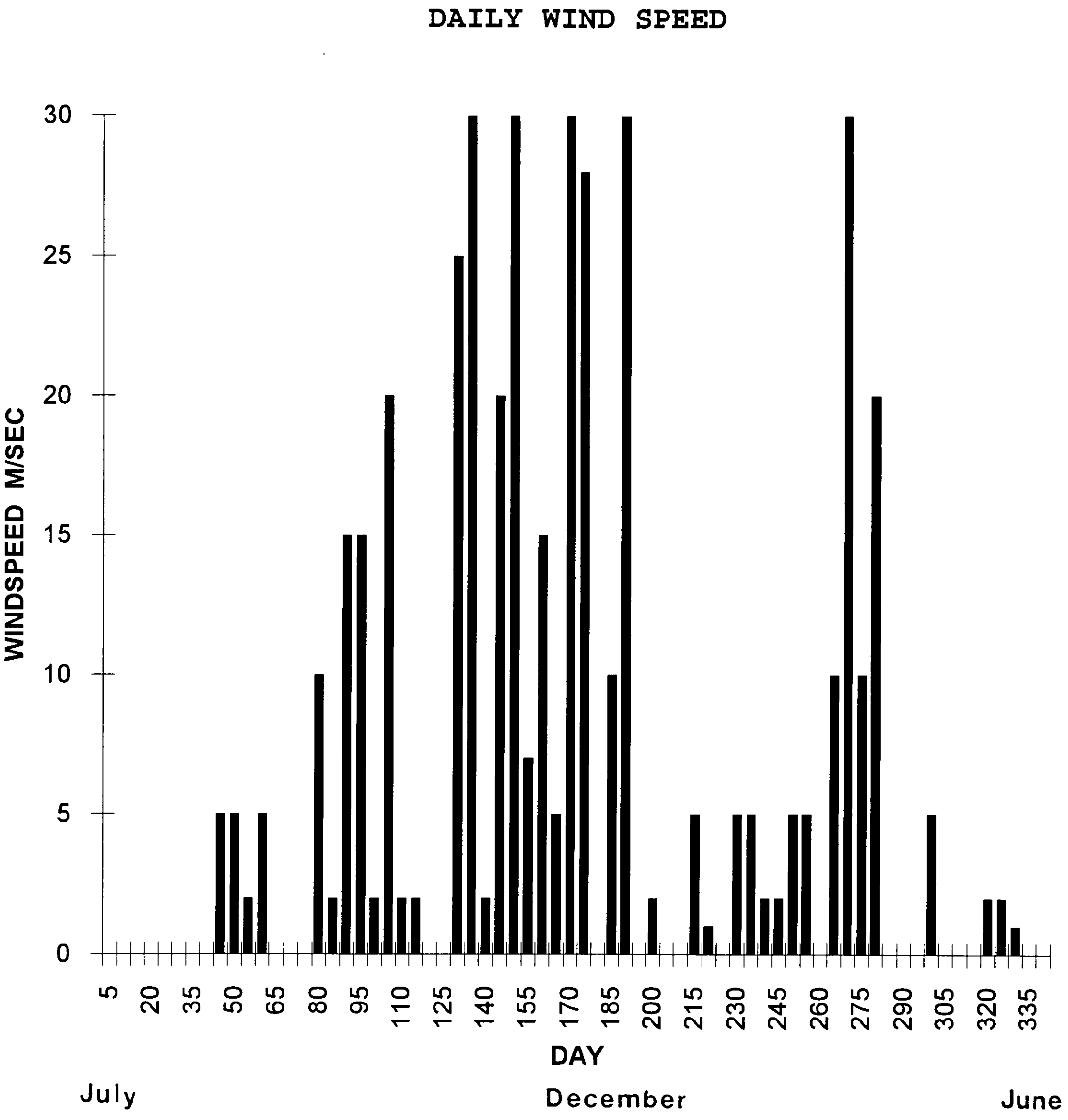


Figure 4.15 Daily rainfall (mm) during the study period on the farm Biesjiesfontein, as taken on a daily basis.

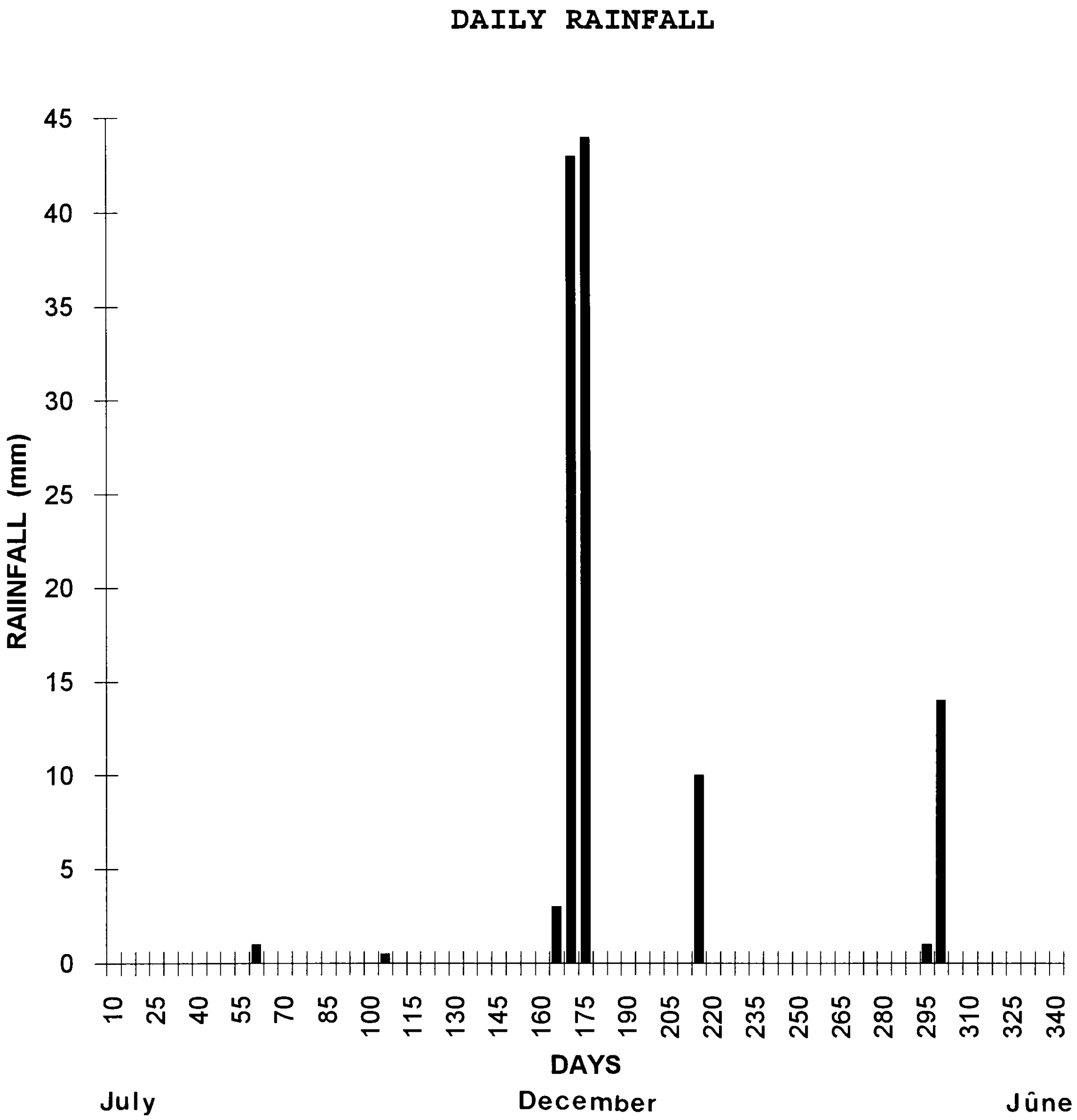


Figure 4.16 Daily temperatures measured at sunrise taken 0.5m above ground level.

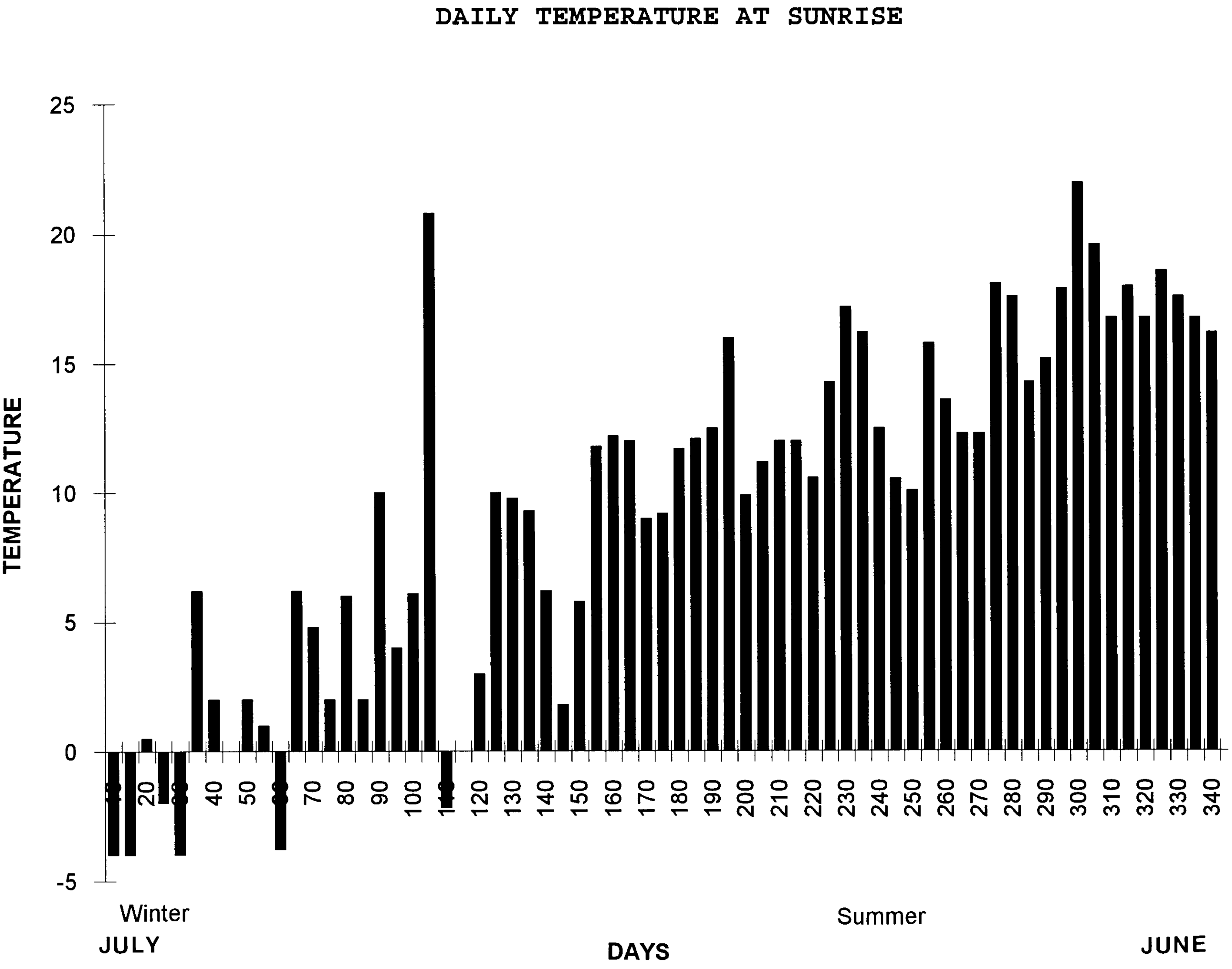


Table 4.9 Summary of environmental parameter statistical data. All correlations shown are time of emergence from burrow in the morning versus named parameters. Pearson's correlation coefficient (r) is given, and the probability level (p). N = number of observation days.

Parameters tested	season	result/range	N	Pearson's r
Time at Home burrow system after sunrise (minutes)	winter summer	142,2 +-9,4 23,8 +-11,3	345	N/A
Time foraging (hours)	winter summer	10:24 +-1:36 6:05 +-0:45	345	N/A
Sunrise	winter summer	07:28 am 05:12 am	345	r = 0,79 p = 0,05
Temperature	winter summer	-7 to 7 °C 12 to 20 °C	345	r = -0,85 p = 0,05
Windspeed	winter summer	variable variable	345	r = 0,18 p = 0,10
Rainfall	winter summer	non-seasonal	345	r = 0,71 p = 0,10
Cloud Cover	winter summer	non-seasonal	345	r = 0,87 p = 0,05

4.3.1 Temperature

Temperatures increased from winter through summer, often with large fluctuations typically evident from day to day. These results were correlated with emergence times from the burrow and showed an excellent negative relationship (r = 0.83, p = 0.95) i.e. an increase in temperature = earlier activity time.

4.3.2 Rainfall

Rainfall was generally low, with a peak in December and rain occurring in September and March. In addition, the daily rainfall measurements (Figure (4.15) showed that during rain, *Cynictis penicillata* remained within the burrow system (r = 0.71, p = 0.95). The annual rainfall in the Karoo is extremely low, although floods in February 1988 occurred, destroying burrow systems and even drowning individuals (dead adults and juveniles were found).

4.3.3 Wind speed

Wind speed peaked from August through January and again the following June and July. Daily windspeed (Figure (4.16)) was measured in order to determine whether emergence time correlated with this parameter, but no relationship was found (r = 0.18, p = 0.90). The wind blows fairly consistently for *ca* 8 months in the Karoo, but has little effect on *Cynictis penicillata* activities.

4.3.4 Time of sunrise

Marked differences in the time of sunrise indicate breaks in observation days (x and y). The time of sun-rise decreased from winter (July) through summer and began to increase again in January. These figures were correlated with emergence times and showed a strong positive relationship (r = 0.79, p = 0.95) i.e. *Cynictis penicillata* emerged earlier from the burrow when the sun rose earlier.

4.3.5 Time at which *Cynictis penicillata* emerged from burrows

In winter *Cynictis penicillata* appeared later than in summer. The graph peaks during the August and November when breeding took place, and the animals were at the home burrow system for longer periods due to babysitting activities (x) (Fig 4.13).

The times at which *Cynictis penicillata* emerges daily from the burrow system closely follows the times of sunrise (r = 0.79 : Pearson's correlation coefficient p = 0.95) (see Figure (4.13)), temperature (r = 0.83, p = 0.95) and cloud cover (r = 0.87, p = 0.95). In summer (bur not in winter), time of emergence from the burrows is closely related to the time at which the sun's rays first reach the burrow entrances.

It is also for this reason that the majority of the burrows have an easterly aspect (direction in which they face). Due to higher average summer temperatures than in winter, *Cynictis penicillata* spends a shorter time period sunbathing and warming its body at the HBS in the summer. The time of foraging is also earlier.

4.3.6 Time spent at burrow system

There is a decrease from winter to summer (mean time in winter = 142.2 +- 9.4 mins, mean time in summer = 23.8 +- 11.3 mins., n = 280 days).

4.3.7 Time at which *Cynictis penicillata* left burrow system

Cynictis penicillata left increasingly early from winter through summer when the temperatures rose sooner and higher (winter = -3 to 7 'C, summer = 12 to 20 'C), sunrise was earlier (winter = 7:28, summer = 5:12) and *Cynictis penicillata* became active earlier (winter = 10:24 +-1:36, summer = 6:05 +-0:45).

4.4 DIET

Analysis of the gut contents of four dead specimens revealed the following data:

Table 4.10 Gut contents of *Cynictis penicillata* on the farm Biesjiesfontein, Karoo (n = 4)

GUT CONTENTS	Percentage by weight	Number of individuals where found
Insecta	70	4
Reptilia	2	4
Myriapoda	3	4
Fruits	7	2
Mammals	3	2
Amphibia	3	2
Aves	2	1
Muridae	4	4
Scorpiones	3	3
Araneae	3	4
Total	100	ave = 3

The nature of the food resource determines the type of hunting techniques used by *C. penicillata*. *Cynictis penicillata* feeds mainly on insects (70 %), in particular various types of Coleoptera and termites, small birds, reptiles, amphibians and mammals (13 %), and fruit (Jackal berries)(7 %).

The only communal function of social or pair foraging would be for the locating of food patches. However, the following case was recorded:

4.4.1 Foraging in groups

Cynictis penicillata was seen foraging alone and in small groups of two to three individuals. The following data were obtained from a group consisting of two adults (male and female) and a single juvenile male.

This data shows that the females and juvenile generally emerge together and earlier than the male and the female leaves foraging alone before the male. The juvenile remains at the burrow with the male and then leaves the burrows to go foraging and touring the home range at the same time as the male. The juvenile accompanied the male 82,2 % of the time, whilst all three left together 14,4 % of the time. The juvenile only accompanied the female alone 3,4 % of occasions.

Table 4.11 The mean times at which *Cynictis penicillata* appears from within the burrows each day and the corresponding time at which they depart to go foraging. Data is given for an adult male and female and a juvenile. The juvenile accompanied the male on foraging excursions. Data were recorded for a continuous 23 day period during May.

	FEMALE		**MALE**		**JUVENILE**	
	out	**leave**	**out**	**leave**	**out**	**leave**
Days	23		23		23	
time (x)	08h17	09h28	08h04	09h47	08h19	09h47
s.d. (min)	45	91	48	91	36	86

4.5 VIGILANCE, ANTI-PREDATOR BEHAVIOUR AND PREDATION IN *CYNICTIS PENICILLATA*

The avoidance of predators is essential for both individual survival and the survival of a group. The number of predator attacks to which a mongoose or group of mongooses is exposed is very high and hiding from predators accounts for approximately 18,16 % of an animal's possible foraging time (*Helogale undulata rufula*, Rasa 1986).

4.5.1 Vigilance

Observations were carried out to determine the vigilance behaviour of different individuals under different conditions. This was performed to determine whether there is division of labour in *Cynictis penicillata* when they occur in small groups, and, if so, if certain individual/s performed more than others. *Cynictis penicillata* was observed in the following situations:

- Vigilance behaviour exhibited by the dominant adult female was accompanied by the adult male and juvenile male;
- Vigilance behaviour exhibited by the adult MALE when occupying the burrow system with the dominant female and a juvenile subordinate male;
- Vigilance behaviour exhibited by the Juvenile subordinate male when at the HBS concurrently with the adult male and female.

Table 4.12 Vigilance behaviour exhibited by the dominant adult female at K52 HBS when in accompanied by the adult male and juvenile male. The figures indicated are: time (seconds) during which the animal was vigilant, time (seconds) between periods of vigilance (non-vigilant), and the number of times vigilant (N). The Mean (s) period of vigilance or non-vigilance are also given for each day.

DAY	**VIGILANT**			**NOT VIGILANT**	
	No. times vigilant	**seconds**	**s.d.**	**seconds**	**s.d.**
1	22	25,5	22,4	10,7	10,3
2	4	32,5	17,8	26,6	32,1
3	64	15,8	12,7	24,1	18,6
4	1	5,0	0	20,0	0
5	11	18,4	13,9	555,7	78,6
6	12	26,8	25,3	9,4	7,1
7	7	8,8	3,9	8,8	5,5
8	14	18,0	13,5	41,5	89,9
9	12	18,6	13,0	625	95,0
10	4	8,3	0,9	0	0
11	24	24,8	18,0	92,7	20,0
12	24	16,9	13,6	15,2	17,9
13	37	18,8	13,7	43,7	14,0
14	48	13,5	13,0	86,6	14,4
15	4	19,0	12,7	44,3	23,6
16	5	19,4	11,8	51,5	42,0
17	11	17,0	11,6	34,4	64,7
N	X	secs		secs	
17	17,4 +- 16	18,1 +- 5,4		99,4 +- 104,3	

The adult female was alert an average of 17,4 times each day for a period of 17 days. The average duration of each vigilance period was 26,8 seconds (+- 20,4). The average time taken for non-vigilance activities was 99,4 (+-104,3).

Table 4.13 Vigilance behaviour exhibited by the adult MALE when occupying the burrow system with the dominant female and a juvenile subordinate male. Time spent vigilant and time between vigilance are shown.

DAY	VIGILANT			NON-VIGILANT	
	Number of times vigilant	seconds	s.d.	seconds	s.d.
1	6	59,6	45,5	4,5	3,3
2	32	19,4	17,3	79,5	194,0
3	27	14,8	13,6	36,2	49,1
4	52	14,2	12,4	45,2	74,0
5	91	14,5	12,4	39,8	50,0
6	58	21,9	18,4	58,1	257,0
7	42	21,6	17,0	22,4	21,7
8	42	14,8	14,5	116,8	598,0
9	20	22,3	20,3	150,0	570,0
10	34	16,7	11,3	79,0	205,0
11	25	12,1	11,4	13,5	10,9
12	127	18,0	16,2	535,0	322,0
13	38	11,8	10,2	70,6	333,0
14	63	16,7	13,4	23,7	21,0
15	71	12,5	12,8	41,6	52,0
16	44	11,2	9,2	42,8	58,4
17	48	13,5	13,0	86,4	143,0
18	26	19,3	14,3	130,0	467,0
19	80	15,2	13,0	54,0	102,0
20	48	12,6	11,3	82,9	220,0
21	63	11,9	11,5	62,7	93,8
N	X			X	
21	49,3 +- 3,6	15,7 +- 3,6		75,8 +- 37,6	

The adult male was alert an average of 49,3 times for a period of 15,7 (+- 3,6) seconds each day for a period of 21 days. The average time between vigilance spent doing non-vigilance activities is 75,8 seconds.

Table 4.14 Vigilance behaviour exhibited by the Juvenile subordinate male when at the HBS concurrently with the adult male and female individuals. Time spent vigilant and time between vigilance is shown.

DAYS	VIGILANT			NOT VIGILANT	
	Number of times vigilant	Time (seconds)	s.d.	Time (seconds)	s.d.
1	24	19,6	22,2	9,6	11,8
2	49	17,8	17,2	24,1	42
3	19	16,4	17,9	27,0	23,3
4	31	11,1	10,3	36,1	77,7
5	103	11,0	11,0	39,6	53,9
6	39	13,5	13,1	87,8	270,0
7	26	13,6	12,6	157,0	81,6
8	39	14,1	10,4	135,7	387,6
9	49	16,6	15,6	72,7	370,0
10	22	16,1	9,6	235,0	638,0
11	138	11,5	11,3	14,3	14,1
12	122	9,1	11,1	76,4	324,0
13	29	8,4	10,7	100,0	312,0
14	44	15,5	13,0	50,3	78,3
15	61	11,9	10,9	49,5	64,5
16	49	10,6	9,1	40,6	60,2
17	51	10,2	8,6	82,9	118,0
18	25	12,6	9,5	122,5	450,0
19	94	11,7	12,1	50,8	92,3
20	63	11,5	9,7	31,3	61,1
21	89	12,5	21,1	49,8	95,5
N		X		X	
21	55,5 +- 13,3	13,1 +- 2,9		73,2 +- 35,7	

The Juvenile male was alert an average of 55,5 (13,3) times for an average time of 13,1 seconds. Between each period of vigilance, 73,2 (+-35,7) seconds were spent in non-vigilance activities.

Table 4.15 Results of two-sample t-test analysis performed on the data from Tables 10.1, 10.2 & 10.3.

Data analyzed	**Analysis on Number of times vigilant (p = 0.01)**	**Significance level**	**Analysis on Seconds spent vigilant**	**Signif.**
Adult Male & Adult female	-5,99	N/S	0,010	yes
Adult male & Subordinate male	0,064	yes	-3,46	N/S
Adult female & Subordinate male	0,017	yes	0,033	yes
Subordinate male performs more vigilance activities and for longer periods than the adult male or adult female.				

The above analyses show a significant difference in the number of times each animal is alert, and the time spent being alert. The juvenile male spent significantly more time than both the adult male and female and was vigilant more frequently. In addition, the female spent on average more time in each vigilance period than the male.

Vigilance when foraging is *ca* 98 % self executed, the *ca* 2 % balance being performed by suricates when the two species are found foraging together. However, when at the burrow system the situation is far more variable, and the amount of time each individual spends guarding is dependent on the number of animals present at the HBS at the time.

4.5.2 Co-operative hunting

An example of co-operative hunting was observed at 09h40 near the homestead on the farm Biesjesfontein during May. Two *Cynictis penicillata* individuals approached a dam next to the homestead, adjacent to which 12 ducks and 17 geese were housed in a large fenced enclosure (*ca* 50 m^2). Initially, the mongooses approached simultaneously from the south eastern side of the enclosure. At approximately 35 meters from the fence, one individual moved to the eastern side of the enclosure, whilst the second animal approached from the southern side. The northern side was surrounded by a chicken-mesh fencing, whilst the western side was flanked by the dam. Moving slowly towards the feeding fowls, the mongooses approached to *ca* 10 meters, shielded by vegetation. Suddenly, the mongoose on the eastern side dived through a small hole in the fencing, creating a surprise to the fowls which responded with an enormous noise and commotion, running in all directions around the enclosure. Due to the noise and confusion of motion, it was difficult to see whether this mongoose actually attacked any of the birds, but nonetheless none were caught.

During this disturbance, the second mongoose was seen entering the enclosure through a second hole in the fencing. This individual did not make an attempt to attack the birds. As the dust cleared slightly, this individual was seen running away from the enclosure with a large duck egg in its mouth. The first mongoose followed immediately and the two disappeared into the bushes.

Similar incidences (5 in total) were observed by farm staff and the farmer and his family. One individual was ultimately killed by one of the farm dogs.

4.6 ANTI-PREDATOR BEHAVIOUR

Cynictis penicillata utilises various morphological features and behaviour in defense against predators. The behavioural mechanisms contributing to predator detection are iterated below (a detailed description of the behavioural parameters are presented in Appendix A):

4.6.1 Auditory and visual function

Cynictis penicillata has acute hearing and eye sight (pers.obs). Both these attributes are essential in the detection of predators (as in the detection of prey). *Cynictis penicillata* is able to see a medium sized aerial predator (e.g Jackal Buzzard) when it is flying over 3 km away from it. Detection of ground predators appears to be more difficult when they are foraging, but as they often make use of raised features as observation posts to give them greater elevation and hence a larger area of view, these may also be efficiently detected. Rasa (1986), Beynon 1986) and Neal (1984) note that location of potentially dangerous predators is done visually in all viverrids. Similarly, their auditory senses are sensitive to the sounds of bird wings, alarm calls of conspecifics and other species, and other sounds.

4.6.2 Vocalisation

The utilization of vocalization in defense situations, either as an warning call or as a threatening response towards the attacker, may be used to distract the predator in a form of anti-predator behaviour. *Cynictis penicillata* has a limited vocal repertoire (Beynon, per obs; Wenhold, pers.comm.), but the calls elicited under attack situations may distract the predator, and cause it to abort the attack attempt. This behaviour has been observed in the Dwarf mongoose and the Arabian babbler (pers. obs.). The expression of vocal emittance during mobbing of potential predators may serve to ward off the predator and avert an attack. Thus vocalization operates on two levels; as a warning mechanism when the predator is detected, and as a defense mechanism.

4.6.3 Pilo-erection

Pilo erection of the hairs on the back and tail occurs under threat or attack situations, in addition to displays. This increases the apparent size of the body, giving the attacker the impression of a much larger prey. The functional mechanism of this anti-predatory behaviour is similar to that of alarm vocalizations: On a number of occasions *Cynictis penicillata* was seen with pilo-erection whilst raptors were hunting in the vicinity of the home burrow system. The attack may be averted by surprising the attacker and deflecting the attention.

If the attack is not completely aborted, it is often delayed in this manner, giving the prey time to escape.

4.6.4 The physical mobility and agility

Physical mobility and agility in *Cynictis penicillata* should be noted here. In order to adequately detect predators, *Cynictis penicillata* is able to utilize body form and its ability to stand upright on its hind legs, balancing with its tail, to more than double its height and hence its area of vision (elevation). Observations show that *Cynictis*'s reflexes are particularly quick, allowing rapid escape and diving for cover when attacked or threatened. They are able to run fast, and due to the apparent suppleness of their body, are able to enter burrows and cover rapidly.

4.6.5 Morphology

In order to adequately defend itself, *Cynictis penicillata* is equipped with sharp incisors and sharp claws which it uses in fighting or warding off predators.

4.6.6 Home Burrow Systems

Apart from the main HBS in the territory, *Cynictis penicillata* and *S. suricatta* also maintain a number of other burrow systems around the territory within easy access and positioned fairly regularly ($\bar{x}$ = 43 metres, s = 20.6, n = 15). These burrow systems provide shelter from predators, and the mongooses will dive for cover when a potential predator is present. They will remain under cover for variable lengths of time, depending on the nature of the disturbance (mean distance of adjacent HBS's = 14.5 mins, s = 10 mins., n = 65). Ground predators tend to elicit a longer "under-cover" period, whereas raptors and other aerial predators elicit a short response. This is probably due to the different modes of attack, and the fact that *Cynictis penicillata* is not able to escape as effectively from ground predators as from aerial predators : Most major ground predator species are small enough to enter the burrow system in pursuit of their prey (*Cynictis*), and hence *Cynictis penicillata* should select a strategy which will minimize the possibility of detection by the predator. Thus by diving into the burrow before the predator has detected it, ***Cynictis* penicillata** increases its defense, and avoids confrontation. It remains in the burrow long enough to ensure that the potential predator has moved off. In the case of aerial predators, *Cynictis penicillata* will only enter the burrow for a short period, and then usually only when there is an attack situation. The modes of attack are more direct and these predator species will never enter the burrow system. In addition, the ground area covered by an aerial predator is that much greater, and they move faster than a ground predator when hunting.

Many predators hunt in the early hours of the morning, soon after the sun has come up, and in the late hours of the afternoon. These are the times of day when the light is difficult and may cause difficulty in predator detection. *Cynictis penicillata* decreases vulnerability to predators at these times of day by remaining in the HBS until there is sufficient light and visibility for predator detection. In addition, they remain at the HBS until they are warm, and more awake/alert to external stimuli.

Essential to predator detection, is the site and situation of the HBS. The elevation, aspect and relation to surrounding topography are all factors which will assist in the overall anti-predatory mechanisms of *Cynictis penicillata*.

4.6.7 Vigilance

When active, *Cynictis penicillata* is constantly alert. Each individual, apart from being partially dependent on the group vigilance, is largely self reliant. The actual observations of "alertness" were taken when the animal appeared tense and very alert.

Vigilance is a form of predator avoidance behaviour in which the vigilant animal becomes alert to the detection of predators.

It is pertinent to note, however, that *Cynictis penicillata* exhibits a high degree of vigilance behaviour both at the HBS and when foraging. Much of the vigilance behaviour is performed in conjunction with other behaviour patterns, and is also exhibited together with *S. suricatta*, when there is slight variation in the behaviour. Often the effective execution of a vigilance system requires the division of labour within a group.

4.7 PREDATION

4.7.1 PREDATION BY *Galerella pulverulenta*

Predation of offspring by *G. pulverulenta* was observed once in the second week after birth. *G. pulverulenta* and other small carnivore species are relatively frequent potential predators, and although they do not prey on the adult *Cynictis penicillata*, the young are taken. The young are taken from within the burrow system, at night (n = 4 records and observations).

G. pulverulenta is able to enter the burrow system and thus gain access to the burrows containing the young. Evidence of predation on the young, and of agonistic interspecific interactions was seen by the scars and blood on both male and female *Cynictis penicillata* the day after the first such encounter. The indicators were cuts, scratches and bite marks on the face, head and forelimbs of both animals. These indicators were evidence of a head-on encounter at close quarters and within a confined space. *G. pulverulenta* was seen entering a burrow adjacent to the home burrow system at sun-set the evening prior to the above incident. The individual proceeded to leave and enter the burrow repeatedly on forays to the home burrow system only ten meters away. Each time *G. pulverulenta* sniffed various parts of the burrow mound and then dived back to the adjacent burrows. The following day, the burrow mounds were inspected for evidence of the interaction which had taken place. From a few hair samples found at the site, behavioural evidence and personal observations, it was concluded that *Cynictis penicillata* and *G. pulverulenta* had been involved in the interaction. In addition, *G. pulverulenta* was not seen at the home burrow system again during the field-study period. Only one such observation was recorded during the field-study period.

The importance of the threat posed by a sympatric species which lives concurrently and on an irregular basis within the same burrow system as *Cynictis penicillata* is great. *G. pulverulenta* is a solitary species which opportunistically occupies the burrow system. It does not appear to contribute to the construction of the HBS at any stage, and when in occupancy, utilizes the peripheral burrows only, i.e. it has an interspecific relationship with *Cynictis penicillata* which may be regarded as parasitic: the relationship benefits *Galerella pulverulenta* in that it is provided with burrows, whilst *Cynictis penicillata* gains nothing and is threatened by predation of its young.

4.7.2 PREDATION BY MONITOR LIZARDS: *Varanus spp*

Predation of offspring by *Varanus spp*, a large carnivorous reptile, was observed within the first week after birth of the second litter of young. The group preyed upon was observed for the entire field- study period. This was the second incidence of predation on this group, where the entire litter was lost.

Varanus is a species of lizard which is large and able to enter the *Cynictis penicillata* burrow system easily. The observed incident of predation by *Varanus spp* occurred when it entered the HBS during the late afternoon whilst both the adult *Cynictis penicillata* were babysitting the young. A confrontation occurred where *Varanus* sp was mobbed intensely by *Cynictis penicillata* and all three animals entered the burrow system. *Varanus* is slow moving animal with a whip-like tail with which it defends itself. After a brief encounter *Cynictis penicillata* was seen to flee from the HBS. The *Varanus* occupied the HBS for 4 days, during which time *Cynictis penicillata* was seen in the territory only once. The male *Cynictis penicillata* approached the HBS, marked the surrounding bushes, but failed to actually enter the HBS. Only the day after the *Varanus* had left the HBS, did the resident male return to the burrow where he marked the mound extensively. The young were presumed eaten.

4.7.3 PREDATION BY RAPTORS

Nine species of raptors were identified in the study area.

Table (4.16) shows the occurrence of various raptors in the study area over a period of 3360 observation hours. The incidence of attacks was relatively low, but the skull remains at the raptor nest sites suggest that predation of mongooses occurs primarily during the breeding season and on sub-adults leaving the HBS on foraging trips (Davies pers. comm.). It is during the foraging periods that *Cynictis penicillata* is particularly vulnerable.

Table 4.16: Number of raptor sighting and attacks observed around the study area during the study period.

SPECIES	NUMBER OF SIGHTINGS	NUMBER OF ATTACKS
Lesser Kestrel, *Falco naumanni*	15	-
Jackal Buzzard, *Buteo rufofuscus*	14	3
Martial Eagle, *polemaetus bellicosus*	10	1
Pale Chanting Goshawk, *Melierax canorus*	10	2
Secretary Bird, *Sagittarius serpentarius*	5	-
Yellow Billed Kite, *milvus parasitus*	3	-
Black Eagle, *Aquila verreauxii*	2	2
Steppe Buzzard, *Buteo*	2	-
Peregrine Falcon, *Falco peregrinus*	1	-
Total	62	8

Raptors attacked on 8 out of 62 sightings, although no successful attacks by raptors were observed. Small raptors such as Lesser kestrels and Peregrine falcons and the large Secretary Bird were not seen to attack. However, the Secretary Bird elicited warning vocalisations from *Cynictis penicillata* and it can therefor be deduce that this species may be considered a potential predator.

Observations of the vigilance behaviour and behavioural reaction towards raptors showed evidence that raptors form a large threat as potential and successful predators. In addition to behavioural observations, skeletal remains of *Cynictis penicillata* were found at the nest sites of both the Black Eagle and Martial Eagle.

4.8 OTHER MORTALITY FACTORS

4.8.1 INFANTICIDE

Infanticide was observed in *Cynictis penicillata* on one particular occasion where the following sequence of events took place: The adult female carried a juvenile out of the burrow system under observation and dragged it 11 metres to the adjacent man-made dyke system. The young animal was held in the mouth by the neck and shaken to death. It was then prodded with the nose and forelimbs, anal marked extensively and cheek marked. The adult mongoose then marked the immediate surrounding bushes and rocks, toured the dyke over an area of approximately 50 square metres, remarked the dead individual and then left to go foraging. Thirty minutes later the adult returned to the HBS to perform further marking of both the dead individual and the dyke. An interaction between the adult male and adult female occurred at the HBS involving marking of the dead offspring and agonism. As the male approached the dead individual, the female growled and prevented the male from contact. The female then took the dead offspring in her mouth and proceeded to eat it from the tail end, forwards. The whole animal was consumed within 5 minutes. Marking behaviour and intensive auto-grooming by both male and female adults followed this sequence of events.

Infanticide is a phenomenon occurring among carnivores where the most universal context is infanticide by females other than the mother (Corbett 1988). In most recorded cases the female kills or caused the death of offspring of subordinate females. However, in the case of *C.penicillata*, infanticide may also occur under certain conditions which are threatening to the survival of the offspring as well as the adults: e.g. drought or floods where the parents cannot adequately supply the offspring with sufficient food. In addition to this, infanticide may occur during unfavourable or exigent conditions which may stimulate the female to kill the offspring as a defense mechanism.

Infanticide by the dominant female appears to be a reproductive strategy where the adaptive significance is to ensure that she is the only breeding female at the time. This would prevent competition between the offspring and other potential breeding females.

Dominant female infanticide may be just an extension in the chain of behaviours that suppress mating activities in subordinates (Corbett 1988).

It is also important to consider the possibility of infanticide by the parents in the following situation: The adults may kill and eat the young as a defense mechanism to counter the danger of the intruding predator which may/may not have already killed one or more of the litter. During an attack situation the adults may kill the young to avoid predation by another species. This behaviour may occur in species which live in an adverse environment where there is a shortage of resources, and where the energetic costs of failure to reproduce successfully is high. i.e. where the fitness of a species is determined by the survival of the young to their first breeding season, and the loss of the "energetic value" of the offspring to a predator frequent, it is likely that infanticide will evolve in order to "regain" that invested energy to the parents of the offspring, rather than to forfeit it to a predator.

4.8.2 ROADS

Cynictis penicillata suffers a high mortality rate due to road accidents. Many of their home ranges are bisected by roads which makes them vulnerable to being run-over by vehicles whilst on foraging excursions or border patrols. The observed mortality due to vehicles was, comparatively, the greatest when considering other forms of mortality. Five dead individuals were found dead during the study periods on the main road running through the farm between Hutchinson and Victoria West.

4.8.3 DOGS

The presence of feral and domesticated dogs on many farms accounts for a percentage of the mortality of *Cynictis penicillata* in this region. Dogs are swift predators, and invariably out-run *Cynictis penicillata* in attack situations, and, unless within close proximity of a HBS into which they can escape, the mongooses are often killed. The farm dogs were seen killing one *Cynictis penicillata* during the study period.

4.8.4 DISEASE

Mortality due to disease occurs in *Cynictis penicillata* as in other species. Rabies is prevalent in this species and due to the nature of their interspecific interactions is transmitted between various vector species, athough such cases of mortality were observed.

4.9 REPRODUCTION IN *Cynictis penicillata*

General observations on the reproductive behaviour by Zumpt (1968), Ewer (1973), and Smithers (1983) have shown that *Cynictis penicillata* breeds from June through to February, with the latter litters being produced only in cases where previous litters have failed to survive, or when conditions are favourable to support a second litter. In general, however, the number of young to survive to adulthood is fairly low (only three young were observed during the entire two year period at Biesjesfontein).

In this study, detailed observations of the entire breeding behavioural repertoire were achieved. The initial observations included courtship behaviour and copulation, and this was followed by the gestation period, birth of the young and finally three months of parental care before the young dispersed.

Table (4.17) gives a summary of the reproduction factors of *Cynictis penicillata*. Of particular importance is the high juvenile mortality rate, experienced by individuals in the first three months after birth.

Table 4.17 Summary of Breeding Data in *Cynictis penicillata* from June 1987 - July 1988

SUBJECT/ FACTOR	DETAIL	SAMPLE SIZE	COMMENTS
Number of young per year	1 - 3	4	small group size maintained
Juvenile mortality	60 %	4	predation on young
Average mortality	22 %	8	adult mortality low c.f. young. Dependent on natural factors.
Courtship period	3 days	2	this may be shorter if post-parturition copulation
Copulation period	2 - 2,5 days	3	overlaps with courtship period
Gestation	*ca* 62 days	3	
Altricial period - lactation period	*ca* 22 days	2	young remain in burrow
Parental care	*ca* 120 days	2	paternal care is predominant
Juvenile independence	*ca* 120 days	2	juveniles leave territory
Post-parturition oestrus	2 - 3 days	2	induced after loss of previous litter
Extra-pair copulation	yes	2	2nd & 3rd oestrus only if previous litter dead
Time of year	Aug - April	2	depending on survival of young - i.e - early if first litter survives, later if other litter survives.
Number of litters per year	1 - 3	2	Usually only one litter survives from each breeding season

4.9.1 Courtship

Courtship are behaviour patterns, often very elaborate and conspicuous, that precede, accompany and sometimes follow the act of copulation. The duration of courtship varies from several days to a few seconds, depending on the extent to which the males and females establish durable pair bonds. Several functions may be ascribed to courtship, such as attraction of a mate, stimulation of the mate to sexual receptivity, and the synchronization of mating activity so that the sexual act (copulation) occurs at the optimum moment.

Displays used in courtship tend to show typical intensity and a high degree of species specificity, features which enable an animal to recognise a mate. The form of some courtship displays suggests that the motivation of the animal performing it involves a conflict between aggression, fear and sexual behaviour.

After a short period of courtship, the male is able to approach the female and copulation takes place. The courtship behaviour appears to play a pivotal role in female stimulation, as it is only after the female is approached by the male, marked and interacted with that the female comes into oestrus. Thus, although there is as yet no physiological evidence, it is likely that the male pheremones emitted during the intensive marking behaviour are responsible for the onset of oestrus. Mating occurs at a high intensity (*ca* 70 times a day : see Table (4.17)), and is accompanied by a variety of interaction behavioural parameters performed by both the male and female. In particular, there is much growling, wrestling, submissive and overt behaviour (see Table (4.18)). Extra- pair copulations were witnessed on the second and third oestrus cycles. The female mated with the male from the neighbouring home range on 3 occasions during the second oestrus and twice during the third oestrus.

4.9.2 COPULATION

Table 4.18 Behaviour patterns exhibited by the male and female during courtship and copulation. Behaviour includes extensive marking, grooming, vocalisations, chasing and ultimately mounting and copulation. Time is given for total minutes spent on each behaviour category. The total observation period per day was 870 minutes (04h30 to 18h30) and copulation took place in the mid-morning.

Behaviour	8 August		10 August	
	male	female	male	female
Total duration	287 mins		297 mins	
Mark	21	10	27	3
Growl	31	3	32	2
Mount	21		77	
Chase (male -> female)	54		113	
Circle	67		69	
Copulate	13		68	

Sexual interaction in *Cynictis penicillata* begins when the female comes into oestrus. The male initiates with inguinal nosing of the female, sometimes accompanied by similar nosing of the male by the female (this occurs to a far lesser extent). Mounting may or may not follow immediately after the inguinal nosing.

These activities take place both around the HBS and may occur within the burrows. Females frequently avoid the male during his advances, exhibiting agonistic behaviours such as growling, biting, snarling and chasing. The female will also run away in these instances. Even when the male has successfully nosed the female, she may evade mounting by moving forwards, or turning around and snapping, before the male has a firm grasp with his forelimbs. Once the female has been grasped the male will proceed with intromission immediately : the female often escapes prior to a successful intromission by biting, scratching, growling or wriggling free. The two were seen to fall over, or into a hole on numerous occasions during copulation.

When intromission is achieved, the pair stay together for up to 20 seconds in the mounting position. Pelvic thrusts were observed, although it could not be determined whether ejaculation had always occurred (see Table (4.17) for copulation frequency). The two also engaged in the sacral position, where the female was "rocked" whilst clasped to the male's lap which sits back on its sacrum.

After mounting, the male loses the grasp of the female and the sequence begins again: often immediately. The female's attitude is generally alert and she exhibits piloerection of the tail hairs, and growls. She moves away from the male: either bounding away, attacking the male or sitting nearby. If the copulation sequence is not immediately following they both groom themselves. Allogrooming was not observed.

The amount of time spent in courtship and copulation on both days of copulation varied little and was extremely intensive. On both days the male was found to mark more extensively than the female marking more on the second day than on the first ($r = 0.89$, $p = 0.01$). This behaviour coincides with the presence at the burrow on the second day of another male *Cynictis penicillata* and may be explained by competition and resultant territorial demarkation in order to ward off the intruding male. However, the female took advantage of a second and third male as will be highlighted later.

In both instances, the male was considerably more vocal than the female, emitting over 93 % of calls during copulation. Female *Cynictis penicillata* rarely make sounds unless alarming against predators. The few times growls were emitted were due to un-relenting pursuance by the male and physical "abuse" (roughness) to the female (e.g. falling into a hole during mounting, neck-biting too hard).

On the 10 August the copulation intensity increased above that of the first day by 83 % whilst interactive courtship behaviours increased by 78,8 % (+-3,6). The numbers of times the animals copulated reached a peak prior to cessation. During the entire day both animals remained at the burrow system interacting. Of particular interest, however, is that every time (N = 11) the female tried to leave the burrow system to go foraging the male would chase her back to the burrow and resume courtship. In all cases it was the female who wanted to leave the burrow system and the male who prevented her from leaving. The reason for this became evident during the latter part of the copulation period when other males were present in the territory (see later).

The second day of courtship and copulation was more intense than the first day: 50 % more chasing and physical interaction took place (54 incidences on day 1 and 113 on day 3) and mounting and copulation occurred 5 times more frequently (13 times on day 1 and 68 times on day 3). Growling and marking occurred at a similar frequency on both days.

Only 13 of the 21 mountings were successful on the first day of copulation, whilst 68 of the 77 mountings resulted in actual copulation on the second day.

This behaviour ceased after the three days of intermittent copulation. (The pair appeared to rest on the second day and no other mongooses were seen in the territory).

4.9.3 PARENTAL CARE

After a gestation period of *ca* 62 days, a litter of altricial young were born. These offspring required an intensive period of 22 days of parental care by the adults, during which time the male and female shared the babysitting in order to have sufficient time to forage. Once the young emerged from the burrow, however, the adult female's parental care included only lactation, and the male became the dominant parent. Lactation continued until approximately 5,2 weeks of age. After a further *ca* 3 months accompanying the male foraging, the young left the parental Home burrow system and moved out of the territory.

The amount of time spent by the male and female in babysitting fluctuated each day, but the overall function of providing a babysitter at the HBS throughout the altricial period was achieved. Figure (4.17) shows a time table of the various babysitting periods exercised by the adults at the nursery burrows. If one follows both the hatched (male) and the solid (female) lines for each day, it becomes evident that the young are seldom left un-occupied for long periods. Those periods where an adult does leave the nursery burrows are short and occur when :

(a) an adult leaves to greet the mate;
(b) an adult has been babysitting alone for a long period and forages close to the HBS;
(c) the young are able to remain at the HBS alone for short periods without making a noise, and not requiring food or "lactation comfort" consistently.

In Figure (4.17) & (4.18) the histograms of relative daily activity times spent by the male and female in the activities of babysitting and foraging show the differences in the two patterns. However, the overall balance of investment before weaning is clear (see Table (4.20)), with a female peak occurring during the first few days and again during the second week.

The male peaks in the second week, but maintains a steadier level of parental investment than the female. Female investment in time may appear to be similar to the male, but the actual energy expended can be considered much higher due to lactation. Thus in a balance of investment we have:

FEMALE MALE

Babysitting + lactation <--> approximates <--> babysitting + post-weaned care

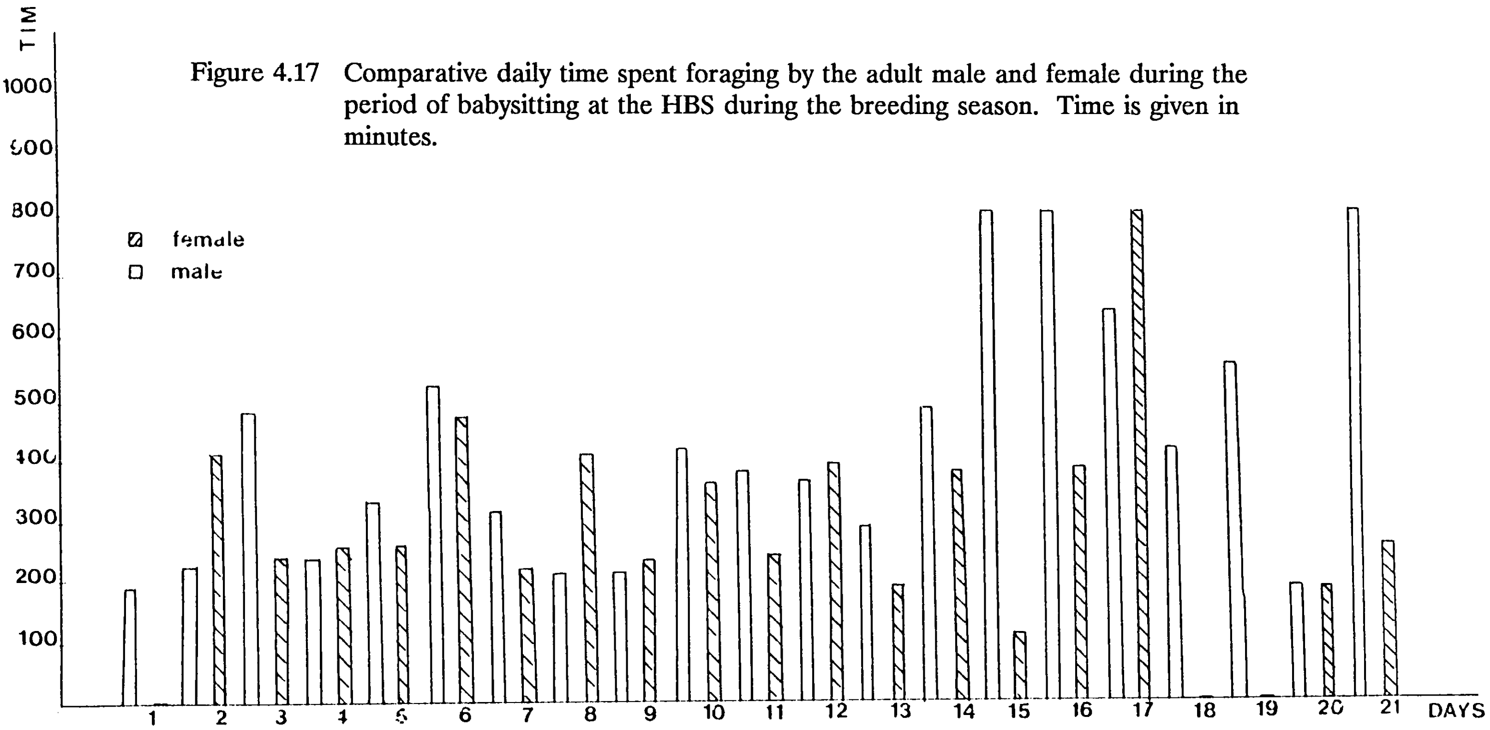


Figure 4.17 Comparative daily time spent foraging by the adult male and female during the period of babysitting at the HBS during the breeding season. Time is given in minutes.

Figure 4.18 Comparative daily time spent babysitting by the adult male and female at the HBS during the altricial phase of the breeding season. Time is given in minutes.

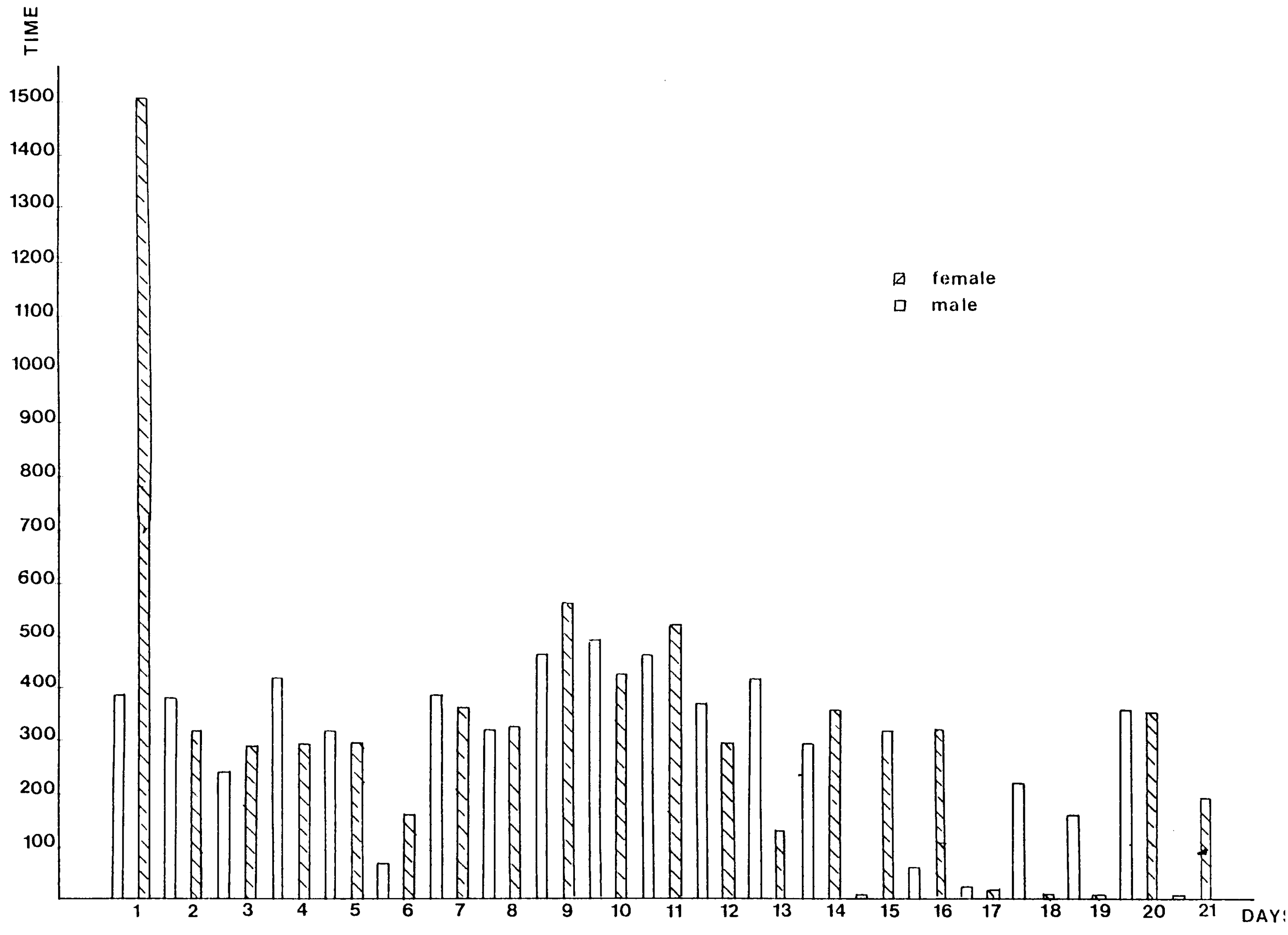
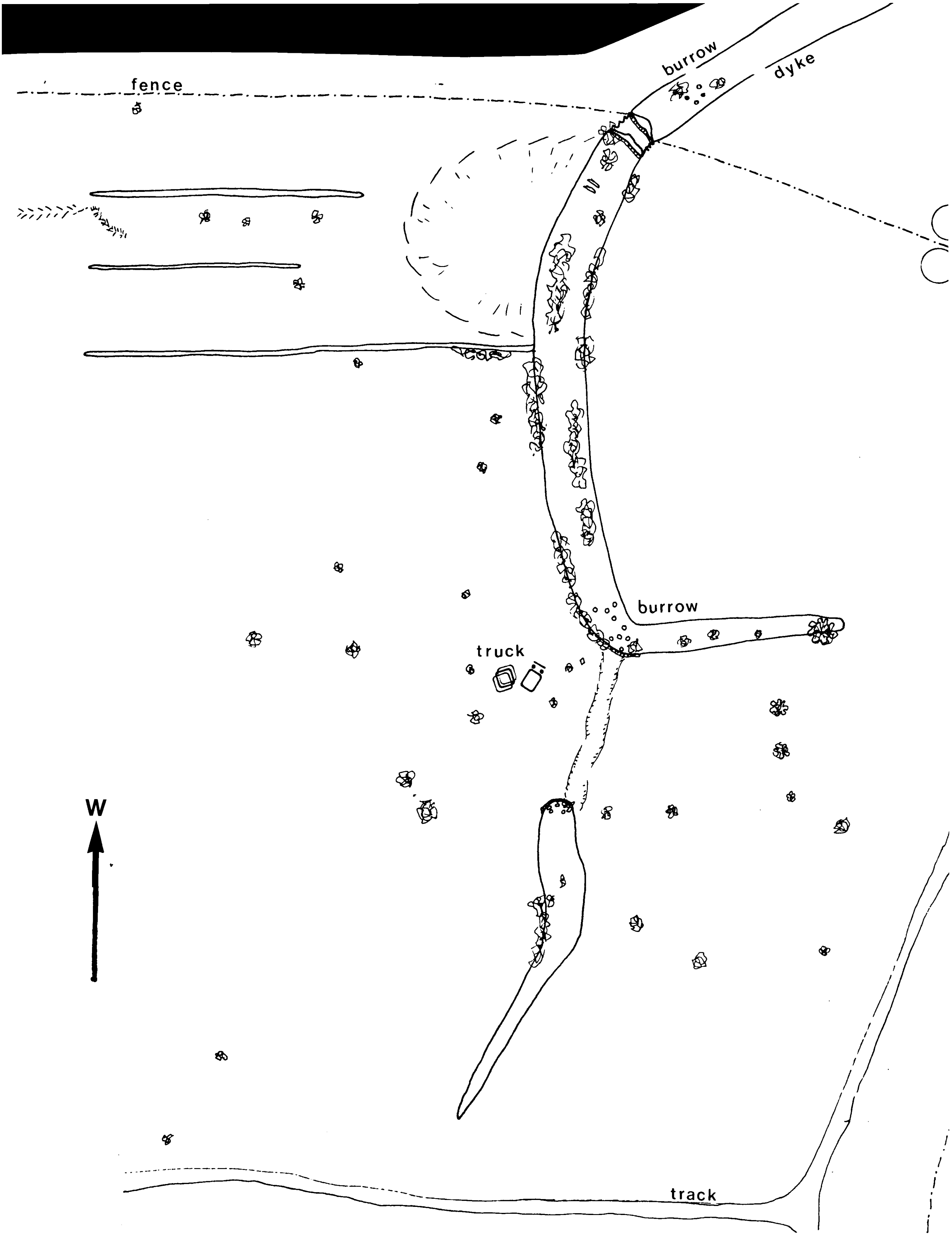


Figure 4.17 shows the relative proportion of each day spent away from the nursery burrows. Note that the time increases towards the end of the altricial phase of development, and that the time invested in foraging by the male and female fluctuates from day to day.

The time invested by the female decreases in the first week, reaching a second peak during the second week. The male investment is fairly consistent. Both male and female decrease their time spent at the HBS at the end of the altricial period, when the young are weaned. At this stage both animals require food to restore invested energy.


fence
burrow
dyke
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truck
W
track

Table 4.19 Male and female parental care, showing the time spent foraging compared to time spent babysitting. The total comparative investment by both animals is shown. The figure given for the total time spent babysitting includes overlapping of the male and female at the burrow system. (The times spent foraging by each animal will thus not add up to the total figure in the right hand column)

DATE	Babysitting time		Total	
	female	male	foraging	babysit
09.10.87	726	382	199	760
10	333	376	650	709
11	295	246	730	541
12	285	422	508	707
13	293	318	590	611
14	167	59	100	226
15	370	386	757	559
16	312	328	607	640
17	567	466	444	103
18	433	484	684	897
19	523	452	624	975
20	298	366	741	664
21	143	414	466	557
22	354	297	849	651
23	323	1	629	324
24	333	61	655	398
25	19	13	784	32
26	9	232	771	241
27	0	163	564	163
28	351	360	377	711
29	187	1	7478	188
Total	6 621	5 827	12 476	10 657

Table 4.20 The mean time periods (minutes) spent babysitting by the adult female and adult male: Time periods are given for the average time spent on each day. On some days the animals only foraged or babysat twice, hence the high standard deviation.

DATE	FORAGING TIME (mins)		BABYSITTING TIME (mins)	
	female	male	female	male
09.10.87	0	66,3 +- 10,7	95,5 +-86,6	2421 +-4151
10	103 +-30,9	79 +-51,4	125,3 +-113	66,6 +-58,4
11	82 +-26	121 +-32	82 +-75,5	147,5 +-176
12	87,6 +-34,4	122,5 +-112	140,6 +-44	95 +-151,6
13	85,3 +-45,7	82,7 +-76,6	106 +-74,5	73,3 +-59,5
14	159 +-80,5	263 +-267	29,5 +-40,3	55,6 +-44,3
15	81,6 +-43,8	157 +-114,5	128,6 +-114	123,3 +-21
16	134,3 +-69,6	51 +-50,5	65,6 +-29,6	104 +-132,8
17	118,5 +-26,2	103,5 +-61,5	155,3 +-225	189 +-21,9
18	72,8 +-61,9	105 +-43,9	96,8 +-144	108,3 +-98
19	62 +- 55,1	94 +-103,2	90,4 +-146	104,6 +-118
20	197 +-52,3	86,7 +-69,9	52,3 +-87,6	59,6 +-32,1
21	61 +- 51,4	70,7 +-71,5	46 +-63,1	35,7 +-45,5
22	93,3 +-63	158,6 +-57,1	49,5 +-41,9	70,8 +-116
23	122 +-0	2057 +- 3457	1 +-1	35 +-30
24	393 +-0	3080 +-4153	30,5 +-41,7	166 +- 231
25	7206 +-	213 +-242,9	4,3 +-2,1	9,5 +-10,6
26	*	83,4 +-89	33,1 +-33,6	4,5 +-4,5
27	*	70,5 +-67,2	40,8 +-50	*
28	98 +-114,5	45,3 +-16,8	40 +- 36,5	70 +-117
29	134 +-104,6	1802 +-3598	1 +-1	26 +-21
TOTAL	+- 9291	+- 8869	+- 1417	+- 4025

Note: * = periods of time when the animal was neither babysitting nor foraging. This behaviour usually included sunbathing, or guarding on top of the home burrow system.

From the data in Table (4.19), the male *Cynictis penicillata* spent on average less time foraging (*ca* 8869 minutes) and more time babysitting (*ca* 4025 minutes) than the female *Cynictis penicillata* (*ca* 9291 minutes and 1417 minutes, respectively)(r = 0,87, p = 0,10). The day the young were born the female spent all her time in the burrow babysitting (726 minutes), whereas the male foraged for 199 minutes.

4.9.4 MALE VS FEMALE PRESENCE AT HBS

Table 4.21 Time spent away from burrows.

	MALE	FEMALE	TOTAL
No of Days	153	106	161
% number of days observed at HBS	95.03 %	65,8 %	100 %

Male *Cynictis penicillata* are more often found at the burrow system than the females. 66% of the females' time is spent at the HBS, whilst the male spends 95% at the HBS. The times spent away may be explained by various factors : foraging; females visiting other male HBS's; reproduction period.

Table 4.22 Parental care and mate care - adult male *Cynictis* penicillata brings food to the home burrow system. N = 22 days.

Day	Time	Food Item	Comment
16	05h10	Frog	Male *Cynictis penicillata* runs in from east carrying frog in mouth. Female greets as he approaches burrow. Enters burrow with frog. Leaves 40 seconds later to go foraging. Female remains in burrow.
17	06h05	Bird - sparrow	Male *Cynictis penicillata* trots to HBS from north east carrying bird. Runs directly into burrow #1. Emerges after 20 seconds without prey. Runs off foraging.
20	15h28	Lizard	Male *Cynictis penicillata* runs to HBS from east with lizard in mouth. Female greets and both run into burrow #2. Both emerge 8 minutes later.

Figure 4.19 The comparative marking routes followed during the breeding and non- breeding seasons. Certain marking routes (A - Red: non breeding season, B - black: breeding season) are followed repeatedly during the breeding period. Foraging maps of the territory utilized by the observed pair of *Cynictis penicillata*. *Cynictis penicillata* covered the territory far more extensively during the breeding season.

The dispersal of *Cynictis penicillata* young occurred at about 5 - 12 months of age, when the young individual appeared fully grown. At this age the juvenile was independent, having accompanied the adult male on foraging trips for the duration of period at the parent HBS. Although reference has been made to the predominance of MALE dispersal in mammals, *Cynictis penicillata* exhibits dispersal in both sexes.

4.10 NURSERY BURROWS

Cynictis penicillata utilizes certain burrows on the home burrow system as nursery burrows. These burrows are used regularly during the babysitting period, but are changed frequently.

Table (4.23) lists the burrows used at the observed HBS, showing the frequency with which they were utilized. Table (4.23) shows the frequency of concurrent occupation. It is evident that Burrow #1 (14 days) was most frequently occupied (63,6 %), followed by Burrow #3 (11 days, 50 %). Both these burrows were also utilized for a maximum of 9 days, during which time, however, other burrows were also used. Burrows #2 and #4 were occupied on 5 occasions each, whilst the remaining 3 nursery burrows were occupied infrequently. Burrows 2 and 4 were also used frequently, and it is these four nursery burrows which provided 85.35 % of the total occupied burrows.

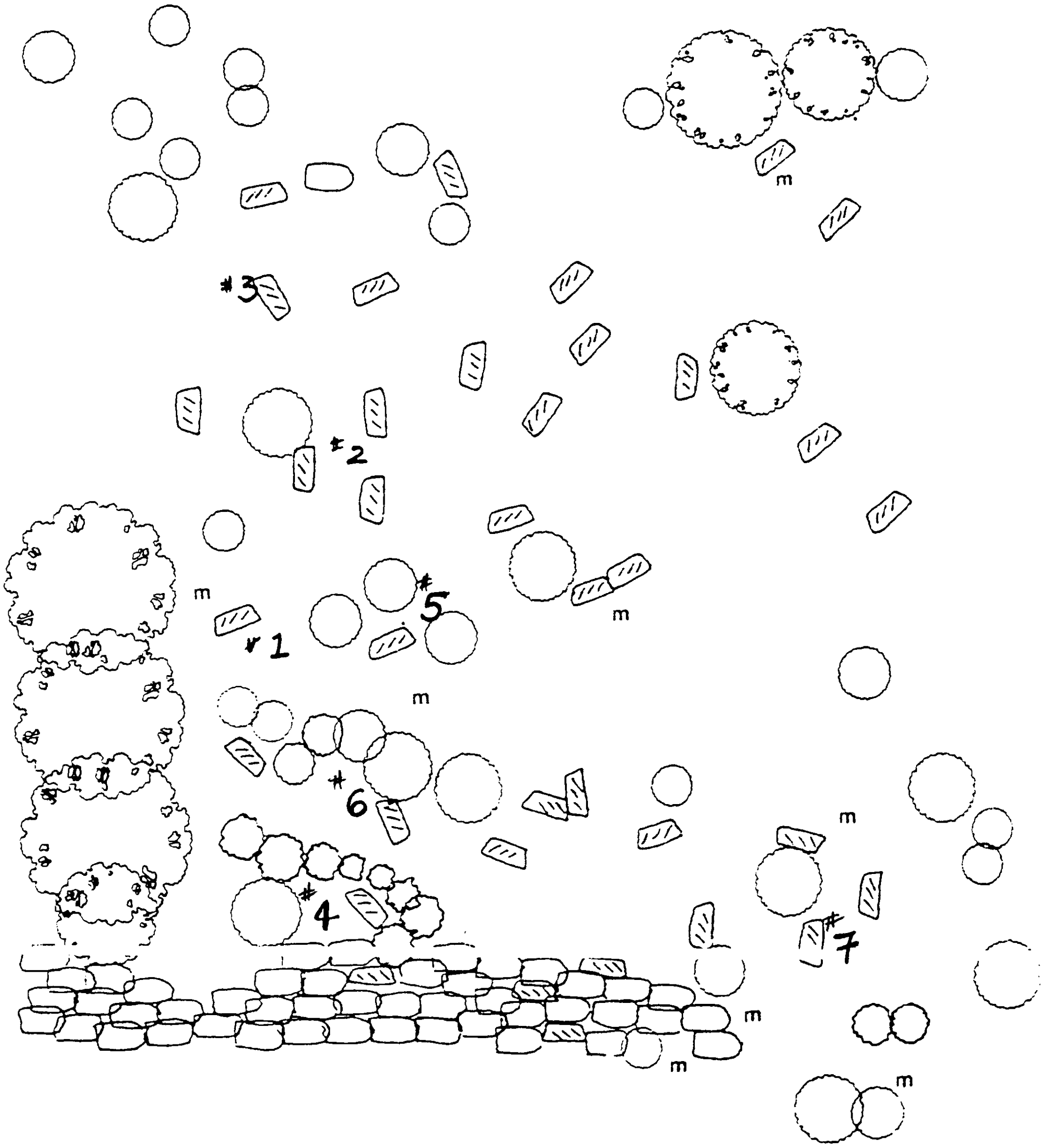
Table 4.23 The frequency of use and occupation of the various nursery burrows by *Cynictis penicillata* during the breeding season. The total number of burrows in the burrow system was 43. *Cynictis penicillata* used more than one burrow on most days. Number of "breeding" days = 22.

Burrow	**Number of days in burrow**	**% of total days N = 22**
# 1	14	63,6 %
# 2	5	22,7 %
# 3	11	50,0 %
# 4	5	22,7 %
# 5	3	13,6 %
# 6	2	9,0 %
# 7	1	4,5 %

Table 4.24 The number of consecutive days during which each of nursery burrows were occupied. The sequence moves from top left to bottom right. Note that the occupation of some of the burrows overlapped, and some of the burrows may have interled into one another underground.

	BURROWS						
	#1	#2	#3	#4	#5	#6	#7
DAYS	8	4	9	4	2	1	1
	1	1	1	1	1	1	*
	2	*	2	*	*	*	*
	3	*	*	*	*	*	*
Total	14	5	11	5	3	2	1

Figure 4.21 Nursery burrows used by *Cynictis penicillata* during the 22 days of babysitting offspring at the Home Burrow System (HBS).



The nursery burrows are situated near, or under, various forms of cover.

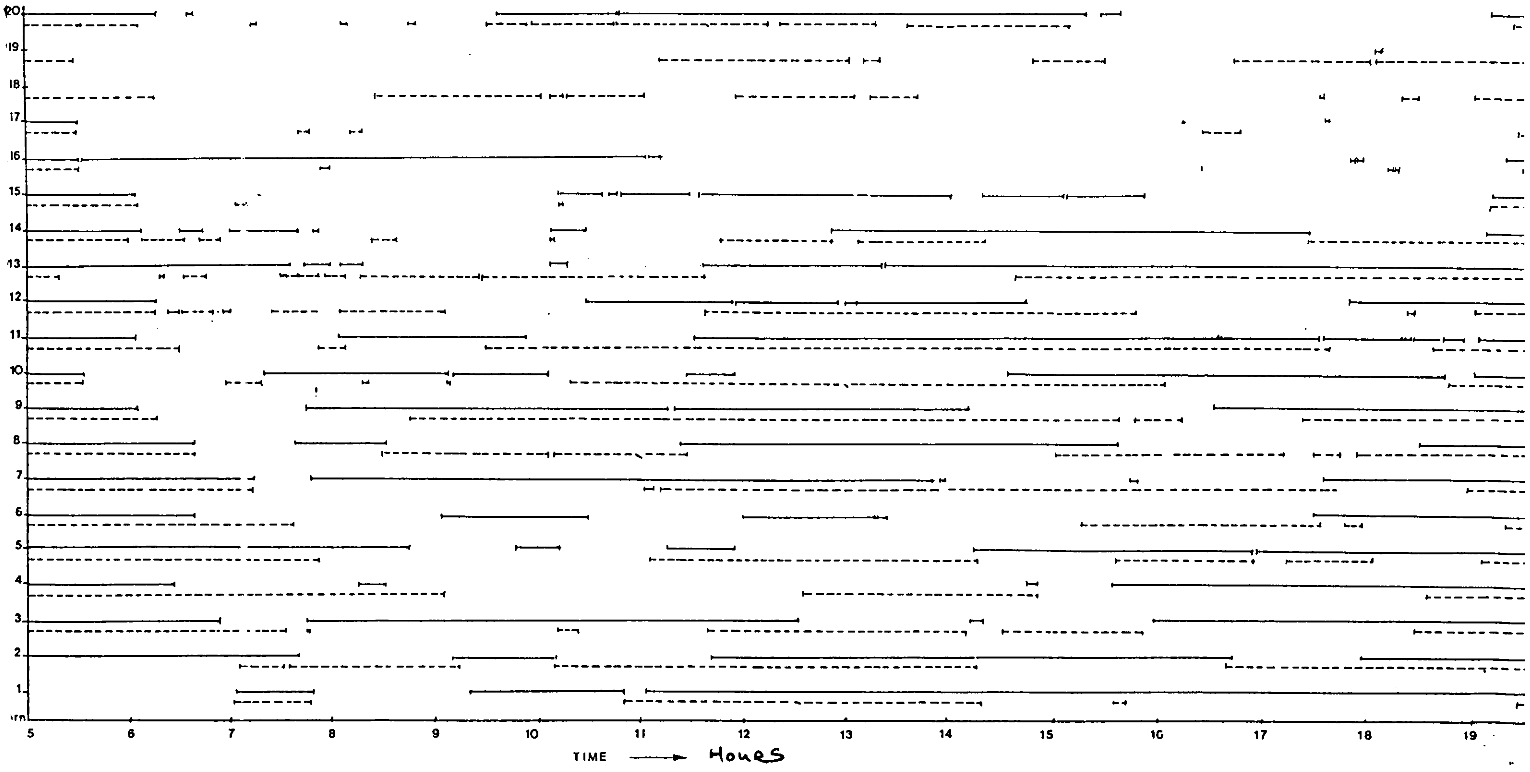
Burrows #1 and #3 were used most frequently and #1 was returned to on the greatest number of occasions. This burrow entrance was well covered by bushes and thus provided:

(i) protection for the adult from predators when exiting the burrow, and

(ii) shade during the hot days for the adults when on the surface of the HBS.

Other burrow entrances were also located near rocks or bushes for shelter. All burrows faced easterly for access to morning sun.

Figure 4.22 Time allocated to babysitting and foraging by the male and female *Cynictis penicillata* during the first 20 days after the birth of the offspring. The "x" axis denotes time in hours, whilst the "y" axis denotes the number of days.



├──────┤ FEMALE } AT BURROW
├ - - - -┤ MALE

┤ ├ (BLANK) FORAGING OR AWAY FROM BURROW

NOTE : EACH DAY EITHER MALE OR FEMALE IS FOUND AT THE BURROW SYSTEM : BABIES NOT OFTEN LEFT ALONE

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The mongooses utilised certain burrows on the Home burrow system as nursery burrows. These burrows were used regularly during the babysitting period, but were changed frequently. Certain burrows were occupied more frequently than others, whilst certain burrows remained un-occupied during the initial 3 week period of parental care. *Cynictis penicillata* male and female appear to share time spent at the Home burrow system with the young, alternating the babysitting function so that there is usually an adult at the HBS with the young ($r = 0{,}79$, $p = 0{,}01$).

Babysitting and foraging could thus be achieved by both members while young were kept safe. e.g. Note that on day 3, 7, 13, and 16 the combined babysitting performed by both male and female accounts for the entire day. The young were only left for very short periods during the first 2 weeks, after which the adults tended to spend an increasing amount of time foraging.

CHAPTER 5

DISCUSSION

5 DISCUSSION

The results presented above have highlighted a number of behavioural and biological features characteristic of *Cynictis penicillata* in the Karoo which may, firstly, be related to the environmental parameters of the Karoo, and, secondly, appear to be determinants of the social structure of this species in this area.

In the Karoo, *Cynictis penicillata* is solitary or pair living for all but 3 or 4 months of the year. During the breeding season the core group at the resident home burrow system (HBS) become increased in size by the addition of offspring. These offspring remain with the group primarily under the parental care of the male, until they are approximately 4 months old. At this stage they disperse and the group size returns to 1 or 2. Thus sociality is partially attributed to by the delayed emigration of the young from the home burrows. The young are unable to attain the weight and maturity needed to fend for themselves as part of a floating population, or big enough to compete for an opening in a vacant territory. Armitage (1981) has found that, in large bodied ground squirrels, complex sociality is associated with delayed emigration of young that are not yet reproductively mature as yearlings and hence remain with the parents until they are. Here the size and maturity of the young (ie, their life-history traits) are instrumental in the social structure and are also responsible for differences in sociality in many species of ground squirrels.

5.1 HOME BURROW SYSTEMS

Distribution and Density

The distribution maps of *Cynictis penicillata*, *S. suricatta* and *Galerella pulverulenta* indicate an estimate of the differences in home range size between these species. Owing to different social composition and structure and different habits, the requirements of each species differs. In the Karoo, *Cynictis penicillata* is solitary or pair-living and thus has lower resource demands than the group-living *S. suricatta* (Smithers 1983). Similarly, *Galerella pulverulenta* is solitary, and nomadic (Smithers 1983).

Although home ranges are smaller, *Cynictis penicillata* occurs with half the density of *S. suricatta* in the Karoo. This factor is due to larger group sizes for *S. suricatta* in relation to home range. The average home range size per *S. suricatta* group is 1 000 hectares whereas that for *Cynictis penicillata* is 250 - 500 ha. *Galerella pulverulenta*, on the other hand, have a density one tenth that of *Cynictis penicillata* and occur in home ranges with an average area of 3 000 ha.

Food and space resources determine the size of the territory by limiting the area required for access to a sufficient resources (Carpenter, 1987). In a comparative study of the diet and distribution of various mongoose species, Du Toit (1980) showed that there is considerable overlap in prey items found in scat analysis, and therefore competition for food. Home ranges range in size (100 - 500 hectares in *Cynictis penicillata*) due to possible differences in availability of food and space resources and topography.

Table 5.1 Comparison of prey selection (percentage occurrence in faeces) by small carnivores in the Mountain Zebra National Park as determined by faecal analysis (after Du Toit, 1980). SM = small mammals; R = reptiles; P = plants; I = insects; B = birds; C = crabs; OI = other invertebrates (worms and centipedes)

Species	SM	R	P	I	B	C	OI	Total
Cynictis penicillata	4	0	10	85	1	0	0	100
Galerella pulverulenta	25	18	10	45	0	1	1	100
S. suricatta	12	25	13	85	0	0	0	100

S. suricatta occupies a large territory whilst being semi-nomadic to accommodate resource renewal (resources are rare during dry periods) in addition to the fact that a large group size logistically requires a larger food resource-base (Rasa, pers. comm.). *Cynictis penicillata*, on the other hand, occupies smaller home ranges due to a lower number of individuals per group and thus would have less immediate impact on resource levels. Feeding competition around the burrows shared by the three species is minimal. Feeding generally occurs away from the burrows except during periods of high food availability, when the abundance of food means less competition. Only when the resource becomes limited is there greater competition (Bekoff et.al., 1981), in this case resulting in larger foraging range. Finally, *Galerella pulverulenta* is nomadic in habit and moves over large distances for food and shelter (Smithers 1983). This species therefore requires a large home range.

Competition for resources may thus be minimized due to the differential distribution of these resources between the different species. Resource renewal should therefore take place and all three species occur together even though they occupy a similar trophic niche (see Chapter 6 on Interspecific Interactions).

5.2 TRADITIONAL HOME RANGE

The manner in which conspecifics within a population distribute themselves within an area is termed social spacing. Social spacing includes a number of different kinds of spacing mechanisms, including the maintenance of core areas, and home ranges. Most research into this field has either concentrated on social spacing as a population phenomenon or experimented on an individual basis. *Cynictis penicillata* experiences a sexual bias in its social spacing, with the male defending a home range smaller than the home range of the female. The size of a home range and/or territory is based on the costs and benefits of resource utilization, and the corresponding ability of the resident individual to defend these. The *Cynictis penicillata* male defends his home range for different reasons and resources to those motivating territoriality or spatial defense by the female.

The male actively defends his home range on a daily basis, utilizing various marking and agonistic behaviours. On the other hand, the female performs far fewer such behaviours (see Appendix A).

Most territorial carnivores show the pattern of territoriality in which a single male defends a large territory which overlaps with one or more female home ranges (Rasa 1986).

Territoriality is an integral part in the breeding behaviour of many species. Because the reproductive success of males is often limited by their access to females, breeding males should behave in such a manner as to maximize their potential resources within their territory in order to optimize the chances of female choice.

In the case of *Cynictis penicillata* where the male spends more time in a specific home range or home range than the femle, changes in food production and limiting resources can have different effects upon the individual male's success in parenting offspring, depending on whether the basis of female choice is abundance of food in the home range or another factor that is positively correlated with home range area (Hixon 1987). The situation with *Cynictis penicillata* becomes complicated by the fact that the female has a home range larger than that of the male, and her home range in fact encompasses a number of male home ranges. This causes an increase in the male competitor densities and makes the female a limiting resource. Here the mating system becomes a function of the number of male territories within each female's home range, which varies with the ratio of female to male home range areas. In this case, the probability of polyandry occurring will increase if food production for both sexes increases with concurrent increases in competitor density, and will decrease if competitor density for both sexes increases with concurrent increases in feeding efficiency (Hixon 1987).

Despite the influence the female has on the territorial defense mechanisms and territorial size of the male, *Cynictis penicillata* females are less intense in their defense of the home range, and hence the term home-range applied to this case. The female exhibits seasonal variance in the degree of territorial behaviour, generally showing a greater degree during the breeding season when she becomes sedentary at a single burrow system for the duration of raising of the young. Carpenter (1987) has shown that animals often abandon territorial defense when food is abundant, although the causes of this behaviour are controversial. This fluctuation may be related to any variance in a defendable resource. However, sometimes the cessation of defense is attributed to the increased availability of food, thus nullifying the benefits a monopolizing animal would gain from defending such resources. Thus below a certain level of food production, when food is abundant in an area, or similarly when not in the breeding season of the year, a threshold is reached where it is not necessary to defend a home range. The reasons for relinquishing the uneconomical demands of home range defense for, or reducing levels of territorial defense, at certain times may be energy or predation related.

Carpenter (1987) indicates that the defense behaviour required for territoriality reduces an animal's alertness to predators and may make it vulnerable to intruders. Thus, animals should be selected to "have the capacity to access resource availability and the costs of various territorial and foraging strategies, and to behave flexibly in response to changing net benefits."

- **Function of the home burrow system**

The home burrow system (HBS) utilised by *Cynictis penicillata* is a major part of its biology. In addition to providing members of a group with a protective shelter, it functions as a vital centre for home range (or territory) maintenance and the marking sites as an information centre for conspecifics.

The individuals occupying a HBS require a certain amount of shelter from climatic variables and protection from predators. Each HBS is constructed from earth and/or rocks, has a number of narrow burrow entrances, are situated at an elevation above the surrounding area and are generally orientated towards the rising sun. In this way the HBS's provide a protective function. The requirements would include both subterranean and surface cover, thus including such features as burrows, bushes, rocks and other natural or man-made constructs which may provide a vantage point for defence.

Many small carnivore species and other small mammals utilize burrow systems on a regular basis, the function of the burrows often being collective (e.g. Dwarf mongoose, Rasa 1977; *M.mungos*, Simpson 1964; *Genetta*, Smithers 1983). *Cynictis penicillata* uses its burrows for numerous functions:

- burrows are used for sleeping in;
- to escape from predators;
- raising young and protection of offspring from predators takes place in burrow systems;
- shelter from extremes of temperature and other climatic elements by remaining in the protective microclimate of a burrow system ie, they are occupied for short or long periods during aestivation, torpor and hibernation.
- possible information centre for conspecifics.

Burrows also have other functions, as seen for other species:

- burrows often provide a larder function for animals storing food reserves for periods of food resource depletion. This function is generally found in graniverous species (e.g. Chipmunks store food in burrows to help see them through the winter (Mares & Lacher 1987)).

- **Distribution and density of home burrow systems**

Spatial distribution of the HBS differs in various regions of the study area. A high concentration occurs in the Northern areas of the farm, whereas the Southern areas tend to have fewer HBSs. The population density in the North is also somewhat higher which may be attributable to the differences in geology and topography. The choice of HBS site is obviously dependent on a number of factors, amongst these being the availability of suitable sites and substrates and also predator pressure. Many raptor species were identified in the area of the observation site. The predators provide a constant threat to mongooses which require cover for protection.

The distance between burrow systems appears large, but *Cynictis penicillata* utilises the dense Karoo scrubland vegetation for cover from certain predators (e.g. raptors). The daily distances covered whilst foraging and marking the home range are relatively large, and *Cynictis penicillata* has to utilise burrows and topographical features for cover from predators (pers. obs.).

Nearest neighbour distances of the HBS's is not a constraint in the movements of individuals across the apparent boundaries of the home range, as males enter adjacent home ranges for marking and the females have access to larger home ranges than the males and utilize more HBSs over a greater area.

- **Site parameters of home burrow system**

Size

The size of the HBS varies within a home range. The larger burrow systems function as the home range centres, the sites for raising young and for sleeping in, whilst the smaller systems are occupied predominantly on foraging and marking excursions. The HBSs are often co-occupied by other species of mongoose.

Larger burrow systems, and those sites covered with much vegetation and rocks have a higher number and density of burrow entrances. In addition, burrow systems with more entrances show a higher density of middens.

All burrow systems were located above ground level. Elevation of the burrow systems serves two purposes: a vantage point from which predators can be seen during the periods spent at the burrow system; and during heavy rainfall (which may occur sporadically in the Karoo) the burrows are not easily flooded.

Aspect

Most of the burrows have an easterly aspect, which suggests here that sunrise influences site choice. The relationship between temperature, time of sunrise and the initiation of daily activity patterns has been discussed above, and is supported by the results given above.

Substrates

Both man-made (for example erosion dykes, dam walls, berms) and natural geomorphological features are utilised for burrow sites. Sites are found in sand, rock and gravel. Sand, however, which is relatively easily excavated, comprises the substrate of most sites. Numerous burrows are found in rocky outcrops, although the number is considerably less than those in sand. Rocky outcrops provide an elevated advantage for detection of predators, and often require little excavation. Rocks often have little holes and gaps which are used, as well as providing good cover from predators.

The shapes/form taken by the burrows vary, and are dependent on the substrate used : berms and walls result in longer or rectangular shaped HBS's, whilst naturally occurring substrates tend to be smaller and more varied. There is no correlation between different shapes and any other factors, although the aspect of the HBS was enhanced by a larger east facing side.

• **Middens - Marking at the home burrow system**

Most natural objects on the HBS are marked by the mongooses. These objects may be cheek or anal marked, and appear to serve as information centres for group members, conspecifics and other mongoose species utilizing the burrows. Of these marking posts, bushes are most frequently marked, whilst rocks, sandy mounds and burrow entrances less often.

Middens are widely used in carnivore species (Macdonald 1979). Generally speaking, a midden is and efficient means of dissemination of information about the inhabitants of an area. It has been demonstrated in *Herpestes auropunctatus* (Gorman 1976) and in *Herpestes ichneumon* (Heftz et.al. 1984) that individual recognition of conspecifics takes place through anal gland secretions. Rasa (1973) has also shown this function of faeces in *Helogale rufula*, and that the identifying secretion (pheromone ?) persists for short periods only. The length of time given to effectiveness of the pheremones stipulates that the middens are used regularly in order to renew identifying marks in an area.

Recent work by Apps et al (1991) shows that the anal gland secretion of *Cynictis penicillata* comprises 22 components. The products of these glands are employed in scent marking and allomarking. It was also shown that there is a difference between the anal secretion composition between males and females, although the sample size was too small for a definite conclusion. These differences may only be due to individual variation, but nevertheless indicate the occurrence of individuality and identity between animals by means of using chemical secretions.

In the use of middens - or a central elimination place - it is important to determine whether the site is chosen and reutilized

(i) because of other excretory products making it attractive

(ii) because of the position of the site of the midden.

Rasa (1973) has shown that dwarf mongooses are influenced both by site and the presence of elimination products at a site in their choice of defecation area, but found that the presence of faeces and urine have the greatest effect on this choice. She notes that the influence of position is short-lived and is only effective within the first 24 hours, suggesting that a learning factor is involved in changing to the new site where the stronger influencing factor of faeces and urine is involved.

The presence of the midden on the HBS, which carries the odours and secretions of the individuals occupying the burrows may provide assurance for the animals. These middens may thus serve a multiple purpose in message content (Rasa 1973) :

a) recognition and identity for resident occupants of the HBS;
b) to inform intruders that the HBS is occupied by other individuals;
c) the marking may also serve as a bonding mechanism in a similar sense to the function of allomarking between individuals of a group.

Mustelids, which are also solitary animals, convey dominance by increased marking intensity (Erling et. al., 1982). In this species, and as shown later by Baker (1988) in the Water mongoose, the dominance of the pair during the breeding season became reversed as the female approached readiness to copulate. Initially the male was dominant whilst the female exhibited avoidance and escape behaviour. In response to the increased intensity of the male marking the HBS and surrounding areas, the female responded by similarly increasing her marking frequency and changing her behaviour.

The average marking frequency of males and females was significantly different, with the males marking more than the females. This sexual dimorphism in the marking behaviour of the yellow mongoose is also demonstrated in the water mongoose (Baker 1988), where the female marks significantly more than the male; the dwarf mongoose (Rasa 1973a); and other carnivore species. The dimorphism occurs particularly in anal marking behaviour, and with other marking mechanisms during the breeding season. In addition to possibly changing the female's receptivity, the divergence in marking behaviour in the male can be related to territoriality in the male, and his defense of the female as a scarce resource. The male defends a fixed home range or territory which he marks regularly whereas the female's home range is less defined. However, it has been noted by Barrette and Diamond (1976) that to assess direct relationships between marking and territorial behaviour is of limited value as marking displays may simply be an expression of sexual and reproductive status, or of familiarizing an animal with its environment.

• Nomadic or sedentary characteristics *Cynictis penicillata*

Cynictis penicillata is essentially a sedentary species. The dominant adult male remains resident at a single HBS for long periods of time: i.e. for at least the duration of an entire season, or year. The male occupies this HBS on a daily basis and leaves the burrows for foraging and territorial activities within a fixed territory. These activities were observed throughout the year.

The female adult *Cynictis penicillata*, on the other hand, appears to be a semi-nomadic individual, occupies two or three home ranges within which she moves from one HBS to another, depending on the season and time of year. The female will tend to spend 2 or 3 days at each burrow system with the resident males. In particular, the female will remained "sedentary" at the HBS for the duration of the breeding season, at which time the pair - bond between the adult male and female was established or strengthened. This situation occurs despite obvious promiscuity in the female and the possibility that the offspring may be parented by a male other than the resident male.

Observations made at the HBS over a long period of time (9 months) indicated that *Cynictis penicillata* does not occupy the same area or the same burrows of the HBS for long stretches at a time. The mongooses will move from one burrow to another after a few days ($\bar{x}$ = 4 days, s = +- 1.2, n = 260), remaining, however, within the HBS as a whole. This localized nomadism amongst the 36 burrows present in a HBS. The function of this movement is thought to be related to the parasite/pest loads within the burrow systems. *Cynictis penicillata* has a extremely high incidence of external parasites and if they remained in one burrow for more than a few days the parasite load would become intense. For this reason they circulate through the different burrows thus providing "fresh" burrows which would contain fewer parasites than those just occupied. Parasites do not remain in an area where there is no host species available, and thus move away or die. After a few days, therefore, the burrows are relatively parasite free and newly available for use by *Cynictis penicillata* (Rasa pers comm.).

The occurrence of localized nomadism in *Cynictis penicillata* during the breeding season may also be a direct anti-predator behavioural mechanism executed to move the young from potential predators which may learn the location of the occupied nursery burrows. The threat of intruders and predators into the burrow system is extremely evident from predation data, and the young are extremely susceptible to predation from within the burrow system. If they remain in one location for more than a few days, this site may become evident to predators, and thus they become vulnerable to attack. If, on the other hand, *Cynictis penicillata* moves around to different burrows it may reduce the chance of the predator knowing which burrow is occupied, and hence reduces the threat posed. This behavioural mechanism is surmised.

Finally, localized movements from one burrow to another, in *Cynictis penicillata*, may be related to hygiene within the burrow system. *Cynictis penicillata* defecate outside the burrow although faeces fall into the burrow entrances because the middens are often situated at or near the entrances. Living in the confined spaces of the burrow would account for the accumulation of waste material (e.g. excreta). Regular burrow changes would decrease this accumulation, and also allow for natural decomposition and diffusion of waste matter to take place.

Cynictis penicillata may utilise one HBS for the following reasons: the availability of food; the limited number of suitable sites for HBS; the high energy expenditure required in the construction and maintenance of the HBS (more than one may be too energetically expensive); and the requisition of a stable and defined territory for the raising of young.

FORAGING BEHAVIOUR

Cynictis penicillata forages alone but can be found foraging in pairs or in groups of three or four individuals. The pair or group is generally made up of adult/s + juveniles. The individuals in the group usually forage independently, but have been seen to participate co-operatively in food acquisition.

Where food (duck and chicken eggs, chicks, waste material etc...) was more freely available compared to the surrounding environment, there was localized variance in the hunting pattern due to local variants and concentrations in the food source. Under such circumstances, *Cynictis penicillata* may forage co-operatively.

Du Toit (1980) reports that on two occasions a pair of mongooses were seen foraging among a flock of Crowned Guineafowl, *Numida meleagris*, with no interspecific interaction. Both species were eating termites. This suggests that the local abundance of food prevented any competition between the two *Cynictis penicillata* nor between *Cynictis penicillata* and the birds. Similar mechanisms must work when *Cynictis penicillata* forages with *S. suricatta*: both species feed off the same or similar resources, and it would seem likely that only in situations of resource abundance would they tolerate each other's presence during feeding (see chapter 6 for interspecific interactions).

ACTIVITY PATTERNS

Various factors appear to influence *Cynictis penicillata* activity patterns:

The time of sunrise may be linked to the differences in availability of food during the different seasons, as well as the activity patterns of their prey i.e. *Cynictis penicillata* cannot hunt for prey that is not active or exposed.

Cynictis penicillata is small and the wind appears to have no influence at ground level due to dense vegetation. *Cynictis penicillata* was more active in areas where vegetation cover was fairly dense than in sparsely vegetated areas.

An abundance of fruits and insects is available at the onset of the rains in spring and autumn. Rain affects *Cynictis penicillata* activities and the animals remain under cover until the rain has stopped. They appear to have an aversion to getting wet, but after long periods of continuous rain (e.g. 1.5 days) will make short foraging trips.

The mean time spent at the burrow system in the mornings prior to foraging decreased from winter through summer. Thus the time at which *Cynictis penicillata* left the burrow system to begin foraging decreased - becoming earlier in summer than in winter. This was evident in both emergence times and times of departure from the burrow system.

There are strong relationships between *Cynictis penicillata* emergence and foraging times with temperature and time of sunrise. This would suggest that *Cynictis penicillata* activity is influenced by temperature, this is particularly evident in winter when many hours are spent sunbathing before foraging.

PREDATION AND ANTI-PREDATOR BEHAVIOUR

The avoidance of predators is essential for both individual survival and the survival of a group, and vigilance is proposed as being adaptive (Ferguson 1991). Vigilance may also be instrumental in evolution as a mechanism of selection. However, it has been argued by Pulliam (1975) and Treisman (1975) that vigilance systems may be inefficient due to increased probability of false alarms and/or reduced feeding time. In this case it may be more efficient for solitary vigilance. However, Pulliam (1974) has shown that individual starlings in captive groups perform less individual vigilance and obtain better food resources than solitary individuals, thus indicating that it is often more efficient to partake in group vigilance than to be solitary. This poses an interesting question in the case of *Cynictis penicillata*, which is essentially a solitary or pair-living animal.

Rasa (1987) reports that in the majority of mammal species studied to date, vigilance is an advantage of group living, where the group structure has evolved in association with factors such as reproductive efficiency, territorial defense and predator avoidance. In such cases vigilance evolves as a task shared between relatives or mates so that the feeding efficiency and resultant protection of the group increases as a whole (Rasa 1987).

The majority of cases where vigilance systems have evolved, and, in particular, become highly coordinated are those where environmental pressures have selected for this. Mongooses are particularly eligible for an efficient vigilance system due to the high predation experienced and foraging techniques which inhibit maximum predator detection. Rasa (1987) has shown that group protection efficiency in the dwarf mongoose is the major factor contributing to the reduction in mortality, thus increasing the inclusive fitness of a dwarf mongoose group.

The need for safety may inhibit other behavioural drives: a hungry animal may abandon a food source to avoid a predator. But the reverse is also true: the same animal may choose to spend time in competitive activities such as feeding, resting and mating rather than in vigilance. The formation of groups will increase security for each individual as the probability of being detected by a predator increases (Treisman 1975). Here, division of labour occurs within a group, and, as may be the case in *Cynictis penicillata*, this division of labour may be intraspecific (Wenhold 1991) or interspecific. This division of labour frees some of the members for other activities. The incidence of co- operative interspecific vigilance has been recorded for starlings and blackbirds (Powell 1974) and for baboons and impalas (Washburn & De Vroe 1961), although as Leuthold (1977) points out, in such cases secondary gains may also be enjoyed.

Recent work argues that anti-predator behaviour might best be understood in terms of the relationship between potential predator and potential prey (Loughry 1987a). Loughry (1988) suggests that one possible description of this from a prey species's point of view is vulnerability, where vulnerability has at least two components: personal and reproductive vulnerability. Reproductive vulnerability in this case refers to the value at stake in dealing with a potential predator and personal vulnerability refers to the cost of being the target of a particular predator, and the context of the encounter (Loughry 1988).

Another possible influence on the anti-predator behaviour of an individual with its predator is the population's history with a predator. Loughry (1988) found that prairie dogs having different experience with different predators behave differently when confronted with a potentially dangerous predator. In addition, the age, sex and parental status of the prairie dogs; the time of year; and the type of encounter affected the anti-predator behaviour exhibited.

Rasa (1986) has found that species group size is associated with the efficiency of the vigilance system and defense against predators. Only groups comprising five or more individuals over one year old and where sufficient animals are available to maintain an efficient vigilance system are capable of surviving reproductively.

Thus many factors are involved in individual and group survival when considering anti-predatory behaviour. Predator avoidance is a basic need for the survival of many animals (Ferguson 1991).

6 COOPERATIVE BEHAVIOUR AND DIVISION OF LABOUR

Division of labour occurs in social species. It is particularly advantageous in groups where there may be provision of food to group members, cooperative care of the young, protection of the group from predators and intruding conspecifics, and in a vigilance system (Rasa 1979). *Cynictis penicillata* is found to be both social and solitary through its geographical range. Wenhold (1990) found that where *Cynictis penicillata* is found to be social, division of labour occurs. The following section investigates the occurrence of division of labour in *Cynictis penicillata* in the Karoo.

7 VIGILANCE

Vigilance for predators benefits animals because it reduces the chance of being preyed upon, but it is costly in that it makes time away from or interrupts other important but incompatible activities like feeding (Cords 1990). Pulliam and Caraco (1984) point out that one of the main functions of sociality in animals is that members of a group can decrease the risks of being preyed upon without increasing the cost of being vigilant. How this theory applies specifically to *Cynictis* *penicillata*, will be discussed in further detail in Chapter 6. However, it is pertinent to note that the advantages of shared vigilance include earlier detection of the predator, interference with its attack through confusion or active defense, hiding behind other victims, and dilution of its effect.

Cynictis penicillata possesses a degree of co-operative behaviour exhibited primarily in parental care and in vigilance behaviour. *Cynictis penicillata* may not be classified as a social species in the Karoo, however, as it is predominantly found alone or in pairs when not accompanied by the current season's offspring. *Cynictis penicillata* shows various co-operative behaviours because the male and female differ in their behaviour with regards to the young i.e. when baby-sitting when the young are still altricial, in parental care, and in group foraging.

In addition, the amount of vigilance activity exhibited by the parents is lower when the subordinate animal is at the burrow system (see Chapter 6). An hierarchical division of labour is therefore evident.

Depending on the degree of sociality of the species, division of labour may occur to different extents. For example, in the Dwarf mongoose (Rasa 1977) a complex system of group cooperation and division of labour is present. Various members of the group serve different functions in an integrated group life. High ranking males and non-breeding females will perform babysitting and care of the young, whilst group protection involves different group members under different circumstances.

Increasing group size, even if only temporarily or at specific times of the year when predation threat is highest (e.g. prior to the young dispersing from the parental burrow system) can decrease the costs of vigilance without exposing animals to higher predation risks (Cords 1990). By sharing the job of being watchful, individuals can devote less time to vigilance or interrupt their other activities less often.

In the banded mongoose, *Mungos mungo* (Rood 1974) and *Suricata suricatta* (Ewer 1983, Macdonald 1980, Waser 1983) a similar, less structured, system of division of labour is found. Many social, or gregarious species, however, have developed a co-operative group existence where there is substitution of roles and sharing of group "commitments" for the benefit of group members or conspecifics. This may involve similar functions to those described, such as vigilance, care of the young and food resources. The breeding female wolf (Zimen 1976) is brought food by other group (pack) members whilst caring for the young. Young brown hyaena, on the other hand, are raised in a communal den where they are nursed and fed by clan females (Smithers 1983) and fed by males (Mills 1990). Certain cases of communal or group co-operation may draw contention in definition, as they are not correctly included in "division of labour". Rasa (1977) suggests that group organisation through division of labour ensures that individuals of varying status within the group (young and dominants) are protected to some extent by the stronger, experienced and perhaps (often) more expendable members of the group. Thus division of labour or group co-operation are a major advantage of sociality.

5.8 REPRODUCTION

The onset of oestrus and the subsequent courtship and copulation in *Cynictis penicillata* occurred in mid August with the birth of the young in mid October. Prior to weaning, the young of the first litter under observation were killed by a predator (*Galerella pulverulenta*) after which the female went into oestrus for a second time and was re-mated. During the second oestrus the female was mated by more than one male although she remained at the main burrow system. Rasa et.al. (1992) report that a second oestrus period occurs after the birth of the first litter in *Cynictis penicillata* throughout the geographical range (Transvaal, Etosha, Kalahari) and is not subsequent to weaning. Rasa et. el. (1992) concludes that *Cynictis penicillata* appears to be polyoestrus. Thus it appears that the second oestrus period evident in the Karoo after the death of the first litter may be an example of the polyoestrus which was recorded at other locations and may have occurred regardless of the death of the first litter.

A possible biological explanation for the small litter size and the rapid production of a subsequent litter may be a reproductive strategy to maximize juvenile survival (Rasa et. al. 1992).

Cynictis penicillata is unique among viverrids in that it is the only species recorded to bring large prey items (rodents, frogs, birds) to the young while they are still in the burrow. This behaviour is more typical of canids and social felids, eg *Panthera leo* (MacDonald 1983). Study of other viverrids have shown that young are not fed at the burrow and must accompany the adults foraging at approximately 4 weeks old. In contrast, *Cynictis penicillata* young only accompany the adults when approximately eight weeks old. Rasa et. al. (1992) suggest that by extending the period the young can remain in the den by feeding them there, the predator spectrum as well as the predation rate on the juveniles can be reduced and hence the juvenile survival is increased.

The breeding system observed in *Cynictis penicillata* thus appears to be a unique breeding strategy for viverrids. This species has evolved the production of small, relatively sedentary, litters which are generally followed by a subsequent litter. This can be considered a means of coping with environmental constraints such a fluctuating food supply and protection against predators (Rasa et. al. 1992). By adopting this strategy, the necessary high level of nutritional investment in the young is spread over a longer period, the young remain at the burrow longer and thereby reducing predator pressure. Predation at the HBS can, however, be very high (Richardson pers comm).

5.8.1 PARENTAL CARE

The data and parental behaviour described above have been only been recorded for *Cynictis penicillata* found in the Karoo. Due to the small group size (2 - 3 individuals) found in the Karoo a system of care for the young which is different from *Cynictis penicillata* found elsewhere in its geographical range has evolved. All group members usually aid in caring for the young. The females play the predominant role in guarding the young at the burrow, whilst the male are primarily involved in provisioning the off-spring.

Parental care by both parents is intensive. After weaning, the young are reared predominantly by the male thus removing the necessity for division of labour within a group situation for babysitters. The young develop rapidly, requiring a relatively short period of post-natal care compared to other carnivore species. In addition, the parents are able to leave the young at the nursery burrow for short periods of time without the young leaving or making a noise which would attract predators. Here again sociality is not selected for due to the adequacy of the existing system. Intraspecific competition may again play an important role in selecting for a solitary social structure.

Paternal care

The male *Cynictis penicillata* spends (89 %) of his total babysitting time in the HBS. On emergence from the nursery burrow, the male shows "lactation" marks on the underside of the belly, indicating that the young have attached themselves to the male's fur with their mouths as they would to the female's teats in suckling. This phenomenon has been observed in the Dwarf mongoose (Rasa pers. comm.), but is unrecorded in the literature. The proposed function of this behaviour is that by attaching themselves to the fur on the male's belly, the young are comforted and kept silent in the absence of the female from the burrow. In addition, the close contact with the male provides warmth to the young and may serve in establishing a parental-offspring bond between the male and the young. This aspect of paternal care is extremely pertinent, as the male maintains the high level of parental investment after the young emerge from the burrow, and is essentially responsible for their rearing until they leave the home range. The strength of the bond is therefore important in establishing a relationship between the father and the offspring that will allow for successful learning development in the period between weaning and dispersal.

The female shows little parental care after the young have been weaned.

The Herpestinae show a great variety of parental care systems. They are generally all solitary hunters and gatherers, even though many species live in groups (Rasa 1986). Mongoose prey is usually small and there is no co-operative hunting, with each individual hunting for itself. The solitary nocturnal Herpestinae retain the typical carnivore parental care pattern although the prey is not carried to the young at the nursery but may be shared when they begin to accompany the mother foraging. *Cynictis penicillata* young, however, accompany the father (or resident male) and the female becomes relatively independent of the young and male soon after the young become mobile and old enough to leave the burrow system.

Rasa (1986) reports that mongoose young, in contrast to most other carnivore species, are very vocal and active from birth onwards. When body contact is not maintained the young are insecure and emit continual vocalizations and may move about: both of which behaviours would attract predators. It is therefore necessary for at least one of the adults to remain with the young at the nursery during the period prior to them accompanying the adults when foraging. It becomes necessary, therefore, in *Cynictis penicillata*, which has been shown here to be solitary or pair- living species, for the male to participate actively in parental care and to spend time at the burrow system with the young. The mother is lactating and hence has a high energy requirement, needing time to hunt and collect food to sustain these energetic demands.

A high degree of co-operation takes place in the parental care behaviour of *Cynictis penicillata*. On three occasions *Cynictis penicillata* was seen bringing prey items, for example a frog, lizard and bird, to the burrow system during the latter phase of the babysitting period (after day 16). These various prey items were brought to the HBS after which the animal left immediately. The short time between arrival of the male at the burrow with the food and his leaving to resume foraging activities was an average of 40 seconds: it can be assumed that the prey could not have been eaten by that individual (generally the male) during this short period of time and therefore the food item must have been left with the female and/or the young. *Cynictis penicillata* is the only species of viverrid where the adult animal (parents) bring food to the young (Rasa pers.comm). This is the first record of such behaviour in viverrids.

In many aspects of parental care, *Cynictis penicillata* can be more typically associated with the canids. Here the male in a pair-bond is primarily responsible for bringing food to the mate and the offspring at the home burrow system, thus reducing the pressure on the female to provide food.

Foraging activities during the babysitting period are intense due to the necessity to obtain food items as quickly as possible so that the animal can return to the nursery burrows. The routes followed allow *Cynictis penicillata* to mark the entire home range regularly and to thus ward off invading individuals and other species. The intense marking that takes place appears to be recognised by conspecifics and *Suricata* because during the initial period of raising the offspring no other individuals were present at the HBS.

Biparental care is widespread among the generally monogamous birds (Lack 1968), yet there may be differences in the optimal level of investment for each partner (Wright & Innes 1989; Trivers 1972). This kind of parental investment where males play an important role is uncommon among mammals, however, and may have evolved because (i) the males have a relative certainty of paternity in *Cynictis penicillata* due to the close association with the female during the height of oestrus; (ii) two parents are necessary to raise the young due to the harsh ecological conditions of the Karoo (scarce food and space resources); and (iii) both male and female parents may remain close to the young due to the limited home ranges available and the fact that the male is forced to stay at the burrow system and therefore may as well help (Williams 1975).

The level of investment by each partner may be influenced by many factors (parent offspring relatedness, age and number of offspring, condition of parents and offspring, time of season). The optimal response to a reduction in the investment by one partner is for the other to increase effort (Wright & Cuthill 1989) so that an optimum balance is achieved. This optimum may fluctuate with the prevailing ecological conditions. I also suggest that if the female comes into oestrus again whilst still lactating the investment in parental care by the male will increase proportional to the energy demands required by the female as she enters the second term of gestation.

Parental investment may be defined as any investment or expenditure on a given offspring that reduces a parent's capacity to produce future offspring. The notion conveyed here is that if a parent invests care and provisioning in an particular offspring this improves the viability and reproductive success of the offspring, but reduces the number of future offspring that can be generated because the parent has a limited total reproductive effort. The relative parental investment of each sex in a given species is important in determining the intensity of intrasexual competition. Males of most species show less parental investment than females; often male parental investment is virtually nil. Thus the theoretical maximum of a male is far higher than that of a female, and intense competition is likely to occur between males over females (Triver et al 1972).

Paternal care in the monogamous swallow, *Hirundo rustica*, measured in terms of frequency of feeding young, was positively related to the certainty of paternity (Moller 1988). Here male parental care increased with the absolute number of pair copulations and decreased with the absolute and relative number of extra-pair copulations by his mate.

In swallows (Moller 1988) female parental care is inversely related to that of male parental care, and parents appear to adjust their contribution to that of their mate, perhaps as a response to the cues given by the offspring.

The suggested benefits of extra-pair copulations may be that the female benefits from copulating with already males of higher quality which have already copulated. A second is that females obtain "helpers" to feed their young by engaging in extra-pair copulations. A third reason may be to avoid infanticide (Crook & Shields 1985; Trivers 1972). Fourthly, females may benefit from these copulations by increasing the chance of fertilization.

5.8.2 DISPERSAL OF YOUNG

The young *Cynictis penicillata* disperse from the adult burrow system three to twelve months after weaning. The variation in age was seen throughout the farm Biesjesfontein where subordinate individuals accompanied the adults for various periods of time. The reasons for this variance in ages of dispersal have been considered by Barash (1974), who suggests that when conditions are severe increased sociality or delayed dispersal will make local population control easier and will decrease the competition for home ranges and/or mates. On the other hand, during favourable conditions (e.g food abundance) the dispersal will be sooner.

Loyalty of individuals within a species to a site or group is well documented in mammals, and occurs particularly in adults which return to a certain site to breed (Greenwood 1989). Although many species are philopatric, often only a portion of individuals of any species can be faithful to any one locality (Greenwood 1980). The dispersal of the remainder must occur, and may be voluntary or enforced, environmentally determined or innate (Howard 1960). Dispersal in a species is of great importance as it may have a role in population regulation (Lidicker 1975) and spatial distribution (Taylor & Taylor 1977). Dispersal may also have an influence on the genetic structure of the population in its role in enforcing gene flow. In this sense it reduces inbreeding and genetic differentiation of neighbouring groups (Wright 1946). Hamilton (1972) has also discussed the consequences of dispersal to evolution of social and disruptive behaviour.

Dispersal in this context can be defined as by Howard (1960) :

> "Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate."

i.e. The definition makes particular reference to juveniles only, and does not include the dispersal which may occur when adults undergo dispersal when breeding.

In most species where dispersal takes place, it is the young which disperse more than adults. In *Cynictis penicillata,* dispersal of the young takes place at about 5 months of age. At this age the juvenile is independent, having accompanied the adult male on foraging trips for the duration of this period. Evolutionary theory proposed to explain the occurrence of sex bias are generally related to the type of mating system practised in the species (Greenwood 1980). In particular, dispersal in a pair living, non-social species would provided increased access to mates and reproductive enhancement. The defense of the home range by the adult male *Cynictis penicillata* for the acquisition of a mate and for the rearing of offspring and the subsequent competition amongst males for females, influence a female bias in dispersal (Greenwood 1980).

5.8.3 REPRODUCTIVE SUCCESS

Reproductive success is a measure of the number of offspring produced by a given individual which manage to survive to a given age (Emlen & Oring 1977).

MATING SYSTEM

When one sex becomes a limiting factor for the other, the result is an increase in the intrasexual competition among members of the available sex for access to mates of the limiting sex. As a result, the male *Cynictis penicillata* defends a female within his home range. The male may encounter other males during the oestrus periods which may attempt successfully to copulate with the female within this home range. Thus the female is able to mate with more than one male.

The cumulative advantage of multiple matings to the female could far outweigh the decreased reproductive success of individual males. In such conflict situations, males could be forced into assuming a larger fraction of the total parental care.

Polygamy is the term used to describe a particular type of mating system where a male can mate with one or more females and a female with one or more males. Sometimes cooperation of both sexes in rearing the young is found. Polygamous and monogamous mating relationships are both contrasted to promiscuous mating behaviour, where restricted mating relationships of substantial duration are not evident. These three types of mating systems occur with varying frequencies in different animal groups, and there have been attempts to describe and explain the ecological and social correlates of mating systems on the basis that they result from natural selection (Krebs & Davies 1981).

Emlen & Oring (1977) stipulate two major preconditions for the evolution of polygamy :

(i) Multiple mates, or resources sufficient to attract multiple mates, must be energetically defendable by individuals i.e. there must be economic monopolizing of several mates;

(ii) An ability of the animals to utilize this potential.

Because male mammals have no direct role in gestation or lactation, male contributions to prenatal and early post natal rearing of their offspring are necessarily secondary to those of the female. Continued presence of a male following mating is not essential to the reproductive success of most mammals (Getz & Hofmann 1986). Consequently, monogamy is presumed to be relatively rare among mammals (Eisenberg 1966; Witteberger 1979; Orians 1981). Kleiman (1977) noted that less than 3 % of mammalian species are monogamous.

Although monogamy implies exclusively the mating between a single male and female, this has not often been demonstrated for a specific species. Monogamy is usually recognised by characters such as (Getz & Hofmann 1986) :

1. Close spatial association between a heterosexual adult pair even during non-reproductive periods;
2. the absence of unrelated conspecifics within a home range or territory of a pair;
3. mating preference;
4. delayed sexual maturation of the offspring to enable the dominant adults or original pair to breed (Kleiman 1977 in Getz & Hofmann 1986).

Facultative monogamy may occur at low population levels because opportunities to encounter other conspecifics are few (Kleiman 1977). Field and laboratory test results suggest that variation in mating systems and social organisation occur among species.

Getz & Hofmann (1986) show that microtine rodents have a mixed mating system between closely related species. There are indications, for example, that monogamy may be the basic mating system of *Microtus pinetorum* (Fitzgerald & Madison 1983) whereas *Microtus montanus* (Janett 1978) appears to have a non-monogamous mating system (Getz & Hofmann 1986). Here the theory may be proposed that large, continuous, stable habitats would promote monogamous mating systems, whereas species occupying small, isolated or ephemeral habitat patches would have non-monogamous mating systems. Emlen and Oring (1977) stated that monogamy would evolve in mammalian species in which animals are widely dispersed throughout a relatively uniform environment.

Mating success measures the net effect resulting from the interaction of many components and, as Gregorius & Hattemer (1987) propose, sexual selection may then be the equivalent to a particular system of mating. Thus sexual selection will operate differently, and is not restricted to single aspects, such as female choice or male competition.

When one sex becomes a limiting factor for the other, the result is an increase in intrasexual competition among members of the available sex for access to mates of the limiting sex (Emlen & Oring 1977). The operant sexual selection tends to be intense in polygamous groups, whilst fairly mild in monogamous groups. Hence the yellow mongoose displays a high degree of competition between male individuals which compete for access to females. This situation is enhanced by an apparent female bias in the sex ratio of the population resident within an area, where there are more males than females in a said area. Each female within her home range is able to monopolize several males. The males are, in effect, too busy to partake of extra-pair copulations due to the intrasexual competition existing between neighbouring males. i.e. the amount of time spent maintaining the home range (in defense and displays) is great and may restrict the male both energetically and temporally to the female at his resident HBS. The female, on the other hand, is far less territorial and moves between the home ranges of several males. Emlen & Oring (1977) suggest that certain environmental factors determine the degree to which mates can be defended or monopolized. In effect, ecological constraints impose limits on the extent to which sexual selection can operate. In addition, Emlen & Oring (1977) point out that the greater the potential for multiple mate monopolization, the greater should be the potential intensity of sexual selection and the tendency for polygamy.

This high degree of competition between the males for females and the resultant mating system applies to *Cynictis penicillata* in the Karoo only, and not to other areas within *Cynictis penicillata's* distribution range.

As the female is the limiting sex in the *Cynictis penicillata* mating system, mate choice takes place by the female. This appears to be dependent on the social status of the particular male, and his status relative to neighbouring males. Evidence suggests that an hierarchy exists between the males which is perhaps reinforced by the female rather than only between the males themselves.

Obviously, competition and home range maintenance will determine the status of the male in the first place and subsequently reflect his status, in terms of fitness and quality as a potential mate, to the female.

Thus the observations of promiscuity or polyandry in the female can be explained within the structure of an evolutionary stable system. Mating success for the female is high and up to three males have been observed mating with the dominant female in one day. As described above, male *Cynictis penicillata* displays a high degree of parental care. Emlen & Oring (1977) suggest that the evolution of polyandry is a possible outcome of a high degree of male parental investment. This, however, is most common in avian species : the female is able to produce multiple clutches if the male is rearing the previous brood. In the case of *Cynictis penicillata*, polyandry as a result of increased paternal care is unlikely. The promiscuous mating observed by the female is to maximize the chances of successful fertilization. Seventy percent (70 %) of matings occur with the dominant male, with the remainder taking place with one or two other males.

Ecological parameters impose limits on the range of types of social organization that will be adaptive. Emlen & Oring (1977) stress that with differences in the dispersion of a critical resource; the availability of mates; or other factors, the optimal social strategies shift resulting in a parallel fluctuation of social structure to ecological parameters. i.e. There is likely to be corresponding change in the potential for a particular mating system with changing environmental selective pressures. Thus we may expect variations to occur between different populations of *Cynictis penicillata* occurring in different environments. This is easily demonstrated when comparing the populations of the Karoo and the Southern Transvaal (Wenhold, 1991).

5.8.4 CUCKOLDRY IN *Cynictis penicillata*

In the past it was generally accepted that parentage was synonymous with the observed sociological pairing of animals. However, extra-pair fertilizations have been reported in so many different species that the true genetic parents of progeny can no longer be accepted on the basis of field observations alone (Birkhead et.al. 1987). Perhaps where population levels are low, a promiscuous mating system would reduce the level of inbreeding in the population whilst still allowing individuals the security of group living in a stable territory?

'Cuckoldry is a form of sperm competition peculiar to organisms exhibiting extensive male parental care and can be defined as a male's involuntary rearing of another male's offspring as a result of the latter male (the "cuckolder") having inseminated the mate of the former (the "cuckold")' (Beecher & Beecher 1979).

Cynictis penicillata displays promiscuous or polyandrous tendencies where the female mates with more than one male. In this situation, there is a high probability that the offspring of a litter may have multiple paternity, or even paternity belonging to a male other than the male at the resident HBS. Thus the possibility of cuckoldry occurring, where the dominant resident male raises the offspring fathered by another male, is present.

Cuckoldry in mammalian species is rare, and has only been recorded in the aardwolf (Richardson 1987) and a couple of species of mice (Richardson pers comm). It has, however, been recorded for numerous apparently monogamous birds (Gladstone 1979).

Trivers (1972) has predicted that in monogamous species with a high degree of male parental care, "a mixed strategy will be the optimal male course - to help a single female raise young, whilst not passing up opportunities to mate with other females whom he will not aid".

This is clearly reproductively successful for the male strategist, but from the female's side, such behaviour may be maladaptive to the secondary female if she already has a mate, because her mate may defect from his paternal duties if he realises he is being cuckolded (Beecher & Beecher 1979; Gladstone 1979; Richardson 1987). It has been argued, therefore, that in order to prevent the possible defection by her mate, a paired female should avoid having extra-pair copulations with opportunistic males. In *Cynictis penicillata* this theory slips up, however, due the promiscuous or polyandrous nature of the females. The female WILL mate with more than one male. HOWEVER, in this species the intrasexual competition which occurs between the males prevents the males from actively seeking out mates. The competition creates a 'dominance hierarchy' between the males in adjacent home ranges which in turn structures the access to female/s. It may be described as being a "side-track" to the males who, should be looking for females.

Paternal care in the yellow mongoose is extensive, and continues after weaning in the raising of the young (see chapter 11). The male spends extended periods alone with the offspring. Paternal care in the aardwolf is exhibited primarily by guarding of the young at the den (Richardson 1987). By contrast, most other carnivore species perform paternal care by bringing food items back to the young, or by regurgitating food (Macdonald 1983). Thus the investment in the offspring is high. There is always the possibility from the females point of view that the male may defect to another female where he may have a higher chance of paternity. If the intrasexual competition is strong enough, however, this should not occur.

Provided the cuckolded male has copulated with the resident female, he is still likely to have paternity of the offspring (Richardson & Coetzee 1989). Therefore he should not defect unless :

(a) he has an alternate female with which he can breed exclusively;
(b) by devoting his energy into raising the young he is likely to effect his future reproductive output negatively (Maynard-Smith 1977).

It appears, therefore, that an apparently monogamous female can preclude the threat of her resident mate defecting when she is promiscuous, if she mates with him as well as with the competing neighbour, thereby potentiating paternity by both males. The advantages to this system to the female are that :

(a) her offspring will gain from higher quality of genes of the intruder (Gladstone 1979);

(b) she may produce "sexy sons" which have the cuckolding tendencies of their fathers, and hence will benefit her fitness through her grandchildren (Weatherhead & Robertson 1979);
(c) if she is fertilized by both males, she will increase the genetic diversity of her offspring (Maynard-Smith 1978);
(d) the likelihood of fertilization of the ova is greater when mated by two mates.

As oestrus may last for up to three days, the female clearly has the opportunity to mate with more than one male. Richardson (1987) reported this observation in three aardwolf females during single oestrus periods. In addition, the female has the ability to terminate a mating attempt by an unapproved mate. In this case the possibility of sperm competition becomes evident (Parker 1984). Richardson (1987) suggests that sperm competition occurs in the aardwolf, although physiological and genetic data are needed to draw conclusive evidence (Richardson pers. comm.). He believes, however, that the aardwolf is an established case of cuckoldry in a mammalian species.

Similarly, physiological evidence is required to prove the paternity of the offspring in the yellow mongoose groups studied, but in this apparently pair living species the behavioural data suggests the occurrence of cuckoldry.

5.9 NURSERY BURROWS

The Nursery burrows utilized by *Cynictis penicillata* were changed a number of times. A possible explanation for this behaviour is related to the hygiene of the burrow system and the presence of parasites. It is possible that there was a build-up of parasites such as fleas, mites and ticks within the confines of the burrows system resultant upon the continual occupation during the ongoing period of babysitting. The warmth within the burrows would naturally induce an increase in the parasite population, and this may have caused *Cynictis penicillata* to move to a "fresh" burrow to escape the "infected" area and to give it time to clear.

In addition to parasites, excreta from the offspring would make the burrows uninhabitable for at least the length of time it would take to dry out or be decomposed. This may be another reason why *Cynictis penicillata* moved from one burrow to another. An additional consideration is that predators watching the HBS over a period of days may become familiar with the nursery burrows, and hence the location of the young. Thus the adults may continually move the young from one burrow to another in order to detract attention of potential predators. It is important to note that it was at this stage of their development that litters were taken by predators from within the burrow system.

CHAPTER 6

6 INTERSPECIFIC INTERACTIONS

6.1 *SURICATA SURICATTA* BREEDING AT THE *CYNICTIS PENICILLATA* HOME BURROW SYSTEM

Interspecific interactions take form in various ways and in different intensities. Cooperation is when individuals work together to achieve a common purpose - and generally occurs between members of the same species. Cooperation due to "enlightened self-interest" even occurs between members of different species, where both partners benefit from the relationship (Zimen 1976).

In order to establish whether the relationship between *Cynictis penicillata* and *Suricata* is symbiotic or commensal, the nature of the association must be clarified/defined. By definition, a symbiotic relationship implies an association between two dissimilar organisms to their (mutual) advantage. This includes mutualism and various forms of parasitism. On the other hand, commensalism includes those associations between different species without much mutual influence e.g. a sharing of a common resource.

6.2 *GALERELLA PULVERULENTA* INTERACTIONS WITH *CYNICTIS PENICILLATA* AND *SURICATA SURICATTA*

Galerella pulverulenta are an elusive, secretive, diurnal, solitary species. They utilize any available site to provide shelter at night. This may be vegetation cover, holes in the ground, rocks or even manmade structures. Smithers (1983) notes that the claws of the front feet are not well developed, resulting in *Galerella pulverulenta* being poor diggers and, while they have not been observed to dig their own burrows, commonly rely on the burrows dug by other species.

Data referring to the interactions between *C. penicillata, S. suricatta and G. pulverentula,* collected over a 7 month observation period in Camp W21 (see Figure 1), are presented below in Tables 6.1, 6.2 and 6.3.

Table 6.1 INTERSPECIFIC INTERACTIONS: SPECIES PRESENT AT HBS. Data collected over a 7 month observation period. The number of days each species was observed at the HBS in camp W21 are presented. The total number gives the number of days on which a viverrid species was seen at the HBS and NOT the total number of observation days.

	Cynictis penicillata Female	*Cynictis penicillata* Male	*Suricata*	*Galerella pulverulenta*	Total
Total sightings	106	153	49	7	161
x = Mean number of sightings of animals per day	15,1	21,8	7	1	23
s = standard deviation	5,7	8,7	3,4	1,2	6,8

Table 6.2 MONTHLY OBSERVATIONS OF VIVERRID SPECIES AT THE HBS : expressed in number of days recorded in a 7 month continuous observation period.

Species	July	Aug	Sept	Oct	Nov	Dec	Jan
Cynictis penicillata(f)	19	15	21	22	12	8	9
Cynictis penicillata(m)	30	23	28	31	17	17	7
Suricata	8	8	8	7	12	1	5
Galerella pulverulenta	3	1	2	0	0	1	0
Total	30	23	28	31	17	18	26

Table 6.3 PERCENTAGE OCCURRENCE OF VIVERRID SPECIES AT THE HBS. Species observed at the HBS per daily observation.

Species	July	Aug	Sept	Oct	Nov	Dec	Jan	Ave
Cynictis(f)	63.3%	65,2%	75,0%	70,9%	70,6%	44,4%	34,6%	60,5%
Cynictis(m)	100%	100%	100%	100%	100%	94,4%	26,9%	88,7%
Suricata	26,6%	34,7%	28,6%	22,5%	70,5%	5,5%	19,2%	29,6%
Galerella pulverulenta	10%	4,3%	7,1%	0	0	5,5%	0	3,8%
Total	100%	100%	100%	100%	100%	100%	100%	

6.3 *SURICATA* BREEDING AT THE *CYNICTIS PENICILLATA* HOME BURROW SYSTEM

Suricata occupy the same HBS as *Cynictis penicillata* 29,4 % of the time, spending more time at the HBS during the winter months than during the summer. When in occupation the *Suricata* contribute significantly to the vigilance investment in time spent at the HBS before moving off on daily foraging excursions. If, as proposed, the suricates are benefitting *Cynictis penicillata* by performing the majority of vigilance behaviour when residing concurrently at the HBS, then *Cynictis penicillata* may be reciprocating a beneficial function to *Suricata*.

Interactions between *Cynictis penicillata* and *Suricata* show that a mutualistic relationship could be recognised at the time of the *Suricata* breeding season.

Suricata have also been observed to breed in the burrow system whilst occupied concurrently by *Cynictis penicillata*. Here observations showed that *Cynictis penicillata* behaviour altered at the time of birth of the young. Before the young *Suricata* were born, *Cynictis penicillata* left the HBS soon after emerging from the resident burrow to forage.

However, the day of the *Suricata* parturition *Cynictis penicillata* behaved similarly to when their own young were born: both the male and female remained at he HBS continuously during the first day after the birth, leaving only briefly to forage (ave = 13,4 mins, no. of times = 5,2 +- 4,1, N = 5 days). The behaviour then took on the pattern exhibited during their own parental care period when the adults alternated their babysitting duties.

This behaviour characterized the 5 days during which the *Suricata* were resident in the observed HBS. Following *Suricata*'s departure (to another HBS within their homerange) *Cynictis penicillata* resumed foraging and marking behaviour as exhibited prior to the *Suricata* and babies being at the HBS.

6.4 *Galerella pulverulenta* INTERACTIONS WITH *CYNICTIS PENICILLATA* AND *SURICATA*

The nature of *Galerella pulverulenta* is noticeable in its habit of utilizing available shelter. Its irregular presence at the *Cynictis penicillata* home burrow system is thus typical of its ranging behaviour as it moves about its home range.

6.5 ESTABLISHING THE NATURE OF THE INTERSPECIES RELATIONSHIPS

Interspecific interactions were observed between *Cynictis penicillata* and a number of other carnivore species. Notable amongst these species were *Suricata suricatta* and *Galerella pulverulenta*, whose presence at the HBS accounted for *ca* 30.4 % of the interactions at the Home burrow system, and 28 % of the total observed interspecific interactions. Other species which were found to interact with *Cynictis penicillata* at a superficial level, whether competitively or incidentally, are *Otocyon megalotis* and *Ictonyx striatus.*

In order to establish the nature of these relationships, various data was collected in order to model and hence to quantify these interspecific interactions. i.e. To help establish whether these animals co-exist as interdependent functionaries. The nature of these relationships was investigated to determine their classification as either:

(i) opportunistic,
(ii) mutualistic,
(iii) parasitic, or
(iv) incidental

The following analytical procedures were used:

(a) The frequency of species concurrence at the HBS was calculated as a percentage of total observation days. These data were then divided into groups in which different species occurred together. i.e. *Cynictis penicillata* + *Cynictis penicillata*; *Cynictis penicillata* + *Suricata*; *Cynictis penicillata* + *Galerella pulverulenta*; and *Cynictis penicillata* + *Suricata* + *Galerella pulverulenta*. This provided simple statistical data.

(b) The vigilance behaviour of *Cynictis penicillata* was documented in order to compare this behaviour under different circumstances of species associations.

(c) An "Index of Mutualism" was created using parameters of vigilance and physical parameters at the HBS. In order to do this the HBS was mapped in detail and all bushes, burrow entrances and rocks plotted. A grid system was plotted over this to enable accurate measurement of the indices (see Results: Home Burrow Systems, Table 4.7).

Each day the positions and movements of *Cynictis penicillata* individuals were plotted, and these positions measured as distances form the nearest form of cover. The distance measures then provided an index which could be used in an equation designed to give an index of Mutualism. In addition to the measured indices from cover, an index of vigilance - taken as the number of times the animal was alert in a certain time period - was also assigned to each animal at that time.

Thus we have:

I_{cover} = distance from bush or rock
I_{burrow} = distance from burrow
$I_{vigilance}$ = no. of times alert in time period x
k = constant : number of species
$\frac{1}{\text{no.Individ.}}$ = inverse of number of individuals.

The index of Mutualism can be calculated using the following equation:

$$I_{mut} = I_{cov} \times I_{bur} \times I_{vig} \times k \times 1/\text{no.indiv.}$$

This index of mutualism can be calculated for any of the situations in which *Cynictis penicillata* interacts with another species at the HBS, and thus a standard representative figure can be obtained. The advantage of this Index is that it can then be used to test for statistical distribution once an hypothesis has been set up. If it is found that the hypothesis initially set up - i.e. That no difference is found in the index of mutualism when *Cynictis penicillata* is present with other species - is either significantly different or not, a distribution curve can been drawn. If there IS a significant relationship we may deduce that *Cynictis penicillata* is influenced in some way by the presence of another species.

6.5.1 RESULTS

Behavioural data were recorded over a period of 8 months at a single home burrow system in a familiar home range. The *Cynictis penicillata* group composition in this home range ranged from : 1 resident dominant male; the resident male and female; the resident male, female and juvenile/s; the resident male and juvenile/s; and the group in association with a varying number of *Suricata* (1 - 9)(Tables 6.4 & 6.5).

Random samples of n = 10 days were taken from 4 of the above categories to enable a detailed analysis of the vigilance behaviour:

Categories studied:

1. adult male alone
2. adult male + adult female
3. adult male + adult female + juvenile
4. adult male + *Suricata*

In Table (6.4) the mean values and standard deviations of various behavioural parameters relevant to vigilance behaviour are shown for categories 1, 2 and 4.

When the male *Cynictis penicillata* is alone at the Home burrow system he was alert an average of 75.7 (s = +-45.5) times during the period prior to foraging. Alternatively, it was alert an average of x = 0.59 (s = +-0.1) times per minute.

When accompanied by the adult female the average number of times the male was alert was X = 0.63 (s = +-0.16) per minute. This shows no significant difference (z = -0.529, p = 0.59 : Mann- Whitney test). However, of significant difference between these two group categories are the positions on the HBS and the behaviour of the male when he is alone as opposed to being accompanied by the female: when the male is alone the average distance to the nearest burrow entrance (i.e. an escape from predators) is X = 0.28 metres, and that from the nearest bush or rock X = 0.16 metres. On the other hand, when the female is present and is also performing vigilance behaviour, the male remained an average of only X = 0.482 metres from a burrow, and X = 0.303 metres from alternative cover. This difference was statistically significant (z burrow = 3.423, p = 0.001; z cover = -2.747, p = 0.001. Mann-Whitney test). See Table (6.5).

When the male was accompanied by *Suricata* at the HBS, the situation became more favourable for *Cynictis penicillata*. Here the male was more often vigilant but for shorter periods of time (0.95 times per minute vs 0.59 times per minute; z = 1.89, p = 0.05) (Table (6.6)).

However, *Cynictis penicillata* remained x = 1.27 metres from the burrow entrances and X = 0.75 metres from an alternative form of cover. This is significantly different to when alone (z burrow = 3.636, p = 0.001; z bush = 3.518, p = 0.001) or when accompanied by the female (z bush = 3.169, p = 0.001; z burrow = 2.627, p = 0.001 - Mann-Whitney z- test).

In addition to significant differences found in the vigilance behaviour of *Cynictis penicillata* when alone versus when at the HBS concurrently with other individuals, significant results were obtained for the Index of Mutualism.

The mean data of Indices of Vigilance, Cover and Burrow for each of the above categories were applied to the Mutualism Equation to calculate the Index of Mutualism :

Case 1 : male alone

$$
\begin{aligned}
I^{\mathrm{mutualism}} &= I_{\mathrm{cov}} \times I_{\mathrm{bur}} \times I_{\mathrm{vig}} \times k \times 1/\mathrm{no.ind.} \\
&= 2.5 \times 4.32 \times 0.59 \times 1 \times 1/1 \\
&= 6.37
\end{aligned}
$$

Case 2 : male + female

$$
\begin{aligned}
I_{\mathrm{mutualism}} &= I_{\mathrm{cov}} \times I_{\mathrm{bur}} \times I_{\mathrm{vig}} \times k \times 1/\mathrm{no.ind.} \\
&= 4.6 \times 7.32 \times 0.63 \times 1 \times 1/2 \\
&= 10.6
\end{aligned}
$$

Case 3 : male + *Suricata*

$$I_{mutualism} = I_{cov} \times I_{bur} \times I_{vig} \times k \times 1/\text{no.ind.}$$

$$= 11.4 \times 19.3 \times 0.95 \times 2 \times 1/4$$

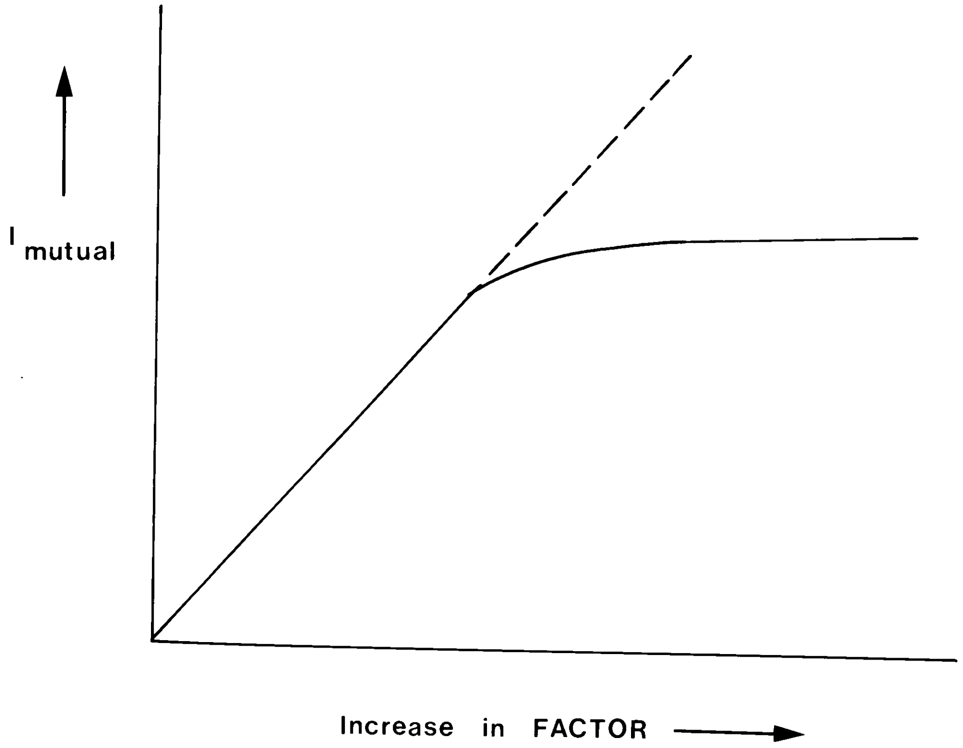
$$= 52.2$$

The Index of Mutualism ($I_{mutualism}$) increases with an increase in the number of individuals at the burrow system. The difference in $I_{mutualism}$ when the male is accompanied by the female and when accompanied by *Suricata* is significant ($z = 2.98$, $p = 0.005$, Mann-Whitney test). Thus as $I_{mutualism}$ increases we find an increase in the difference in the vigilance behaviour performed by the adult male : less vigilance because it is safer.

These data can be plotted on a graph of $I_{mutualism}$ vs Number of Individuals. When the number of individuals reaches an optimum level, the $I_{mutualism}$ stabilizes, and then decreases again when the number becomes too high. Here the system becomes suboptimal and *Cynictis penicillata* must begin to increase its levels of vigilance again. Figure (6.1) represents the relationship between an increase in the index of mutualism, and an increase in the number of animals present at the burrow system. The Index of mutualism increases steadily, and then reaches a level where an increase in the number of individuals at the HBS does not increase the Index of mutalism significantly. The point where the "plateau" is reached may be considered the point of optimization: ie for an optimal system - although not always the most frequently utilized system due to the nature of *Suricata*'s habits - this has been calculated to occur when there are approximately 7 *Suricata* at the HBS.

These data strongly support the theory that *Cynictis penicillata* exists mutualistically with *Suricata* on a partial basis.

Figure 6.1 Graphic representation of the relationship between parameters of vigilance.



The Index of Mutualism ($I_{mutualism}$) increases exponentially as "k" (number of species) and the number of individuals increases. An optimum level is reached at a certain group size when vigilance is most efficient and *Cynictis penicillata* is able to remain a maximum distance from cover remaining relatively safely due to shared vigilance activities. As the group size increases beyond this the system becomes suboptimal and inefficient and this is indicated by a levelling in $I_{mutualism}$. i.e. When group size is large predators may be attracted to the HBS, communication breakdown may occur and vigilance not optimal. Beyond this level it would benefit *Cynictis penicillata* to perform an alternative strategy. (The skew distribution suggests that it would then become feasible to associate rather with a small number of conspecifics e.g. female and juveniles).

Table 6.4 Parameters of vigilance behaviour performed by the resident adult dominant male at the HBS taken from random samples of 10 days during an eight month observation period. Data recorded shows observations in 3 different categories of group structure at the HBS : (i) *Cynictis penicillata* male alone; (ii) *Cynictis penicillata* male + *Cynictis penicillata* female; (iii) *Cynictis penicillata* male + *Suricata*. In all cases the mean value.

Social Structure	N	Total Time (min)	No. x Vigilant	Index Vigilance	Index Burrow (m)	Index Cover (m)	k	No Ind
Male	10	75,7 45,5	57,5 26,3	0,59 0,10	0,285 0,099	0,165 0,105	1	1
Male + Female	10	47,3 32,8	31,4 15,6	0,63 0,16	0,483 0,158	0,303 0,092	1	2
Male + *Suricata*	10	44,3 46,6	26,5 16,6	0,95 0,38	1,273 0,733	0,752 0,348	2	7

Table 6.5 Results of the Mann-Whitney test performed on data for vigilance behavioural parameters of the resident dominant male *Cynictis penicillata* when present at the HBS under different group composition.

Social Structure	parameter	z - value	probability
male vs male + female	*Ibur* *Icov* *Ivig*	3,423 -2,747 -0,527	0,001 0,001 N/S
male vs male + *Suricata*	*Ibur* *Icov* *Ivig*	3,636 3,518 1,890	0,001 0,001 0,05
male + female vs male + *Suricata*	*Ibur* *Icov* *Ivig*	2,627 3,169 2,295	0,001 0,001 0,001

An increase in the Index of Mutualism reflects an increase in the Indices of vigilance, cover and burrow. Thus, with an increase in the number if individuals and an increase in the number of species at the HBS, the *Cynictis penicillata* male tends to become more "confident" and spends more time further away from the burrow entrances and sources of cover from predators. Thus *Cynictis penicillata* appears to be relying upon the vigilance activities of other individuals and a shared vigilance system for detection of predators and defense.

Thus:

Increased $I_{\text{mutualism}}$ = Increased number at HBS

SOLITARY **GROUP COOPERATION** **MUTUALISM**

Tables (6.4), (6.5) and (6.6) show the time periods spent in vigilance and non-vigilance activities by an adult female, adult male and juvenile *Cynictis penicillata* respectively. All animals were occupying the same HBS. Important figures to note are the mean values for time spent in both activities.

Table 6.6 Vigilance behaviour exhibited by the <u>dominant adult female</u> at K52 HBS when in accompanied by the adult male and juvenile male. The figures indicated are: time (seconds) during which the animal was vigilant, time (seconds) between periods of vigilance (non-vigilant), and the number of times vigilant (N). The Mean (s) period of vigilance or non-vigilance are also given for each day.

NUMBER OF OBSERVATION DAYS	VIGILANT			NOT VIGILANT	
	No. times vigilant	seconds	s.d.	seconds	s.d.
1	22	25,5	22,4	10,7	10,3
2	4	32,5	17,8	26,6	32,1
3	64	15,8	12,7	24,1	18,6
4	1	5,0	0	20,0	0
5	11	18,4	13,9	555,7	78,6
6	12	26,8	25,3	9,4	7,1
7	7	8,8	3,9	8,8	5,5
8	14	18,0	13,5	41,5	89,9
9	12	18,6	13,0	625	95,0
10	4	8,3	0,9	0	0
11	24	24,8	18,0	92,7	20,0
12	24	16,9	13,6	15,2	17,9
13	37	18,8	13,7	43,7	14,0
14	48	13,5	13,0	86,6	14,4
15	4	19,0	12,7	44,3	23,6
16	5	19,4	11,8	51,5	42,0
17	11	17,0	11,6	34,4	64,7
N	X	secs		secs	
17	17,4 +- 16	18,1 +- 5,4		99,4 +- 104,3	

The adult female was alert an average of 17,4 times each day for a period of 17 days. The average duration of each vigilance period was 26,8 seconds (+- 20,4). The average time taken for non-vigilance activities was 99,4 (+-104,3).

Table 6.7 Vigilance behaviour exhibited by the adult male when occupying the burrow system with the dominant female and a juvenile subordinate male. Time spent vigilant and time between vigilance are shown.

NUMBER OF OBSERVATION DAYS	**VIGILANT**			**NON-VIGILANT**	
	Number of times vigilant	**seconds**	**s.d.**	**seconds**	**s.d.**
1	6	59,6	45,5	4,5	3,3
2	32	19,4	17,3	79,5	194,0
3	27	14,8	13,6	36,2	49,1
4	52	14,2	12,4	45,2	74,0
5	91	14,5	12,4	39,8	50,0
6	58	21,9	18,4	58,1	257,0
7	42	21,6	17,0	22,4	21,7
8	42	14,8	14,5	116,8	598,0
9	20	22,3	20,3	150,0	570,0
10	34	16,7	11,3	79,0	205,0
11	25	12,1	11,4	13,5	10,9
12	127	18,0	16,2	535,0	322,0
13	38	11,8	10,2	70,6	333,0
14	63	16,7	13,4	23,7	21,0
15	71	12,5	12,8	41,6	52,0
16	44	11,2	9,2	42,8	58,4
17	48	13,5	13,0	86,4	143,0
18	26	19,3	14,3	130,0	467,0
19	80	15,2	13,0	54,0	102,0
20	48	12,6	11,3	82,9	220,0
21	63	11,9	11,5	62,7	93,8
N	X			X	
21	49,3 +- 3,6	15,7 +- 3,6		75,8 +- 37,6	

The adult male was alert an average of 49,3 times for a period of 15,7 (+- 3,6) seconds each day for a period of 21 days. The average time between vigilance spent doing non-vigilance activities is 75,8 seconds.

Table 6.8 Vigilance behaviour exhibited by the Juvenile subordinate male when at the HBS concurrently with the adult male and female individuals. Time spent vigilant and time between vigilance is shown.

NUMBER OF OBSERVATION DAYS	VIGILANT			NOT VIGILANT	
	Number of times vigilant	Time (seconds)	s.d.	Time (seconds)	s.d.
1	24	19,6	22,2	9,6	11,8
2	49	17,8	17,2	24,1	42
3	19	16,4	17,9	27,0	23,3
4	31	11,1	10,3	36,1	77,7
5	103	11,0	11,0	39,6	53,9
6	39	13,5	13,1	87,8	270,0
7	26	13,6	12,6	157,0	81,6
8	39	14,1	10,4	135,7	387,6
9	49	16,6	15,6	72,7	370,0
10	22	16,1	9,6	235,0	638,0
11	138	11,5	11,3	14,3	14,1
12	122	9,1	11,1	76,4	324,0
13	29	8,4	10,7	100,0	312,0
14	44	15,5	13,0	50,3	78,3
15	61	11,9	10,9	49,5	64,5
16	49	10,6	9,1	40,6	60,2
17	51	10,2	8,6	82,9	118,0
18	25	12,6	9,5	122,5	450,0
19	94	11,7	12,1	50,8	92,3
20	63	11,5	9,7	31,3	61,1
21	89	12,5	21,1	49,8	95,5
N		X		X	
21	55,5 +- 13,3	13,1 +- 2,9		73,2 +- 35,7	

The Juvenile male was alert an average of 55,5 (13,3) times for an average time of 13,1 seconds. Between each period of vigilance, 73,2 (+-35,7) seconds were spent in non-vigilance activities.

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Table 6.9 Results of the t-test performed on vigilance behaviour performed by three *Cynictis penicillata* at the HBS. The test was performed to prove differences in the behaviour between individuals.

	female	**male**	**juvenile**
female		t = -0,01 p = 0,001	t = -0,01 p = 0,005
male	N/S		
juvenile	t = 0,093 p = 0,030	t = 0,064 p = 0,005	

6.6 DISCUSSION

How do we interpret this influence or relationship ? In looking for an interspecific relationship of a symbiotic nature one's attention is drawn to certain factors which may promote this kind of relationship. Thus, in *Cynictis penicillata* one has to look for those factors which may benefit it by becoming involved with another species.

In order to do so, the basic ecology and behaviour of *Cynictis penicillata* must be outlined so that clues may be suggested. For instance:

1. *Cynictis penicillata* is solitary/pair living;
2. *Cynictis penicillata* is largely sedentary;
3. Foraging occurs mostly alone or in pairs due to the nature of their food resource which is very patchy;
4. There is a high risk of predation;
5. Spatial resources appear to be a limiting factor;
6. Females may be a resource competed for due to their promiscuity.

The major factors which can be highlighted from the above list which have possible influence in leading to the establishment of an interspecific interaction (e.g. mutualism) are pointed out below:

- primary factor = predation
- secondary factor = spatial resources (may be interchangeable with Food, depending on the season
- tertiary factor = food resources

```
            - PREDATION
      -
     -
GROUP SIZE ---- FOOD
      -      -
       -    -
     - SPACE -
```

In this context the factor of predation is primary due to the lack of a counteracting external factor in the system. Thus if predation gets too high there is a collapse in the system i.e. the mongooses will be unable to adequately defend themselves. The secondary factor of spatial resources comes into play due to the shortage of suitable sites for the establishment of HBS in the Karoo. The maintenance of a suitable HBS, and subsequently a home range, are interrelated factors with food resources and group size as can be seen below.

- SPACE

Space is a limiting resource due to the nature of the burrow systems, and the specific requirements for establishment of a HBS. In addition to this, space is influenced by both group size and food availability in its role as determinant in home range size. *Cynictis penicillata* utilizes the same HBS over a long period of time in its sedentary mode of existence. On the other hand, *Suricata* utilize the HBS on a traditional basis - moving nomadically from one system to another throughout their homerange. The *Suricata* have a larger homerange than *Cynictis penicillata*, and one group appears to utilize many HBSs. The HBS thus occupied may or may not be shared systems, and therefore the *Suricata* do not always live concurrently with *Cynictis penicillata*. The same group of *Suricata* reappears at a single HBS every 14 - 18 days, thus implying a rotation or a homerange size 7 times the size of *Cynictis penicillata*'s if they consume the same amount of food/area covered. Finally, the importance of the spatial aspect in posing a factor in the occurrence of mutualistic relationships is in the fact that space is a shared resource. If it can't be competed for then it must be shared.

- PREDATION

Predation is an integral common factor in the ecology of all above mentioned small carnivores: They are predated upon by similar species and their predator avoidance strategies are similar. These common factors thus provide foundation for mutual accommodation of defense resources.

The major difference between the species is found in the group size which has an effect on the different modes of predator detection. The *Suricata* have a complex vigilance system structured from division of labour within the group. Certain members of the group are designated guards and the animals co-operate in the detection of predators, utilizing a complex vocalized communication to alert conspecifics (also in the Dwarf mongoose (Beynon & Rasa 1989)). Here visual senses are the primary mode of predator detection, supplemented by the complex vocal alarm repertoire.

On the other hand, the solitary *Cynictis penicillata* perhaps cannot afford to spend as much time as *Suricata* in utilizing visual predator detection, as this would detract from time available to search for food (optimal foraging theory, Belovsky 1984), and to advertise the home range (marking behaviour).

As a result, it appears that *Cynictis penicillata* utilizes auditory senses as a primary predator detection mechanism, whilst visual detection also remains acute. Personal observations of *Cynictis penicillata* at the HBS indicate that *Cynictis penicillata* is acutely aware of sound and is alerted to many intruders in this way. However, the importance of visual perception cannot be dismissed. *Cynictis penicillata* is also far less vocal than *Suricata*, and was rarely heard to alarm against a predator (see Appendix A).

Galerella pulverulenta is an extremely elusive species, remaining solitary throughout the year. Its solitary nature and nomadic existence make for an extremely difficult animal to study closely in the field. *Galerella pulverulenta* spends very little time at the HBS, and for this reason it may be deduced that the interspecific relationship between this and the other two species is not predator related.

Consider the aspects influencing the evolution of social systems :

(i) cooperative hunting
(ii) maintenance of territories
(iii) predation avoidance
(iv) cooperative breeding
(v) spatial resource limitations

These factors are influencing parameters in becoming group living or SOCIAL. However, a parallel argument stands equally strong for the case of solitary animals where these aspects - or socializing factors - are the evolutionary driving forces which keep them solitary. In a species such as *Cynictis penicillata* which occurs in both solitary and social group structures, the social structure can be justifiably demonstrated as being reflective of ecological conditions. The result being that under some conditions *Cynictis penicillata* is found in social groups of up to 20 individuals, whereas under others, e.g. the Vaal Dam (Wenhold pers.comm.), the groups comprise -+ 10 animals. In the Karoo, however, *Cynictis penicillata* occurs solitarily or in pairs.

An explanation of this dichotomy may be the theory that *Cynictis penicillata* has NOT given up its traits as a social species at some localities, but has rather compromised according to conditions.

Perhaps *Cynictis penicillata* is the evolutionary link between the solitary and social species. Consider the following hypothesis :

A. The *Cynictis penicillata* at the Vaal Dam study site (Wenhold pers.comm.) are socially bonded at the HBS and particularly during the breeding season. They forage alone or in pair, although all prey capture and foraging behaviour is independent. Most foraging pairs comprise an adult and sub-adult where the existence of the "pair" is thought to be functional in information transference of foraging techniques from the adult to the young. At the Vaal Dam *Cynictis penicillata* is the only carnivore species present. At the HBS, *Cynictis penicillata* benefits from being social in aspects of defense from predation, cooperative breeding, spatial availability and the maintenance of the home range.

On the other hand it reverts to a solitary state when foraging. Solitary foraging for an opportunistic carnivore feeding primarily on insects and small vertebrates is far more efficient than group foraging: the prey is simply too small.

B. The case for the *Cynictis penicillata* population in the Karoo is essentially different in that *Cynictis penicillata* remains solitary or pair-living. Here the individual has a different predator-defense system, which may be considered a disadvantage of being solitary. This, however, may be outweighed by the advantages gained from aspects of spatial availability, home range availability and foraging efficiency. Although there is no cooperative breeding, parental care is shared between the male and the female.

This system looks very different in isolation but is possibly different (and hence similar to *Cynictis penicillata* in a social situation) when considering the INTERSPECIFIC INTERACTIONS occurring with *Suricata*.

If the Index of Mutualism shows that *Cynictis penicillata* exhibits altered vigilance behaviour when associating with *Suricata*, the *Cynictis penicillata* are perhaps augmenting their group size by entering into an interspecific relationship. The existence of this relationship at the HBS is to be expected, and the model would thus fit that present in social *Cynictis penicillata* populations.

Obviously there is a dichotomy of influencing factors - the species must exercise both social structures in order to function maximally under given conditions.

When *Suricata* is present at the home burrow system, vigilance activities performed by *Cynictis penicillata* decreases significantly and it appears that *Cynictis penicillata* takes advantage of the *Suricata* vigilance at the burrow and therefore decreases its own costs of vigilance. While most studies demonstrate that an increase in group size reduces an individuals vigilance time have been made on single- species groups (Lipetz & Bekoff 1982; de Ruiter 1986) this has also been observed in mixed-species flocks of birds whose members share common predators and respond to one another's alarm calls (Metcalfe 1984; Sullivan 1985; Cords 1990).

In mixed-species groups of primates, predation pressure has been noted to be the most important selective pressure for interspecific sociality (Cords 1987). The advantages of reduced vigilance may not, however, be sufficient explanation for mixed-species associations between the *Suricata* and *Cynictis penicillata* as these association are not continuous, and may vary in the number of individuals participating in the association. Other factors, such as home range size, group size and diet will also play a role in the nature and occurrence of the association.

The co-existence of three mongoose species (*Cynictis penicillata*, *Suricata* suricatta & *Galerella pulverulenta*) within the same burrow systems, and their shared food and spatial resources, provides for various forms of interspecific interactions. In addition to the mongoose species, interactions occurs between above species and other viverrids (e.g. the small spotted genet, *Genetta genetta* and the Bat-eared fox, *Otocyon megalotis*).

- ***Suricata suricatta* breeding at the *Cynictis penicillata* home burrow system**

A number of mechanisms may contribute to the interspecific interactions present between these two species, with an interplay of costs and benefits working towards an ultimately cooperative system. More than one mechanism is likely to work from both species, thus creating a complex situation of relationships working on long-term costs and benefits as opposed to immediate costs and benefit. The apparent nature of the mechanisms at play in these relationships are such that they operate out of unison and are thus possibly rewarded out of phase :

Consider the following supposition: *Suricata* occupy the established HBS of *Cynictis penicillata*, benefitting in provision of an established shelter for which it was not necessarily a primary excavator even though it may temporarily occupy other burrow systems which it may have excavated independently. These burrow systems do exist, but they are less elaborate and are occupied only in defensive or anti-predator situations. *Suricata*, however, excavate the HBS to modify the burrows. This may function as "spring cleaning".

This behaviour may have two explanations:

a) The behaviour is a complex form of reciprocal mutualism in performing a babysitting function for the protection and raising of the young *Suricata*. The similarity in the behavioural repertoires of *Cynictis penicillata* during this period and the period of their own breeding is noted. It is important to note that the general lack of aggression between the *Suricata* and *Cynictis penicillata* during this period suggest an association between the two species. Previous agonistic interactions are common between these two species, where *Cynictis penicillata* appeared submissive to *Suricata*. Thus had the situation warranted it, the *Suricata* would clearly have expressed aggressive interjection, and chased the *Cynictis penicillata* away.

b) The behaviour exhibited by *Cynictis penicillata* in remaining at the HBS during the first few days after the birth of the *Suricata* could be predatory behaviour. *Cynictis penicillata* may remain at the HBS waiting for an opportunity for the *Suricata* babysitters to slacken in their duties at the nursery burrows thereby allowing *Cynictis penicillata* the opportunity to prey upon the young. Although *Cynictis penicillata* feed primarily on insects and fruits, they also eat small mammals and birds (Lynch 1979) and thus it is possible that they take the offspring of other viverrid species should they become available. This possibility is likely, although the lack of aggression from *Suricata* suggests that the first explanation may be relevant.

Cynictis penicillata will benefit for tolerating *Suricata* presence at the HBS in the following ways:

a) *Cynictis penicillata* appears to utilize the *Suricata* vigilance system for the detection of predators. *Suricata* have a functionally integrated guarding system whereby certain individuals within a group warn against attack by predators. Due to the lack of visual contact and the problem of communicating in well vegetated habitats, information conveyance is most effectively carried out by means of vocalization (Beynon 1986). Primary to this, and to the advantages of sociality, is the function of vocalizations in the avoidance of capture of mongooses by predators (Beynon 1986).

This aspect is important in the ecology of *Cynictis penicillata* because the mere fact that predator presence is vocalized in *Suricata* means that *Cynictis penicillata* can benefit from these calls by utilizing in interspecific communication. In addition, flight and appeasement behaviour by *Suricata* may be signals which are clearly interpreted by *Cynictis penicillata* as indications of danger.

b) *Suricata* have often been observed excavating the HBS. In these instances the HBS is "cleaned" as debris, faeces and loose soil are removed from the burrows. The excavations are generally performed over a period of 2-3 days and are less extensive than those carried out by *Cynictis penicillata*. Thus *Cynictis penicillata* may benefit from this in removal of parasites and waste from the HBS.

c) *Cynictis penicillata* and *Suricata* often forage together. The function of this may be that of mutual benefit in locating food resources. In addition, the ostensibly augmented group size may increase proficiency of vigilance against predators.

Figure 6.2 The factors contributing to a mutually beneficial interspecific relationship between *Cynictis penicillata* and *Suricata*.

CYNICTIS <--------->	*SURICATA*
provision of HBS	vigilance
babysitting (questionable)	hygiene
feeding (questionable)	

Thus the question of the nature of the interspecific interaction between *Cynictis penicillata* and *Suricata* may be determined by the balance between the above factors. It is important to conceptualize a holistic or long-term view of the relationship when considering mutualism in this case, as there are staggered inputs and returns of the overall "equation". On a daily basis the complexity of this subtle system may be overlooked, but the interchange of mutual association, though sometimes indirect and subsequent, is relevant and substantial.

Evidence thus presented suggests the occurrence of mutualism i.e. association between two species resulting in mutual benefit, in *Cynictis penicillata* and *Suricata*.

• ***Galerella pulverulenta*** **interactions with** ***Cynictis penicillata*** **and** ***Suricata***

Galerella pulverulenta is prone to moving along existing tracks and paths in touring its home range and is repeatedly seen trotting over the same ground. This often intersects with a burrow system excavated by *Cynictis penicillata* or *Suricata*.

Both *Cynictis penicillata* and *Suricata* react aggressively toward *Galerella pulverulenta* when encountered. Agonistic behaviour exhibited includes tail raising, chasing, threat jumping, growling and even biting. *Galerella pulverulenta* generally responds submissively and retreats soon after detection by either species. The reaction elicited by *Galerella pulverulenta* is likely related to predation threat factors. *Galerella pulverulenta* has been recorded to prey upon *Cynictis penicillata* young at the HBS.

CHAPTER 7

SUMMARY

The major factors influencing the evolution of a solitary social structure in *Cynictis penicillata* (or at least for reduced sociality) are:

- Intrasexual competition
- Intraspecific competition

The interspecific differences in sociality between closely related taxa are generally attributable to differences in habitats, foraging ecology, predation and resource distribution (Rubenstein & Wrangham 1986). The social organisation of mongooses can be placed along a continuum ranging from aggregated, asocial individuals (e.g. *Galerella pulverulenta* (pers. obs.)), through moderately social female/male kin clusters and familial groups (e.g. *Cynictis penicillata* (pers. obs.)), to highly social groups (e.g. *Helogale* sp. (Rasa 1977), *Suricata* (pers. obs.). The most social of the mongooses tend to be the smaller diurnal species living in matriarchal groups. Rasa (1976) has noted that viverrid species inhabiting exposed plains areas with little or no cover have almost all evolved a relatively high degree of sociality (*Helogale*, *Suricata*, *Mungos*, *Crossarchus*) whilst larger, nocturnal and arboreal species occupying denser habitats have a tendency to solitary or pair living (*Ichneumon* sp., *Herpestes* sp., *Atilax*). The major factor involved in the evolution of sociality in the smaller species appears to be predation pressure in an exposed environment and the subsequent necessity for effective anti-predation mechanisms.

Sociality among carnivores is generally related to in terms of cooperative hunting (Kleiman & Eisenberg 1973; Kruuk 1972; Schaller 1972) and group defence against predators (Rasa 1986). Group size in many species of carnivores may be determined by the food resource size and availability (Bekoff & Wells 1980; Caraco & Wolf 1975). However, as Waser (1980) points out, the apparent success of models relating the degree of sociality to resource dispersal falls short when considering viverrids. As an alternative, Waser suggests that the renewal rate of a prey resource, rather than its actual distribution, is instrumental in the selection for sociality in viverrids.

Table: 7.1 Summary of selection pressure factors influencing the sociology of *Cynictis penicillata*, in the Karoo. "yes" indicates whether the factor is considered to be relevant to the development of the specific social system in a particular geographical area.

SELECTION PRESSURE	SOCIAL	SOLITARY OR PAIR LIVING
HBS availability	-	yes
Food availability	-	yes
Foraging technique	-	yes
Predation	yes	-
Parental care	-	yes

Cynictis penicillata is solitary or pair living for all but 3 or 4 months of the year. Only at times of breeding does the core group at a resident HBS become increased in size by the addition of offspring. These offspring remain with the group, primarily under the parental care of the male, until they are approximately 4 months old. At this stage they disperse and the group size returns to its original number. Thus in *Cynictis penicillata* sociality may in part be attributable or associated with the delayed emigration of young that are unable to attain the weight and maturity needed to fend for themselves as part of a floating population, or big enough to find an opening in a vacant home range. Armitage (1981) has found that, in large bodied ground squirrels, complex sociality is associated with delayed emigration of young that are not yet reproductively mature as yearlings and hence remain with the parents until they are. Here the size and maturity of the young are instrumental in the social structure and are also responsible for differences in sociality in many species of ground squirrels.

The question, however, lies in whether intraspecific differences in life-history traits and environmental factors will result in differences in social structure between populations. The length of time over which intraspecific alterations in habitat, behaviour and life-history traits could cause changes in sociality is variable. Any changes in sociality should be a balance between opposing factors of cooperation and competition within the social group that allows its members to maximize their life-time reproductive success (Wrangham & Rubenstain 1986). This is achieved by increasing the probability of juvenile survival to reproductive age (Rayor 1988). Sociality, which permits juveniles to remain in the relative safety of the natal area until they are reproductively or otherwise mature, increases the probability of survival, regardless of the sources of mortality (e.g predation, Hoogland 1981a). However, offspring remaining for too long in the natal area will ultimately provide competition for the parents for space and forage (Rayor 1988). Evidence for competition in various social ground squirrel species is emerging. In the yellow-bellied marmots mother-daughter competition reduces fecundity of the daughters (Armitage 1986). Infanticide in the black-tailed prairie dog has a high frequency of occurrence (Hoogland 1985), where the grandchildren are killed to prevent competition with new generation offspring.

Cynictis penicillata offspring leave the natal HBS relatively soon. The young move off into adjacent areas, fending for themselves. The costs of remaining in the natal home range include vulnerability to infanticide, and increased pressures, due to competition from the parents, of resources such as food and limited availability of HBS's. The predation rate should be lower at the HBS due to increase in the vigilance activity when more animals are involved. It is known that space is an important factor in the ecology of *Cynictis penicillata*, and is a limited resource. Here the costs of competition obviously exceed the benefits of cooperation and selection is for a decrease in sociality.

APPENDIX A

BEHAVIOURAL PARAMETERS OF *Cynictis penicillata*

To enable the analysis and description of intra- and interspecific interactions, an abbreviated ethogram of the behaviour patterns observed in *Cynictis penicillata* is necessary.

An ethogram may be defined as: the complete behavioural inventory of a species - the listing of easily recognisable units of behaviour whose occurrence in various contexts, and sequences, can be used to provide a comprehensive description of behaviour (Schleidt 1979). A total of 40 behavioural patterns were identified. These are listed below, with detailed descriptions of each following.

Table 6.1 Behavioural parameters of *Cynictis penicillata*

INDIVIDUAL			**SOCIAL INTERACTION**		
No	Behaviour	Abbrev.	No	Abbrev.	Behaviour
POSTURES			**COMMUNICATION**		
1	sit up	stu	27	mrk	mark
2	sit high	* sth	28	mrkc	cheek mark
3	sit medium	* stm	29	mrka	anal mark
4	sit low	* stl	30	lc	lick
5	stand	std	31	alarm	alarm
6	stand high	stdh	32	grl	growl
7	lying	* ly	**AGONISTIC**		
8	sunbathe	* sn	33	chs	chase
9	in burrow	bur	34	ft	fight
10	looking	* lk	35	wrs	wrestle
11	alert	alt	36	bt	bite
12	yawn	* yn	37	scr	scratch
13	stretch	* str			
LOCOMOTION			**BREEDING**		
14	walk	wlk	39	sub	submissive
15	run	rn	40	chs	chase
16	gallop	glp	41	cop	copulate
17	trot	trt			

INDIVIDUAL			**SOCIAL INTERACTION**		
No	Behaviour	Abbrev.	No	Abbrev.	Behaviour
18	forage	frg	41		
19	dive	dv			
MAINTENANCE			**OTHER**		
20	urinate	mrku	42	exc	excavation
21	defecate	def	43	pl	play
22	groom	grm			
23	groom stomach	grsmst	44	algrm	allogroom
24	groom tail	grmt			
25	groom genitals	grmg			

6.1 DESCRIPTION OF BEHAVIOUR PATTERNS

POSTURES

Sit up (stu):

The animal is characteristically squatting with the fore limbs straight and close to the body. The general appearance is relaxed. This position is used when in general alertness, during sunbathing activity when varying the degrees of exposure of the body are presented, and when looking from the home burrow.

sit high (sth):

Squatting on the hind legs with the forelegs cocked horizontally from the mid body when very alert. This posture gives an added advantage of height.

sunbathing (sn):

The animal positions itself in the sun exposing as great a surface area as possible. This behaviour is thought to help regulate their body temperature and is particularly evident in winter when up to three hours are spent sunbathing. Various postures are used when sunbathing.

sit medium (stm):

The animal squats on its hindlimbs as in sit up but the forelimbs are extended further forward and the head is bent downwards to rest on the legs. This is still an upright posture with most of the body off the ground. This position is used primarily during sunbathing although the animal may sometimes be alert.

sit low (stl):

The animal sits on its hindlimbs as in sit medium but the forelimbs are further forward and the head is completely curled in towards the body. This position is used predominantly during sunbathing and maximises the area of the head, neck and shoulders exposed to the sunbathing. Often one or both of the hindlimbs are extended forwards under the body, thus increasing the area exposed to the sun. The animal is generally very relaxed when in this position.

stand (std):

The animal is stationary on all four limbs (sometimes with one cocked). This position is usually maintained when the animal is alerted to a possible danger (when foraging or at the burrow), when marking and smelling the home range, or foraging.

Stand high (stdh):

The animal stands up on its hind legs with its fore legs cocked horizontally off the ground. The animal's back is generally arched concavely. Balance is maintained using the tail. This posture allows the animal maximal head elevation above ground.

lying (ly):

The animal's entire body is on the ground - spread out either laterally to maximise the surface area exposed to the sun or hearth-rugging (ventrally) in the shade to cool.

in burrow (bur):

The animal has entered the burrow and is out of site. It incorporates all times when the animals are underground.

looking (lk):

The animal is semi-alert but does not change its position, apart from head movement. The animal will look regularly when sunbathing to scan its surroundings for predators or intruders.

alert (alt):

The animal is highly alert to environmental factors indicating danger, predation or a food source. Both auditory and visual senses appear to function acutely (pricked up ears and eyes scanning). The animal may also sniff the air. The animal may be sitting, standing or standing high - often the posture is changed when the animal becomes alert e.g. sitting low to standing high.

yawn (yn):

Whilst stretching and after waking up, the animal may yawn with a full gaping, open mouth

stretch (str):

The animal stretches whilst standing with the back bowed concavely. The front of half of the body is lower than the back half, both front and hind legs are straight and at +- 35° from the ground, facing forward.

LOCOMOTION

Locomotion postures are usually associated with other behaviour patterns. Such behaviour includes touring the home range, foraging, overt and agonistic expression towards outsiders, etc.

walk (wlk):

A slow pace of quadrupedal locomotion using alternate feet. The animal may be fully alert, foraging, touring the home range or moving between points. This behaviour is generally compounded with other behaviour patterns, and the intent is generally found in the other behaviour - e.g marking and touring the home range.

run (rn):

Fast pace of quadrupedal locomotion using alternate feet. Running is used on home range inspections, when foraging, and when returning to the home burrow system. The average speed is +- 6 km^{-1}.

gallop (glp):

Fast pace of locomotion using front and hind feet together when running from danger.

trot (trt):

Medium pace quadrupedal locomotion using alternate feet with undulating motion of shoulders. Used when relaxed and moving around the home range.

forage (frg):

Cynictis penicillata often chases and catches insects by pouncing on them with a bounding movement, sometimes swiping them out of the air with the forepaw. During the pounce, the forepaws are extended forwards with the palms down: this enables the pinning down of the insect on landing. *Cynictis penicillata* remains standing on all four legs when eating, generally using one paw to pin the prey down, whilst tearing and biting. Small mammals, birds and reptiles are eaten in a similar manner. Pieces of flesh are bitten off directly or torn off by pulling motion with the head. Regurgitation of food and its immediate re-ingestion occurs. Collection and transportation of food to the burrows during the breeding season was also observed.

dive (dv):

This is a flight behaviour exhibited when predators or intruders are spotted/detected in the vicinity of the animal. The animal dives into the nearest form of cover, preferably a burrow or small cave in rocks. The motion is swift and head-first, after which the animal may turn around inside the shelter and cautiously peer out, with only its head exposed.

MAINTENANCE

urinate (mrku):

The animal is in a squatting position with its back slightly arched. The tail is lifted off the ground either horizontally or in a vertical curve with the tip towards the ground. No incidences of cocked leg urination were observed.

defecate (def):

Defecation occurs at a midden. The animal stands and arches its back towards the ground with the anus parallel to the ground, and then defecates one faeces. The heads is extended forward with the eyes staring fixedly ahead. The tail is lifted up and way from the body, horizontal to the ground (sometimes found to be held vertical).

groom (grm):

Grooming is a toilet or cleaning behaviour used to remove parasites and dirt. This includes any form of auto-grooming (self-grooming) which was not distinguished in detail. The behaviour is generally carried out when the animal is sitting medium or low. Grooming involves licking the body (tongue) and nibbling and biting with the incisors. Scratching with the hind leg is used for the neck and rib-cage area. The different parts of the body groomed include: the stomach, tail, and genitals.

allogroom (algrm):

Any form of grooming which involves a dyadic interaction where one individual grooms the other and/or vice versa. Allogrooming is generally social behavioural pattern and seems to serve little function in toilet in *Cynictis penicillata*. It occurred rarely and generally involved mutual grooming by nibbling.

COMMUNICATION

mark (mrk):

Marking includes all acts of scent deposition. Both object and allomarking take place. Predominant marking techniques include anal marking, cheek marking, urination and defecation.

cheek mark (mrkc):

The cheek glands are stroked across an object alternately from nose to ear approximately three times (f = 2.84 +-2.08, N = 32).

anal mark (mrka):

The animal raises its tail and anal marks in two distinctive ways: firstly by anal dragging, where the secretory glands around the anus are dragged along the object or ground being marked; secondly the animal may spray an object or other animal with a substance produced in the genital area.

lick (lc):

The animal licks an object or individual where a scent mark has been previously left. This is generally preceded by smelling the object, followed by a short pause in activity (t= 1.2 +- 0,3 sec, N = 37).

Behaviour complexes

Low intensity threats comprised staring intently either in silence or with snarling and teeth bared. In response the subordinate animal would lower its head in attempt to avoid eye contact. More intensive threats involved close or actual body contact accompanied by much snarling, spitting and pronounced baring of teeth. Lunging and snapping, often accompanied by biting, was also exhibited.

In response to threat behaviour, *Cynictis penicillata* (subordinates: juvenile and adults) would perform passive submission (Schenkel 1947) and either crouch or flatten itself against the ground. The ears are typically drawn back against the head, the lips pulled back and the tail kept low.

The response of the male to threat behaviour by oestrus or lactating females can be defined as "tolerance behaviour" (Corbett 1988). Instead of passively submitting or returning the threat, the recipient male stood in a semi-threat posture without snarling, then averted his head and moved away. Often this behaviour is accompanied by vigorous genital grooming.

Active submission (Schenkel 1967) occurred when an individual went up to the front of a recognised dominant animal in a slightly crouched posture, with it ears and tail low. In response the dominant animal would either jump over the rear end of the submissive animal followed by allogrooming of the dominant's genitals , or would acknowledge the behaviour by simply allogrooming.

Pilo-erection of the tail occurs in agonistic encounters, or when there is a new or unfamiliar animal around. Accompanying pilo-erection is often tail-flicking and jumping.
The function of "tail displays" or the tendency to bush the tail in certain circumstances, has probably evolved because it provides information for the assessment of size during agonistic encounters (Petrie 1988).

VOCALISATIONS

alarm (alarm):

This is a vocalisation given in a surprise attack situation, or when an animal is frightened by something. The call is low and rasping, and may be short or repetitive - resembling a bark.

appeasement call:

A soft call given by a subordinate animal when interacting with a dominant animal. The call is continuous and low frequency, and is given when the animal is in a crouched position.

courtship calls:

Low growl given by the female during courtship. Predominantly given when the male advances on the female. The growl may increase in intensity and volume turning into a harsh bark.

AGONISTIC

chase (chs):

Animals run after one another with the intent of removing the one being chased from the immediate vicinity. Chasing was observed in the following situations:

- when the male is chasing an intruder from his home range
- during the breeding season when the female chases the male when he makes advances to her
- the adults chase the young when they climb on them
- chasing away from a prey item.

fight (ft):

An Agonistic or aggressive dyadic interaction usually occurring between the territorial male and an intruder or subordinate. Fighting involves growling, biting, wrestling and chasing.

wrestle (wrs):

Wrestling occurs during courtship and copulation or in an aggressive situation. The animals face each other and inter-lock (clasping each other with fore-limbs) their necks alternately left and right in attempt to bite each other's neck and/or head. Sometimes they may use their forepaws to wrestle, standing upright on their hind legs. This serves to push the opponent away.

bite (bt):

The bite is aimed at the head and neck region of the opposition. During the courtship period prior to and during copulation both the animals involved bit each other with an inhibited bite i.e. the mouth is gaped but the jaws do not close on the opponent.

scratch (sct):

The animal scratched the ground with a fore paw whilst in a crouched position. This is also performed in a threat situation, often as a warning before fighting.

BEHAVIOUR COMPLEXES

Male dominance behaviour

Agonism between the dominant or adult male and the subordinates occurs at the HBS during the period of parental care after the young have emerged from the burrow. Most often the adult (Male) will leap over the back of the individual, anal marking (pers.obs) the back of the subordinate as it does so. The adult circles the subordinate, moves away a few feet and grooms vigorously for a few seconds. During this behaviour complex, the subordinate takes on a crouching pose when the adult is close, and then resumes normal posture. It often runs off the HBS, with the adult following a few seconds later.

Juvenile submission behaviour

Submission behaviour is shown when the subordinate approaches the adult in a submissive crouch, and invites the adult to perform agonistic (dominance) behaviour. The young animal is subordinate to the adult, and this is indicated by means of crouching behaviour when approached by the adult. The young will arch its back and crouch down onto its fore limbs so that its head is against the ground and lower than the tail. The animal will then snarl, bare its teeth, and may growl softly. This behaviour pattern complex was taken to indicate submissiveness. The adult responds by leaping over the subordinate's back. This behaviour appears more frequently than the above, and in many instances the adult ignores the often persistent juvenile.

Threat behaviour

Both male and female *Cynictis penicillata* approach the intruder (eg *C.penicillata*) growling and baring teeth. There is pilo-erection of the tail and back which serves to increase the apparent size of the animal. Chasing and jumping take place and the animal may rapidly "tour" around the HBS, marking and smelling marking posts as it does so. Direct attacks are not made towards the intruder.

BREEDING

submissive (sub):

The female becomes submissive to the male during the courtship for a short period, and the young and subordinates are submissive. This is demonstrated variously by: crouching, appeasement calls, turning the back on the dominant, allogrooming etc as dealt with above.

chase (chs):

(see above)

copulate (cop):

The act of copulation involves a sequence of behaviours ultimately resulting in the male mounting the female and ejaculating. The entire act is repeated many times throughout a two to three day period and begins with the two animals circling. The male is next to the female and slightly behind her. Mounting takes place from the side or the rear and the male holds onto the female with his forelimbs and paws. Penal penetration takes place almost immediately after mounting, when the male holds the female even tighter and performs pelvic thrusts. The male's head is often laid against the females back and quiet low vocalisations are emitted. Alternately, the male draws the female right over until he is in the sacral position, and she is above him. The male then "rocks" the female over himself. There is neck nibbling (inhibited neck biting) during the copulation process, and often agonism (see later).

BEHAVIOUR COMPLEXES

Courtship behaviour is an important precursor to mating in *Cynictis penicillata*. The male initiates the sequence by approaching. For a few days before mounting is accomplished the male marks the home range at a very high rate and intensity. The female is generally very aggressive towards the male, and the male towards the female. The persistent approaches of the male are accompanied by snarls and growls from other members. (The actual behaviour is complex, and is dealt with in a later chapter).

The female performs submissive behavioural sequences as described above. These displays during courtship apparently indicate mate acceptance: the marked change from aggression to submission (and promiscuity) during the few days of courtship are communicated to the male/s in this way. These few days may defined as the oestrus period.

OTHER

excavation/digging (exc):

Using the forepaws and claws to dig away sand and gravel which is kicked backwards between the hind legs. This behaviour is performed either during foraging or when the animals alter the burrow system. Sometimes the hind feet are used to kick back excavated material.

play (pl):

There were no records of distinctive play behaviour in adult *Cynictis penicillata*, although certain behavioural play sequences were performed by young. Here the animals performed stand high, chasing, neck-wrestling, digging, jumping, running in circle, etc.

BEHAVIOUR COMPLEXES

The excavation behavioural sequence combines digging, HBS touring, smelling and marking in a vigorous activity combination. It is exhibited exclusively by the dominant resident male and performed:

(a) prior to the onset of courtship behaviour;
(b) when the male has taken over or moved into a new home range;
(c) in a lesser form every morning prior to leaving the burrow system.

As a result, display of the courtship or the occupation of a new burrow system takes place in which the male may be overtly "advertising": primarily to the female in the home range, and secondarily to neighbouring males.

This behaviour is shown when an overt change in the state of the territorial "status quo" due either to the onset of oestrus in the female, or to a change in the dominance status of the male concerned occurs.

The excavation behaviour complex is performed by the male only, and is not only done in the presence of the female. The behaviour may have the secondary effect of a longer term message on the recipient of the display: that effect being the more permanent alterations to the immediate micro habitat, or HBS, which is often re-dug.

Throughout the sequence, the animal is extremely alert and nervous with a high degree of vigilance for predators, or perhaps conspecifics. (The vigilance can be regarded as first level alertness, where the animal stands on its hind legs and appears fully alert). Marking behaviour includes cheek marking and anal dragging. The objects marked range from burrow entrances (most) to bushes and other animals at the HBS at the time.

The most commonly occurring behaviour pattern in *Cynictis penicillata* is foraging, both in the number of days it was observed and the percentage daily time budget spent on this activity (see table 6.1).

Although detailed behavioural observations could only take place at the home burrow system, it is obvious that *Cynictis penicillata* forages for the greatest percentage of its activity time. Foraging varies in duration during the different seasons due to differences in the availability of food resources (pers.obs.). A lower frequency of foraging activities is also seen during the periods after the offspring are borne due to time allocated to parental care of the young by both adults.

Cynictis penicillata also spends a considerable amount of time in the burrow system (bur) during the night, and may return to the burrow several times during the day. This activity is often associated with either:- predation factors,

- parental care,
- climatic factors,
- rest and sleep.

A large increase in the amount of time spent in the burrows is seen during the breeding season, when adult male and female alternate foraging trips with remaining at the home burrow system with the young.

Other activities which *Cynictis penicillata* performs for relatively long periods of time are sunbathing in various postures at the home burrow system before foraging activities begin. Sunbathing is particularly evident during the colder winter months. Sunbathing may raise *Cynictis penicillata's* body temperature after emerging from the burrows in the cold mornings, although no physiological data is available to support this. The amount of time spent sunbathing varies with the ambient temperature and decreases from winter to summer. *Cynictis penicillata* may spend up to 3,5 hours sunbathing in the winter compared to only 2 minutes in the summer. Behaviour associated with sunbathing is marked with "*" in Table 6.1

Those activities occurring most frequently are generally associated with maintenance and territorial behaviour. Foraging activity includes touring the home range and marking.

Marking behaviour occurs with a high frequency (combined total of all marking postures), although time actually spent marking is very short. Similarly, grooming, standing, walking etc are all activities which *Cynictis penicillata* performs every day in routine behaviour. However, there are certain behaviour patterns which only occur under certain circumstances and at certain times of the year. These, therefore, have a low frequency of occurrence, or may not even be represented in this observation period. Interactions with conspecifics and with other species are an example of these types of behaviour complexes.

Table A.2 Summary of frequency of occurrence of behavioural parameters taken over a 40 day continuous observation period which included a breeding season. The observation period occurred during summer.

BEHAVIOUR	**No. of days occurring. N = 40**	**Percentage of behavioural repertoire over 40 day period**
Stand	40	19,09
Walk	38	12,23
Forage	38	26,98
smelling	37	7,30
stand high	37	5,50
mark	37	5,05
run	35	7,08
sit up	33	8,95
burrow	33	12,99
excavate	28	12,90
defecate	16	2,04
interact	14	6,67
scratch	12	1,72

stretch	9	1,58
groom	7	1,62
sunbathe	5	12,06
dive	5	1,03
sit medium	4	12,95
yawn	4	2,45
growl	4	1,23
sit low	3	6,45
sit high	3	0,95
fight	2	3,70
submissive	2	0,60
alert	2	0,40

Vigilance behaviour accounts for a total of 24,19 % of the various behaviour patterns at the home burrow system. This includes activities such as running, stand high, sit up, dive, alert, and growl.

The following behaviours were observed during inter- and intra-specific interactions (some of which may be regarded as ritualized behaviour) they are described above as behaviour complexes:

1. threat behaviour when an unfamiliar, new or non-territorial animal comes onto the HBS;
2. Behaviour between the male and a subordinate member of a group during parental care activities;
3. Female dominance behaviour towards the male: indifference and growls - during both breeding and non-breeding periods;
4. Tail piloerection - exhibited during agonistic encounters;
5. Marking behaviour;
6. Digging and excavation;
7. Tour of HBS combined with marking/digging/smelling;
8. Defecation when another animal is at the HBS;
9. Urination - specially during the breeding season.

The term "display" is used to designate a pattern of social behaviour that is species specific and forms a part of the communicative system within or between social groups, or between individuals. In *Cynictis penicillata*, displays may be classed as part of ritualised behaviour. Here the process of ritualization (Cullen 1966) results in an increase in the conspicuousness of signals with concomitant decrease in ambiguity. Ploog (1970) suggested that ritualization is the "adaptive canalization of expressive behaviour", and gives the example from Ewer (1960) of play in Canids which becomes species typical and more ritualized as they become adults (e.g. re-ordering of sequences, repetition, exaggeration). In mongooses this is particularly relevant when considering exaggerated and repetitive behaviour. This behaviour appears to increase the efficiency of message transmission, which may be further increased by either animal in the interaction. Facial expressions, gestures, body posture, and vocalizations may also increase message reception if ritualized (Bekoff 1980).

The function of this behavioural sequence is to maintain the dominant - subordinate position between the individuals concerned. This may also serve to maintain the bond between the male and the offspring. The young may learn foraging and defence techniques from the male (see later) in this manner.

Behaviour indicating threat to another individual is shown when strange conspecifics or other species approach the HBS, and in particular towards *Galerella pulverulenta*. (The behaviour shown towards the *S. suricatta*, for example, differs and is more an indication of acceptance of their presence. Agonistic behaviour is shown towards *Galerella pulverulenta*, whereas *S. suricatta* moves about the HBS with little interaction from *Cynictis penicillata*.

The term communication has been defined as the passing of information from one animal to another by means of signals that have evolved for the purpose (Deag 1980). In general animals lower in the phylogenetic scale communicate by means of signals that are under direct genetic control and relatively free of learned components. The communication of mammals are under enough genetic control to result in clear-cut, species specific signals but are often marked by individuality, and a subtle relationship to the prevailing context. Often these signals are fixed action patterns, the individual responding according to particular stimuli in a particular way.

APPENDIX B

GLOSSARY and DEFINITIONS

SOCIAL DOMINANCE

Dominance has two meanings. It is usually the ranking of one animal over another in a fairly stable hierarchy of threats. It may also mean the priority of one animal over another for access to a scarce resource, particularly food or mates.

Social dominance and aggression are terms sometimes used synonymously due to their intimate relationship. Separating the two is made difficult due to their amorphousness, and the fact that both terms encompass a broad variety of behavioural patterns and motivational cues (Hinde 1978; Benton et al 1980' Bernstein 1981; Brain 1981). One response to the lack of consensus, in an attempt to provide a coherent framework from which theories and hypotheses concerning the subjects can work, is to dispense with the terms social dominance and aggression, and to substitute more acute definitions.

Some schools of thought (Gartland 1968; Drews 1973; Rowell 1974) disregard the concept of social dominance: that social dominance is an artificial abstraction of little explanatory or descriptive utility (Gartland 1968; Drews 1973; Rowell 1974).
However, in the context of this thesis the concept of social dominance and of aggression is accepted. The question which can be addressed here is: to what extent is dominance in animals a function of aggression: i.e. is the display of aggression an adequate indication of a particular animal's dominance status ?

Francis (1988) found that, in the paradise fish, *Macropodus opercularis*, dominance is not highly correlated with aggressiveness. He gives a possible explanation for this : perhaps in many contexts dominance status is not related to individual differences in aggressiveness, even when the establishment of dominance relationships is obviously mediated by aggressive behaviour.

DOMINANCE

A working definition for any subject is essential before the subject can be fully discussed and analyzed. Three varying definitions for the term dominance are considered (Francis 1988):

a) Dominance has been considered by some as an individual capacity (Dewsbury, 1982). In this definition dominance is the ability of an individual to prevail in a conflict or in which sense dominance can be subject to selection. Dominance in this sense is termed dominance ability.

b) Dominance has been considered a state - the condition of being dominant. This term indicates the condition of being subordinate or of a particular rank, and is often referred to as "dominance status".

c) Dominance has also been considered a relational quality (eg. Bernstein 1981). In this sense dominance is a particular kind of social relationship, usually defined in terms of a polarity in agonistic interactions, and referred to as a dominance relationship (Francis 1988). Of particular importance to this definition is the restricted application of the term to stable non-territorial interactions involving individual recognition.

Functional accounts of dominance are generally associated with access to resources (Popp & DeVore 1979). However it can be argued that in many species dominance is highly context specific. i.e. dominance relationships are largely externally determined. Contextual variables include:

- prior residency,
- seniority

- presence or absence of allies
- prior experience
- resource availability
- territoriality

Finally, dominance relationships are not intrinsic to individual organisms. It is a supra-individual quality (Francis 1988) and is a relationship context in which the behaviour of individuals is involved, and it is thus contextually embedded.

Although many dominance relationships are established and decided through non-aggressive means, aggression is often the easiest way in which to recognise dominance. Alternatively the submissive behaviour of the subordinate individual, which is a manifestation of a dominance relationship,is noted and the dominance relationship established by this means. Both methods were used in defining these behavioural parameters in this thesis. However, the fact that dominance relationships can be operationally defined by means of submissive behaviour does not, as implied by Rowell (1979), imply that the relationship is controlled by the behaviour of he subordinate, or invalidate the notion of dominance (Francis 1988).

Appeasement behaviour by an individual is a ritualised gesture (including vocalizations and scents) of submission. It is commonly the opposite of a threat gesture, taking the form of stances such as crouching which reduces apparent size and hides marking of sex and species. Many appeasement gestures mimic female or infantile behaviour.

The final dichotomy to be mentioned in the concept of social dominance, and which I reject on account of definition, is implicit in the distinction between dominance relationships in group-living animals and dominance relationships resulting from dyadic encounters in less social animals, often referred to as contests. In current research, however, pair-wise testing has been of special interest to ethologists and advocates of game theory. Dominance relationships in group-living animals have fallen primarily under the scope of primatologists and animal sociologists (Allee 1942).

AGGRESSION

Aggression can be defined as an attack or threat of attack. Aggressive motivation is the disposition to behave in this manner. In an ethological analysis of agonistic behaviour it is customary to distinguish between two underlying motivation variables: fear and aggression (e.g. Blurton-Jones 1968; Rasa 1969). These variables are the primary factors which may, however, interact in their effects on behaviour. According to this analysis, dominant individuals exhibit a higher ratio of aggression to fear than do submissive individuals, and this proportion is the major determinant of dominance status.

Aggression plays only a limited role in determining dominance status, and many other factors are involved in distinguishing dominant and subordinate individuals. Size, variation in colour patterns and morphological features (e.g. antlers, horns, wattles, tail length) play significant roles in a variety of animals. Differences in any of these characters have been shown to have an influence on dominance status. Prior experience of successes and defeats are other factors which may effect the dominance of an individual.

Maslow (1936) realized that the apparently sexual mounting and presenting of macaque monkeys is often a ritualized gesture of threat or appeasement. In most straightforward situations the threat hierarchy correlates with access to food or mates. However, there are more complicated situations, such as when status has a geographical factor, when threat and food priority differ between the two sexes, or when the most advantageous strategy depends on the strategy of competitors - i.e. territoriality. In some primate species the sexes are ranked separately, and the females have priority to food while males maintain a threat hierarchy amongst themselves with little reference to the females. There are many far more complicated situations in which there are combinations and variations of social hierarchies and social dominance.

The costs and benefits of high rank depends on the strategies of one's opponents. In some species, or social situations, one may find an ESS in which some animals achieve partial reproductive priority by social dominance, while others may chose to remain subordinate. The advantages of being subordinate depend on the number and status of the dominants, while the advantages of being dominant depend on the subordinance of the subordinates (Maynard -Smith 1972; 1979). True dominance hierarchies with individual recognition have often been interpreted as beneficial for the whole group because they cut down the amount of overt aggression in the group. However, accounts in terms of benefits to the group are not generally thought to have any explanatory power, and the existence of dominance hierarchies has to be explained in terms of benefits and costs to individuals surrendering or not surrendering in particular circumstances.

SOCIAL HIERARCHY

If dominance relationships are randomly formed the dominance hierarchies are significantly linear. An individual can be considered dominant if it wins over 50 % of its interactions with the other member of the dyad.

Many animals display different hierarchies in accordance with a different base point, i.e. a hierarchy may exist for breeding which is different to that for feeding. This is reasonably common in certain species where there's competition for resources such as food or mates. In this circumstance, the dominance hierarchy may change between, for example, breeding and non-breeding seasons, or the different hierarchies may operate simultaneously.

Animals may exhibit various types of hierarchical structure in a group, or in a social interaction, based on one or a combination of the following:

1. Breeding hierarchy
2. Feeding hierarchy
3. dominance reversal (in polyandrous females)

BREEDING DOMINANCE AND DOMINANCE REVERSAL

During the breeding period, the male *Cynictis penicillata* undergoes a dominance reversal and becomes subordinate to the female until the offspring leave the HBS. The onset of subordinate behaviour is at the beginning of the courtship period when the female *Cynictis penicillata* displays and elicits appeasement behaviour from the male. Prior to the onset of breeding, the male is dominant and the female exhibits submissive behaviours.

The dominant status of the animal places it in a favourable position of greater access to foraging time and manipulation of the other sex. The female is seen to dominate copulation in allowing the male to mount. However, the male is extremely defensive of the female "resource" due to intrasexual competition and will monopolizes her by attempting to prevent her from leaving the HBS in the event of other males from other territories mating with her (which does occur).

Because *Cynictis penicillata* is not a social species, the dominance hierarchies in a "group" are difficult to define and are only evident at certain times of the year. The young are always subordinate to the adults, and do not gain biased access to food as reported in (Rasa 1977). The male accompanies the young foraging, but I have not recorded an incident where the male relinquished his food to the young individual.