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SPACE USE AND GROUP LIVING IN THE CAPE PORCUPINE
(*HYSTRIX AFRICAEAUSTRALIS* PETERS, 1852)

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by

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ABSTRACT

Ten Cape porcupines were radiotracked for one year in a savanna ecosystem at Nylsvley Nature Reserve, Transvaal, South Africa. Social organisation was characterised by family groups comprising a monogamous adult pair and immature offspring. Pair members usually shared the same burrow and utilised similar home range areas. Group size is probably determined by the time of offspring dispersal which is dependent upon population density and resource dispersion and abundance. Total home ranges (100% locations) of neighbouring pairs often showed considerable overlap, although areas of intensive use (90% locations) were largely exclusive and are thought to be defended as territories. Temporal space use patterns suggest that neighbours rarely encounter one another, indicating territorial maintenance through scent marking. Natural foragers had larger home ranges in winter than in summer, whereas range size of crop foragers was aseasonal, suggesting that range size in natural environments is determined by seasonal food availability.

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CHAPTER 1: INTRODUCTION

INTRODUCTION

The Cape porcupine (Hystrix africaeaustralis Peters, 1852) is a hystricomorph rodent belonging to the family Hystricidae, the Old World porcupines. Two seperate species, H. capensis Grill,1858 and H. stegmani Muller, 1910, and two subspecies H. a. prittwitzi Muller, 1910 and H. a. zuluensis Roberts, 1936 were formerly recognised, but all of these are now regarded as a single species H. africaeaustralis with no distinct subspecies (Corbet & Jones 1965, Meester, Rautenbach, Dippenaar & Baker 1986). They are distributed throughout southern Africa, extending as far north as Tanzania, northern Zaire and southern Kenya and Uganda where they occur sympatrically with the very similar crested porcupine (H. cristata), although no intermediate forms have been recorded (Corbet & Jones 1965, Kingdon 1974, De Graaff 1981), (Fig.1). There are another seven species in the genus Hystrix which are distributed throughout Africa and Asia (Corbet & Hill 1986). H. africaeaustralis, H. cristata, H. indica and H. brachyura are all similar in appearance and, from what is known, in habits and general biology as well. However, very little is known about the other four species, H. crassispinis, H. javanica, H. pumilis and H. sumatrae, all of which inhabit the forests of southeast Asia (Corbet & Hill 1986).

Porcupines have a wide ecological tolerance and are found in all habitats except rainforests and swamps. They favour hilly, rocky areas where they use caves and crevices as shelter, although they often inhabit extensive burrow systems which they dig themselves or modify from aardvark (Orycteropus afer) burrows (Skinner & Smithers 1990). These burrows may be shared with other species for example aardvark, warthog (Phacochoerus aethiopicus), brown hyaena (Hyaena brunnae) and spotted hyaena (Crocutta crocutta) (Mills & Haagner 1989, pers. obs.); a phenomenon also reported for other Hystrix spp. ,e.g., H.

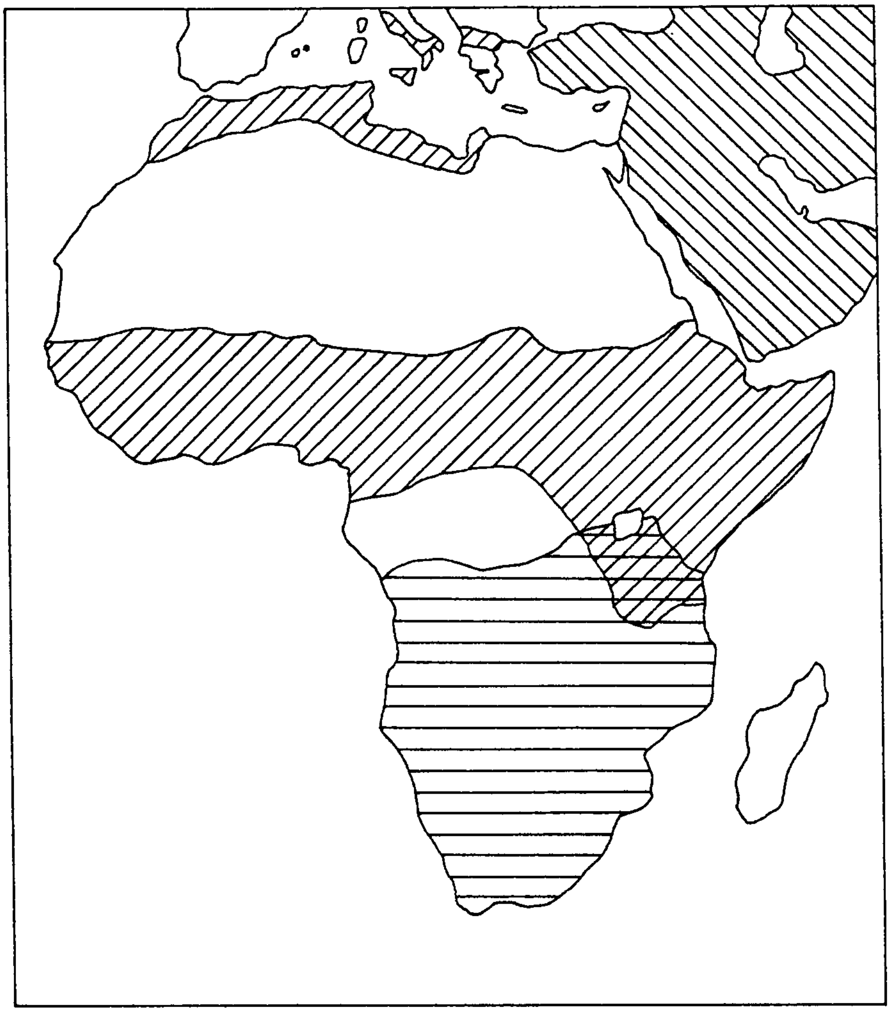

Figure 1: Distribution of *Hystrix* spp. in Africa, the Middle East and Europe.

▤ *H. africaeaustralis*, Cape porcupine (from Skinner & Smithers 1990).

▨ *H. cristata*, Crested porcupine (from Santini 1980).

▧ *H. indica*, Indian crested porcupine (from Von Kumerloeve 1967, Sever & Mendelssohn 1988a).

cristata cohabiting with European badgers (Meles meles) in Italy (Pigozzi 1986) and Indian crested porcupines H. indica cohabiting with Striped hyaenas (Hyaena hyaena) in India (G.B.Corbet pers. comm.*). Burrows often have several entrances with deep tunnels up to 20 m in length which are often interconnected. The ground above the burrow system is often a raised mound of bare earth in which the entrances are situated and large systems are probably used by many consecutive generations of porcupines (Shortridge 1934, Kingdon 1974, Greaves & Aziz Khan 1978).

Porcupines are nocturnal and may travel up to 16 km in a night while foraging, often using regular pathways (Shortridge 1934, Skinner & Smithers 1990). They feed mainly on roots, tubers and bulbs which they excavate using powerful forelimbs equipped with strong claws. A wide variety of fallen fruits and seed pods, the bark of trees and the shoots, stems and leaves of various herbaceous plants are also eaten. In addition, porcupines often eat and cause extensive damage to cultivated crops, for example, sweet potatoes, maize, groundnuts and melons and are therefore regarded as pests in many agricultural areas (Kingdon 1974, Van Aarde 1987a, De Villiers pers.comm.*). Thomson (1974) and Yeaton (1988) have suggested that the ringbarking of dominant tree species by porcupines may be important for the successional change and cyclicity of riperian and savanna woodland communities, as the damaged trees may die or be destroyed by fire so creating space for fresh growth and regeneration. Greaves & Aziz Khan (1978) report that H. indica is considered a serious pest in India and Pakistan due to its ringbarking activities in forestry plantations.

Porcupines are large rodents, adults collected in Cape Province and Orange Free State weighing between 10 and 18 kg with a mean of approximately 12 kg (Gaigher & Currie 1979, Van Aarde 1987b). However, further north in

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Zimbabwe a mean weight of about 18 kg with a maximum of 24 kg has been recorded (Smithers & Wilson 1979). There is some evidence for slight female-biased sexual size dimorphism in H. indica and H. cristata (Alkon & Saltz 1983, Pigozzi 1987) although there is no evidence for this in H. africaeaustralis (Van Aarde 1987b). In captivity, porcupines may live for up to 20 years, although 12 to 15 years is normal (Kingdon 1974, Greaves & Aziz Khan 1979, Van Aarde 1985a).

The porcupines' quills provide formidable protection against their natural predators which include lions (Panthera leo), leopards (P. pardus), spotted hyaenas and caracal (Felis caracal), (Shortridge 1934, Kruuk 1972, Kingdon 1974, Van Aarde pers.comm). Porcupines, although normally shy, become very aggressive when harassed and will charge backwards or sideways at their attacker, being capable of inflicting severe wounds with their quills. Juveniles are accompanied by one or both parents while foraging, and in captivity the parents, particularily the male, are very protective of their offspring (Grant 1984, Van Aarde 1987a). There has been no thorough study of their social organization but most observations suggest that they live in pairs or small groups (Shortridge 1934, Kingdon 1974, Van Aarde 1987b), although up to eight adults may share a burrow and R.J.van Aarde (pers.comm.*) reports one group of 14 individuals cohabiting. Similar observations of parental care and social organisation have been made for H. indica (Greaves & Aziz Khan 1978, Tohmé & Tohmé 1980, Sever & Mendelssohn 1988a, Saltz & Alkon 1989), H. cristata (Santini 1980, G.Pigozzi pers.comm.*) and the Himalayan porcupine (H. hodgsoni) (Gosling 1980). In captivity there appears to be no aggression between mature offspring and their parents, so that an extended family group may develop, consisting of a monogamous parental pair with both

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their mature and immature offspring (Morris & Van Aarde 1985). In the captive Cape porcupine colony at the University of Pretoria's Experimental Farm one group grew to eight members and Mendelsshon reported that over a ten year period one captive group of H. indica grew to 17 members (R.J.Van Aarde pers.comm.). Captive family members have been observed to spend a large proportion of their time in close proximity to each other and they usually huddle together when resting (Grant 1984). The monogamous pair bond appears to be maintained by daily sexual activity (Morris & Van Aarde 1985) which has also been described for H. indica (Sever & Mendelssohn 1988b). However, extra-pair copulation may occur when the opportunity is presented in a captive situation (Morris & Van Aarde 1985). Most observations of porcupines roaming at night indicate that they usually roam alone, or sometimes in pairs of an adult and juvenile or two adults; occasionally small "family" parties have been observed (Shortridge 1934, Kingdon 1974, Van Aarde 1987a).

The reproductive biology of the Cape porcupine has been well studied (Skinner, Van Aarde & Van Jaarsveld 1984, Morris & Van Aarde 1985, Van Aarde 1985b, 1985c, Van Aarde 1987a, 1987b, 1987c, Van Aarde & Skinner 1986a, 1986b Van Aarde & Van Wyk 1991). In the wild, female porcupines give birth once a year, usually during the hot, wet summer months, to a litter of 1-3 precocial young, after a gestation period of about 93 days. In captivity parturition appears to be less seasonal and two litters per year have occassionally been recorded. The young are weaned after approximately ten weeks, although suckling often continues until the twentieth week post-partum (Grant 1984). Sexual maturity is reached at 9-16 months in females and 8-18 months in males. The mature offspring within captive family groups are physically capable of reproducing, the females display ovarian cycles and incestuous copulations occur. However, only the dominant female conceives and bears young. Incestuous reproduction has only been recorded on one occasion, when the female parent died and her mature twin daughters were both mated by their father. Both twins conceived and bore live young, although one sister's offspring were killed shortly after birth, probably by the dominant sister.In the group of 17 H. indica observed by Mendelsshon only the dominant female bred (R.J.Van Aarde pers.comm.). P.U.Alkon (pers.comm.*) also observed a captive male Indian crested porcupine to mate two females, the pups of one female being killed by the other.

Van Aarde (1987a, 1987b) has suggested that porcupine populations may be regulated by a density dependent factor whereby a female may only disperse from her natal group to breed when a vacancy occurs through the death or emigration of a neighbouring female.

Captive porcupines have been observed to scent-mark their enclosures by defecation, urination and perineal dragging (to deposit secretions from their anal glands), and to aggressively defend them against conspecific intruders (Grant 1984, Ferguson 1987). It is therefore possible that free-ranging porcupines may maintain a group territory through scent-marking and/or active defense.

Although it has been established that free-ranging porcupines live in groups, very little is known about their social organisation, behaviour and ecology.

A social group is a permenant or semi-permenant aggregation of two or more conspecifics, in which the individuals within the group presumably derive benefits from group membership. There are many theories as to the advantages of group living. These include anti-predator defence, increased foraging or hunting efficiency, resource defence (including mate guarding), territorial maintenance, territorial inheritance by offspring, increased reproductive opportunities, greater offspring survival and energetic benefits; many of which involve the cooperative behaviour of the group members. In some instances group living may be enforced by the delayed maturity of offspring or

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the inhibition of offspring dispersal (Brown & Orians 1970, Fedyk 1971, Kruuk 1972, Jarman 1974, Crook, Ellis & Goss-Custard 1976, Banks 1977, Eisenberg 1977, Kleiman 1977, Waser & Wiley 1979, Armitage 1981, Clutton-Brock 1984, Lindeström 1986, Bertram 1987, Cowan 1987, Arnold 1988, Rayor 1988, Canals, Rosenmann & Bozinovic 1989, Kruuk 1989).

Whether or not the above factors are evolutionary causes, or beneficial consequences of group living cannot be determined. However, if such factors confer advantages to group members, that are ultimately reflected in increased reproductive sucess, they will be evolutionarily perpetuated as will the practice of group living in the species.

The aim of the present study is therefore to investigate some of the factors related to group living in the Cape porcupine. As sociality is closely interlinked with intraspecific spatial relationships, space use will also be investigated. Due to the difficulties of studying many of these factors, particularily in a shy, nocturnal animal, it was decided to undertake an intensive radiotracking study to determine the social organisation, space use, and activity patterns of the Cape porcupine. Such information is an essential prerequisite for an understanding of the ecology and population dynamics of any species and is vital if conservation or control programmes are to be successfully implemented. Radiotracking allows for the simultaneous investigation of these factors for several animals under undisturbed, natural conditions. Additionally, the body temperature and behavioural circadian rhythms of captive Cape porcupines will be measured to complement the indirect estimates of activity circadian rhythms made in the field. Body temperature is often closley related to activity levels, although a circadian cycle of T_b, independent of activity, may also exist (Hart 1971, Pauls 1979).

KEY QUESTIONS

1. What is the social organisation of the Cape porcupine ?
2. Are Cape porcupines territorial ?
3. How is the home range/territory divided amongst group members ?
4. If Cape porcupines are territorial, how are territories maintained and is group living important for such maintenance ?
5. Are home ranges/territories temporally stable ?
6. What determines home range/territory size ?
7. What is the daily activity pattern of the Cape porcupine ?
8. Are there seasonal differences in social organisation, space use and activity patterns and if so what are the causes, social or environmental ?
9. Why does such a system of social organisation and space use exist ?

The relevance of these and other factors, for which there is sufficient evidence, will be discussed with reference to group living in the Cape porcupine.

THE CONCEPT OF HOME RANGE AND TERRITORIALITY

Harris, Cresswell, Forde, Trewhella, Woollard & Wray (1990) defined a home range as consisting of a more or less restricted area within which an animal moves when performing its normal activities. However, as an individuals range may change over time, the period for which it is measured must be specified in order for the measurement to be meaningful. The exact size and shape of a home range may have little significance in themselves, as they may be largely dependent on the method used to determine them. Alternatively, they may be closely related to factors such as population density, intra- or interspecific interactions and resource abundance and distribution (Sanderson 1966, King 1975, Cooper 1978, Waser & Wiley 1979, Kruuk & Parish 1982, Wolton 1985, Carr & Macdonald 1986, Harris et al.1990, Hewson & Hinge 1990, Horner & Powell 1990, Ortega 1990).

Animals rarely utilize their potential habitat in an entirely random or uniform manner. Departures from random or uniform distribution may result from non-uniformity of habitat, in terms of resource distribution or impassable terrain, or from attraction to, or avoidance of, other animals (Brown & Orians 1970, Samuel, Pierce & Garton 1985). The clumped or patchy use of areas within home ranges requires analyses that emphasise internal structure of home ranges and not merely outlines or total-area measures (Horner & Powell 1990). Disproportionate space use creates areas of concentrated space use, or "core areas" which Samuel et al.(1985) defined as an area where space use exceeds that expected from a uniform distribution. As with home ranges, the size and location of a core area will be dependent upon the method used to determine it.

Having characterised an individuals home range, intraspecific spatial relationships may then be investigated. Firstly, having determined the social organisation of the species concerned, the individuals use of space with respect to other members of its social group, if such a group exists, may be studied. Secondly, spatial relationships between neighbouring individuals or groups can be considered which can lead to the question of territoriality. The degree to which the home ranges of conspecifics overlap, from complete overlap to exclusive ranges, varies between species and also within different populations of the same species (Brown & Orians 1970). Davies (1987) defined a territory as "whenever individuals or groups are spaced out more than would be expected from a random occupation of suitable habitats" but added that such spacing may be referred to as a territory if it is due to interactions between groups or individuals. This recognises the fact that territoriality is as much a behavioural as it is a spatial phenomenon. Territorial behaviour may take the form of active defense such as attacking or chasing intruders or may involve passive defence or maintenance, for example, displays, vocalization or scent marking (Brown & Orians 1970, Hendrick 1984, Davies 1987, Gorman 1990). Brown & Orians (1970) reserved the term territory for strictly defended areas with no overlapping boundaries. However, King (1975) pointed out that unless an animal is highly mobile it may be impossible for it to actively defend a territory, thus many mammals maintain a territory through indirect communication. Such maintenance requires an overlap zone between neighbours to facilitate the transmission of olfactory, visual or auditory signals so enabling neighbours to avoid potentially dangerous close contact with one another. Ewer (1968) noted that "it is not uncommon to find that while the home ranges overlap, the core areas do not". If such non-overlapping core areas are defended, they may be considered to be territories, thus an exclusive territory may exist within a non-exclusive home range. I shall therefore define a territory as follows, "a territory is an area that is largely exclusive to an individual or group and is defended in some manner against conspecifics". It also occupies a fairly stable position over a period of time, although it is not necessarily permenant (Brown & Orians 1970). In addition to spatial overlap, temporal overlap or avoidance should be considered, as an area may be used exclusively by an individual at any moment in time but may be shared with conspecifics over a longer time period (Macdonald, Ball & Hough 1980, Davies 1987).

However, as Hendrick (1984) stated, "The home range of an organism is generally larger than it's territory, but because the aggressive interactions used in defining territorial limits are often difficult to observe, home ranges are often more practical to examine.". Therefore, the initial aim of this study with respect to space use will concentrate on determining home range areas. Spatial, temporal and behavioural evidence for territoriality will then be examined.

STUDY AREA

Fieldwork was conducted at Nylsvley Nature Reserve, situated in the central Transvaal between 24°36' and 24°42'S latitude and 28°40' and 28°44'E longitude (Fig. 2). The reserve covers 3,120 ha of undulating to flat terrain between 1,080 m and 1,154 m altitude and the vegetation consists of mixed grassland and deciduous woodland savanna. The study area comprised approximately 1,000 ha at the southern end of the reserve where an Eragrostis pallens-Burkea spp. woodland savanna community dominates (Coetzee, Van der Meulen, Zwanziger, Gonsalves & Weisser 1976). A small hill, Maroelakop (1,154 m), occupies the centre of the study area and the small, seasonal Nyl River runs approximately 2 km to the north.

The areas adjacent to the reserve are largely bushveld with vegetation similar to that within the reserve. To the south of the study area is Blindfontein Farm on which maize and watermelons are cultivated.

The climate is characterized by hot, wet summers and cool, dry winters. Summer maximum and minimum temperatures are approximately 35°C and 15°C respectively (December) and the corresponding temperatures for winter are approximately 25°C and 0°C (June). The average annual rainfall is 630 mm, the majority of which falls from October to March (Coetzee et al.1976).

Sunset and sunrise at the winter solstice occur at 17:15 & 06:45 and at the summer solstice 18:45 and 05:15 respectively. With approximately 45 minutes of semi-darkness after sunset and before sunrise, a maximum of 12 hours total darkness occurs in winter (18.00 - 06.00) and 9 hours in summer (19.30 - 04.30).

The larger mammalian fauna in the reserve includes over 300 impala (Aepyceros melampus), approximately 100 kudu (Tragelaphus strepsiceros) and 100 reedbuck (Redunca arundinum) as well as large numbers of warthog, common duiker (Sylvicapra grimmia) and steenbok (Raphicerus campestris). There are smaller numbers of blue wildebeest (Connochaetes taurinus), tsessebe

(_Damaliscus lunatus_), waterbuck (_Kobus ellipsiprymnus_), giraffe (_Giraffa camelopardalis_), roan (_Hippotragus equinus_), bushbuck (_Traphelagus scriptus_), zebra (_Equus burchelli_), bushpig (_Potamocherus porcus_) and aardvark, (J.Coetzee _pers.comm._*).

Large carnivores are scarce with only a very small number of resident brown hyaena and possibly caracal (_Felis caracal_). Leopards are rare transients. The largest carnivore to occur in significant numbers in the reserve is the black-backed jackal (_Canis mesomelas_).

The smaller mammalian fauna of the reserve includes springhares (_Pedetes capensis_), scrub hares (_Lepus saxatalis_), tree squirrels (_Paraxerus cepapi_) and several species of Muridae, the most common of which are the bushveld gerbil (_Tatera leucogaster_), the highveld gerbil (_T. brantsii_), the grey climbing mouse (_Dendromus melanotis_), the multimamate mouse (_Praomys natalensis_) and the pygmy mouse (_Mus minutoides_), (Korn 1987, J.Coetzee _pers. comm._).

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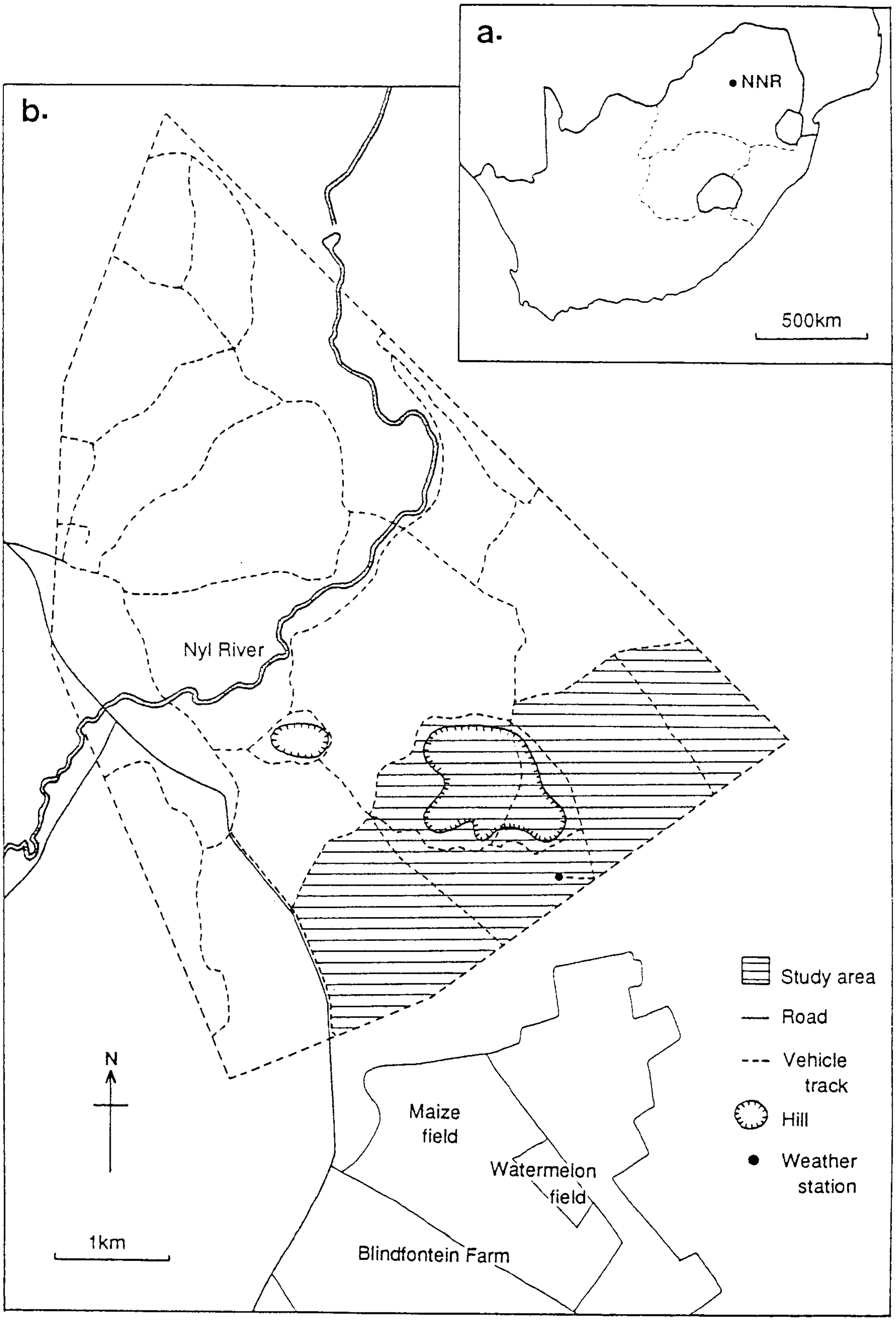

Figure 2: Map of South Africa showing the location of Nylsvley Nature Reserve (a) and map of Nylsvley Nature Reserve showing the study area (b).

CHAPTER 2: MATERIALS AND METHODS

CAPTURE OF STUDY ANIMALS

Trapping

Porcupine burrow systems were located with the help of the reserve rangers. Occupancy was determined by the presence of quills, tail "brush-marks" and/or footprints (rare) around the burrow entrances. Subsequently more burrows were located by identifying the daytime positions of radiocollared porcupines. A total of 28 burrows were located of which 14 were used as trapping sites, Fig.3.

Live traps, (130 x 75 x 75 cm), baited with fresh vegetables, were placed on level ground close to a burrow entrance and checked every morning. To facilitate the trapping of burrow occupants a wire mesh tunnel was constructed between the burrow entrance and the trap entrance. All other entrances to the system, from zero to five, were sealed with wire mesh pegged to the ground. Thus, the only exit from the burrow led straight into the trap. Despite laying seige to five burrow systems in this manner only two porcupines were caught, the other burrow occupants eventually digging their way around the wire mesh. Seige tactics were therefore abandoned and the traps were placed within a few metres of a burrow entrace currently in use by the porcupines.

Initially treadle traps were used but these proved difficult to set and were unreliable. Sometimes a porcupine set off the trap without properly entering it and on other occasions animals managed to enter the trap, eat the bait and leave without setting it off. Only one porcupine was caught in a treadle trap and these were therefore abandoned and replaced by simpler drop door traps (Fig.4), four of which were available. These traps proved to be simple to use and reliable. Sweet potatoes, apples and maize were all used successfully as bait. No captures were made when using pumpkins, squashes or

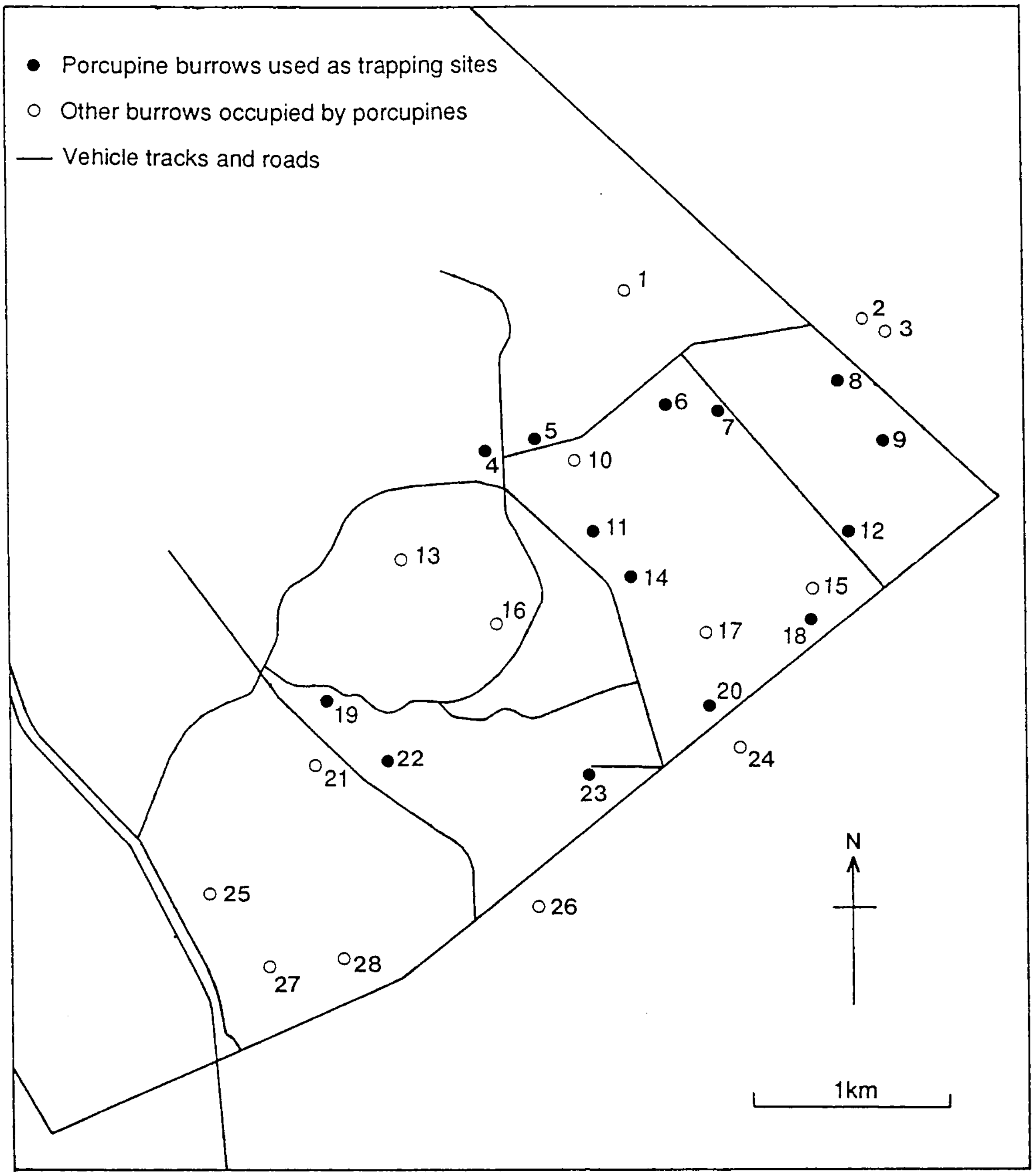

Figure 3: Distribution of porcupine burrows located in the study area.

potatoes as bait, although all of these items were eaten by porcupines kept in captivity. The only problem encountered was that of mice or squirrels occasionally eating the apples used as bait and thus setting off the trap.

A further 11 captures and 31 recaptures were made using drop door traps between July 1989 and July 1990. However, traps were not set continually during this period. The time taken to catch a porcupine after setting a trap varied from one night to three weeks. One or more porcupines were caught at 11 of the 14 trapping sites. All trapping data was recorded for capture/recapture analysis in order to study social organisation and to estimate population density.

Immobilization

Trapped porcupines were transferred from the trap into a custom built crush box (120 x 60 x 30 cm) which was placed against the trap entrance. Occassionally the porcupine entered the crush box of its own accord although usually it had to be forced in using a homemade "porcupine pusher" (Fig. 5) which was inserted through the hinged rear door of the trap. Once in the crush box the porcupine could be pinned against one side and then injected through the bars, thus minimizing stress to both the porcupine and the handler.

An intramuscular injection of 70mg ketamine hydrochloride (Ketamine; Parke -Davis Laboratories (Pty) Ltd, Isando, RSA) mixed with 10mg xylazine hydrochloride (Rompun; Bayer Pharmaceuticals(SA) (Pty) Ltd, Johannesburg, RSA) was administered which normally resulted in a recumbancy time of 10 to 15 minutes (Van Aarde 1985d). If the animal was not fully recumbant after 20 minutes a second injection of 30mg Ketamine and 4mg Rompun was administered. Once immobilized the porcupine was removed from the crush box and placed on a sack. Whilst recumbant the porcupine's breathing was regularily monitored and a 75mg injection of doxapram hydrochloride (Dopram-V; Keating

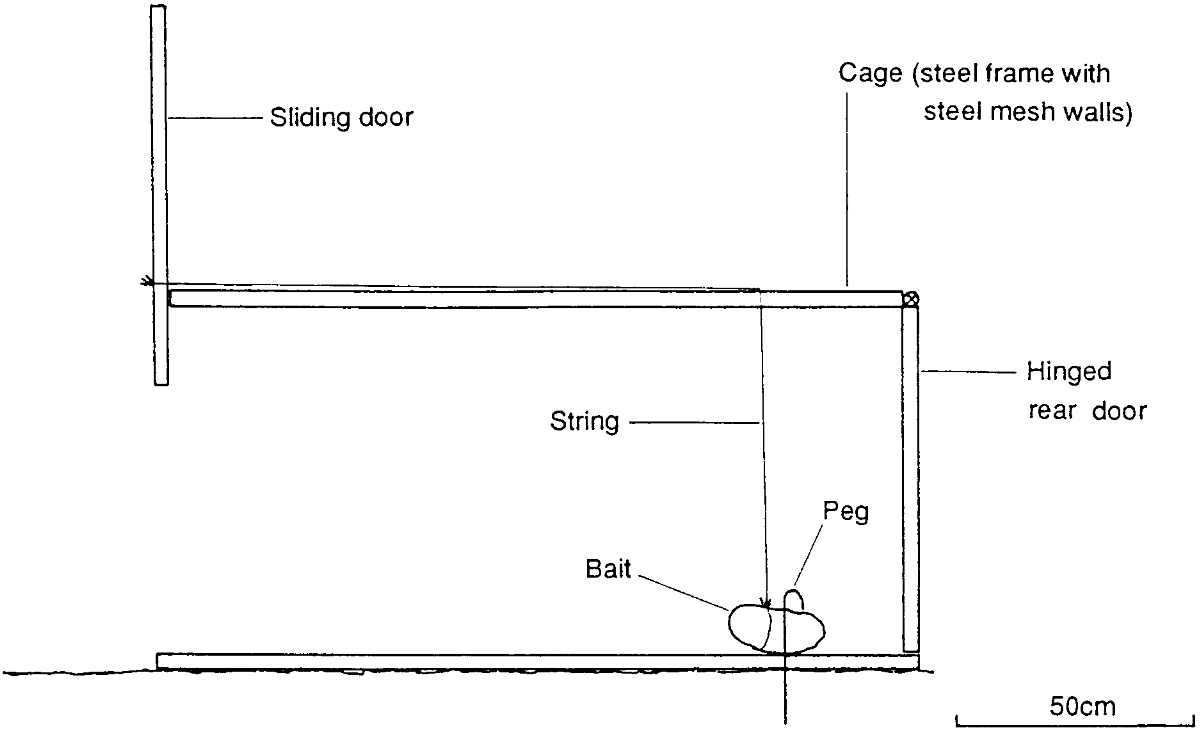

Figure 4: Cross-section of a baited drop-door trap.

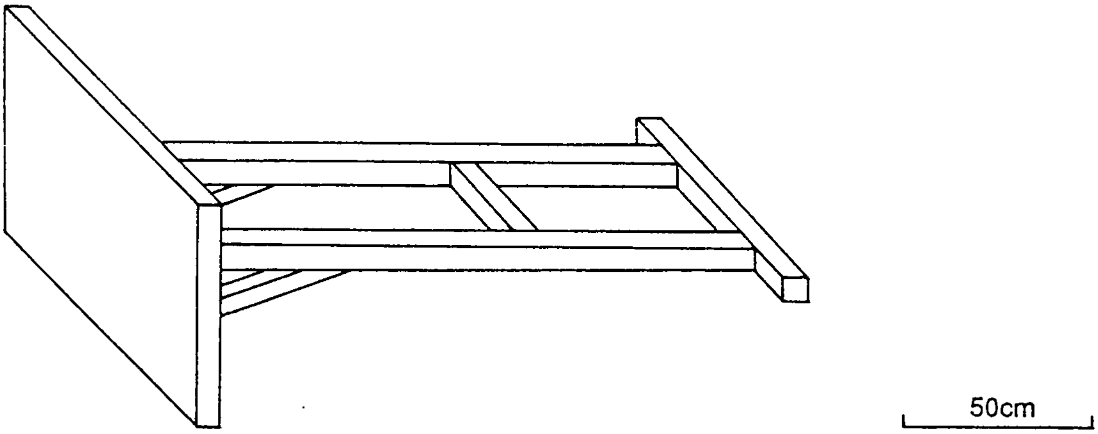

Figure 5: "Porcupine pusher" - a custom built device used to facilitate the transfer of porcupines from the trap to a crush box.

Pharmaceuticals Ltd, Johannesburg, RSA) a respiratory stimulant, was kept available in case of respiratory problems. Fortunately this was never required. A booster injection of 30mg Ketamine and 4mg Rompun was also kept available in order to maintain sedation, although this was only rarely necessary.

Any minor cuts to the head or feet incurred while attempting to escape from the trap were treated with an antiseptic spray (Airbiotec; Bayer Pharmaceuticals (SA) (Pty) Ltd, Johannesburg, RSA).

After collecting data on sex, age and weight, and fitting a radiocollar, the porcupine was placed next to it's burrow entrance and watched until it had recovered sufficiently to stagger into the burrow. This recovery period varied from approximately one to two hours. During recovery care was taken to shield the porcupine's head from direct sunlight and after recovery an apple or sweet potatoe was placed in the burrow. Occassionally a porcupine was transferred to a permenant concrete cage where it was kept for a few days before release, for example, if a radiocollar was not immediately available.

Determination of age, sex and weight

Once immobilized the captured porcupines could easily be sexed by examination of the external genitalia. The teats of the females were examined for swelling and milk secretion in order to indicate the latter stages of pregnancy or lactation (Van Aarde 1985b). Age was determined by examination of the teeth to identify the dental pattern and tooth attrition. Individuals were thus assigned to one of nine dental age classes from which approximate real age, up to two years old, may be determined (Van Aarde 1985a). Beyond two years of age, ageing with any degree of accuracy becomes very difficult. Porcupines were weighed to the nearest 0.5 kg in a sacking sling suspended from a hand-held 50 kg spring balance.

Individual codes

Each porcupine was assigned a code consisting of a letter and a number, whereby M = male and F = female. The number identifies an individual and it's partner, e.g., M1 is the partner of F1.

RADIOTRACKING

Radiotracking theory

The position of a radiotagged animal can be determined by triangulation which involves taking two or three bearings on the animal from different known sites, it's position being the point where the bearings intersect each other (Kenward 1987). Bearings may be determined using either the loudest signal method or the null-average method (Springer 1979). The accuracy of triangulation however, may be affected by a variety of errors of which there are four main types, site errors, reading or user errors, inherent or system errors and errors due to the movement of the animal. Locations obtained by radiotracking triangulation are therefore only estimates, and not exact determinations of an animals position (Heezen & Tester 1967, Taylor & Lloyd 1978, Springer 1979, Kenward 1987, Schmutz & White 1990).

Site errors are those caused by the physical environment such as woods, hills, buildings, wire fences and electricity pylons which can cause reflection, absorption or refraction of radio waves.

Reading errors are due to the inaccurate determination of the loudest signal or the null peak, and also to inaccurate allignment of the compass.

Inherent errors are associated with the equipment but should be minimal as long as the receiver, aerial, transmitters and compass are not damaged.

Errors due to the movement of the animal may be of two types. Firstly, movement will result in changes in both the orientation of the transmitter and in it's proximity to the ground and other objects, all of which can affect the signals amplitude and consequently the accuracy of the bearing. Secondly, if an animal is moving, the first bearing will be taken on a different point to the second bearing, and so on, the greater the animal's speed the greater this discrepancy will be. Ideally therefore, two or three simultaneous bearings should be taken on a moving animal. However, if this is not feasible the time interval between bearings should be reduced as much as possible in order to minimise such inaccuracies. Taking two rather than three bearings reduces this interval, although a third bearing should be taken to check the reliability of the first two. As long as the initial pair of readings appear to be reliable the third bearing need not be included in the data set.

If the 95% confidence limits of the standard deviation (S.D.) of the mean error are calculated (S.D. x 1.96), through tests which involve taking bearings on known points, then error polygons may be plotted . These comprise a polygon, at the centre of which is the point where the bearings intersect, and within which there is a 90.25% probability of the animal being located. The greater the distance at which the bearing is taken the larger the error polygon, assuming equal inaccuracy at all ranges (Heezen & Tester 1967, Springer 1979, Runyon & Haber 1980).

If a map of the animals movement is to be plotted, the sample interval, i.e., the length of time between successive locations, is important. As the sampling interval, and the animal's speed increase, the map becomes less and less representative of the animal's true movements. The lines connecting successive locations then merely show a progression of locations and not the actual route travelled (Heezen & Tester 1967, Springer 1979). Sampling interval will therefore also affect the calculation of distance travelled and speed of movement. Harris et al. (1990) described two main types of radiotracking, "continuous" and "discontinuous". Continuous radiotracking involves determining locations at small sample intervals of approximately 5 to 15 minutes which can give a fairly accurate estimate of the route travelled by the animal. Discontinuous radiotracking involves determining locations at discrete or random time intervals. It can be used to calculate home range areas and allows the concurrent study of several individuals or groups of animals. The shorter the sample interval between successive locations, the greater the degree of autocorrelation of the data, i.e., the less independence there is between locations. Autocorrelated data are unsuitable for certain methods of home range analysis as will be discussed later. It is therefore important to choose a sample interval that is suited to the aims of the study and the chosen method of analysis.

Equipment

Receiver: Yaesu FT290 R2 G Model, (144-152 MHz), (Yaesu Musen Co. Ltd, Tokyo, Japan).

Antenna: Hand-held Telonics RA-2AK H-antennas, (144-148 and 148-152 MHz), (Telemetry-Electronics Consultants, Mesa, Arizona, USA).

Compass: Suunto 360° RL KB-77, (Wild & Leitz RSA (Pty) Ltd, Johannesburg, RSA).

Transmitters: Telonics MK5 transmitters with SAFT 3.5V C size lithium batteries and a 30 cm TA-5HT7 Ext. antenna, (Telemetry-Electronics Consultants, Mesa, Arizona, USA).

Transmitter frequencies :	146.200 MHz	146.260 MHz
	146.210 MHz	146.270 MHz
	146.220 MHz	146.280 MHz
	146.230 MHz	146.290 MHz
	146.240 MHz	150.743 MHz
	146.250 MHz	150.750 MHz

The transmitters and batteries were embedded in dental acrylic (Taylor and Horn; Pretoria, RSA) and attached to a Trekflex belting collar (SA Belting, Pretoria, RSA). The antenna was sewn into the collar so that a 15 cm section extended vertically from the top. Different combinations of coloured reflective tape were stuck to the sides of the collar in order to facilitate identification of individuals seen at night. However, this tape did not generally last for very long. The collars were fastened with a pair of nuts and bolts and could be adjusted to fit individual animals. They were fitted quite loosely so as to avoid causing discomfort to the porcupine; no chafing or infection was observed in any recaptured animals. The total weight of a radiocollar was about 200 g, approximately 1.3% of an adult porcupine's bodyweight.

Two of the collars slipped off over the heads of porcupines but were later recovered. A certain amount of damage was caused to the collars through being chewed by the porcupines partner(s). Fortunately no collars were lost in this manner although two were rendered useless by the destruction of the antenna. On completion of the study all but one of the radiocollared porcupines were recaptured and the collars were removed.

The expected lifespan of the batteries was approximately 12 months. The batteries were in use for up to 13 months and only one failure occured.

Marking and mapping of radiotracking sites

Triangulation sites were marked at 400-500 m intervals on all vehicle tracks within the study area. Their positions were then accurately recorded on a 1:10,000 map traced from an aerial photograph. These sites were initially marked with a numbered, wooden plaque nailed atop a white painted wooden pole. However, these markers were very short-lived, as within a month of their installation about half the plaques had been ripped off, were knocked down or had disappeared completely. Brown hyaenas were the suspected culprits in the majority of cases. The plaques were therefore nailed to trees which also had the appropriate number painted on their bark. These markers all survived for the remainder of the study period. Additionally, a length of white electrical tape was bound around the trees to which was stuck small squares of reflective tape. This enabled the sites to be easily identified from a distance of up to 50 m while driving at night. All markers were removed from the study area after completion of the fieldwork.

Determination of accuracy

To establish the accuracy of radiotracking and to test the equipment, a testing session was undertaken. Several radiocollars were placed in small bushes close to the ground at various known localities throughout the study area. Bearings were then taken on these collars from the marked sites at ranges from 200 to 2000 m. For the initial testing session the null-average method was used to take bearings. A second session using the strongest signal method was also conducted. Results are presented in Table 1.

Accuracy, ie, standard deviation (±) of the mean error, was similar for all ranges so the data were combined. This gave accuracies of ±10.4° and ±11.3° for the two methods respectively. The loudest-signal method gave a negligible mean error (+0.3°) compared to the null-average method (-5.6°) and also allowed bearings to be taken considerably faster, thus reducing the time interval between bearings. It was therefore used for all subsequent radiotracking. Using an accuracy of ±11°, and assuming that the two bearings are taken at 90° to each other and at approximately the same range, approximate error polygons were calculated (Table 2). These estimates of error were confirmed by plotting pairs of intersecting test bearings, taken using the loudest-signal method, and measuring the distance of the plotted location from the real location of the collar to give a "distance error" (Table 3). Error polygons were not actually used when mapping points or calculating distances moved but it is important to know the accuracy and therefore the limitations of the data base.

Site errors could account for much of this inaccuracy, for example, the fairly dense woodland through which most bearings were taken, the presence of Maroelakop in the study area and a large wire fence around the perimeter of the reserve. An electricity pylon running close to the reserve's southern boundary often made it difficult to take precise bearings in this vicinity due to signal interference.

Table 1: Accuracy of bearings taken using the null-average and strongest-signal methods.

METHOD	RANGE (m)	N	MEAN ERROR (°)	S.D.(±°)
Null-average	0- 500	38	-4.6	10.4
	501-1000	43	-6.3	9.7
	1001-1500	47	-5.9	11.7
	1501-2000	19	-6.2	8.3
	0-2000	147	-5.6	10.4
Strongest signal	0- 500	12	+1.9	8.5
	501-1000	23	-1.0	13.5
	1001-1500	17	+2.7	10.0
	0-1500	52	+0.3	11.3

Table 2: Dimensions of error polygons for bearings taken using the strongest-signal method.

RANGE (m)	ERROR POLYGON (m^2)	ACCURACY OF LOCATIONS (±m)
	(90.25% confidence limits)	
100	75	37
200	150	75
300	225	112
400	300	150
500	375	187
600	450	225
700	525	262
800	600	300
900	675	337
1000	750	375
1500	1125	562
2000	1500	750

Table 3: Accuracy (distance errors) of locations taken using the strongest-signal method.

Mean distance error = 119 m	(n=59)
100% of locations accurate to within 300 m	(n=59)
95% of locations accurate to within 250 m	(n=56)
90% of locations accurate to within 200 m	(n=53)

Trial tracking

During June 1989 the first two porcupines caught, one male and one female, were tracked for two and three nights respectively using a 30 minute sample interval. This allowed estimates to be made of home range size, movement patterns, distance travelled and speed of movement which enabled the planning of a radiotracking programme. The first full month's radiotracking in July 1989 also effectively served as an extended trial period.

Radiotracking programme

As discussed on page 8 the length of time over which a home range is measured may drastically affect it's estimated size and shape. Similarily, the number of locations used to determine a range will affect these estimates.

Theoretically, the longer a home range is measured or the more locations that are obtained, the larger the range will become until it reaches an asymptote, i.e., the point at which additional locations do not increase range size. Thus, by plotting the number of locations against range size, this critical number of locations may be calculated. Ideally, the number of locations required should be calculated during the initial trial tracking period. This number will vary depending on the sample interval between successive locations, the space use pattern of the animal and it's home range size. However, some ranges may never reach an asymptote over the study period, for example, if the animal focuses it's activities successively in different subsections of it's total range. In this case the cumulative range area may reach successive "asymptotes" over varying periods of time such that a graph of number of locations against range area forms a stepped pattern. To avoid the problem of asymptotic ranges, a standard number of locations may be chosen to represent every home range within a given time period, thus making all such ranges comparable (Waser & Wiley 1979, Harris et al. 1990).

It was decided to determine home range areas on a monthly basis. A shorter time period was considered impractical and a longer period, e.g., seasonal or annual would produce successively larger and less meaningful ranges due to the variation in space use over that period which could obscure details of social organisation and reveal little about the interactions within a dynamic system. Each monthly range was required to represent a similar time period to enable comparisons to be made between ranges. Thus, as the number of hourly locations per night varied seasonally, due to changes in day length, it was decided to specify the number of nights data to be collected, rather than the number of locations. Therefore, it was decided that each monthly home range estimate would be based on 15 nights data as it was considered that this would be sufficient to reach at least the first "asymptotic" step.

Radiotracking study

Ten porcupines were radiotracked between July 1989 and June 1990 inclusive. It was not possible to regularily obtain 15 nights data per month for each animal, due to the number of study animals, and also as a result of technical problems with receivers and vehicles. Thus, four to eight animals were tracked for 5 to 15 nights per month throughout this period. Tracking took place from dusk to dawn with a sample interval of approximately one hour which enabled several porcupines in different parts of the study area to be tracked concurrently. A sample interval of one hour falls somewhere inbetween Harris et al.'s (1990) continuous and discontinuous radiotracking types, reducing the autocorrelation of data and facilitating home range analysis while still allowing rough estimates to be made of route travelled, distance moved and speed (for a slow moving animal).

Although bearings could sometimes be obtained at ranges of up to 2000 m, almost all were taken at less than 1000 m in order to reduce errors, with an average range of approximately 500 m. This gave an average error polygon of approximately 400 m^2, or an average location accuracy of about ±200 m (see Table 2). This is comparable to the distance errors measured between plotted test location and real collar location for which 90% of locations were accurate to ±200 m with a mean distance error of 119 m (Table 3).

Using the loudest signal method, the time interval between bearings was reduced in most instances to less than five minutes, and with practice an interval of two or three minutes was usually acheived. As the mean speed of a porcupine was found to be approximately 5 m per minute, the inaccuracy due to the movement of the animal between bearings is probably relatively small when compared to that from other sources of error.

The following data was recorded each time a bearing was taken: Date, animal's individual code, observer's position, time (to the nearest minute) and bearing (°).

OBSERVATIONS OF PORCUPINES IN THE STUDY AREA

All observations of porcupines seen while radiotracking were recorded. Attempts were made to follow porcupines on foot using a hand-held torch fitted with a red filter. This however, proved impossible as the porcupine's black and white striped quills provide excellent camoflague at night in the long grass which covers most of the study area, such that they were effectively invisible if more than about 5 m away. To approach this close was not feasible as it was impossible to move silently through the fairly dense and usually dry vegetation. This noisy movement alarmed the porcupines which then fled at high speed.

Porcupine burrows were watched at dusk on 22 occasions, in October, November, January, February and March, in order to provide information on social organisation and emergence times. Observations using a powerful, red-filtered searchlight to sweep the area around the burrow entrance were unsuccessful, the porcupines possibly being alarmed by the searchlight and therefore using alternative exits concealed from the observer by long grass or bushes. Porcupines were seen on 11 occasions, most successful observations being made at burrow entrances that were situated on bare patches of ground and observed from vantage points in trees or parked vehicles, no more than 10m from the burrow. The use of a pair of 10 x 50 binoculars on clear moonlit nights greatly enhanced observation.

CLIMATIC DATA

Daily records of rainfall, minimum temperature and maximum temperature were obtained from the weather station in the study area. These records were collected by the Foundation for Research and Development (FRD) staff at Nylsvley. Total monthly rainfall and monthly mean minimum and maximum temperatures and humidity were then calculated. Temperature data were not available for the period March to May 1990 due to faulty equipment at the weather station. The above climatic variables will be compared with seasonal changes in range size and activity levels.

During radiotracking sessions, hourly records were kept of rainfall, moon status and cloud cover.

Rainfall was scored from 0-3: 0 = No rain
3 = Torrential rain.

The moon was scored from 0-1: 0 = Absent
1 = Present.

Cloud cover was estimated and scored from 0-8: 0 = No cloud cover
8 = Complete cloud cover.

Relative mean moonlight intensities could then be determined for each night of radiotracking. These values were calculated as follows:

$$M_x = \left(\sum_{i=1}^{n} MI_i \right) \div n$$

where: M_x = Mean moonlight intensity for night x.
n = Number of hours observations.
MI_i = Moonlight intensity at hour i, (possible values of 0-24),
$= (M_i \times MP) - CC_i + 8$

where: M_i = Presence or absence of moon at hour i.
MP = Moon phase scored from 0-16 according to the lunar cycle,
i.e., 0 = new moon, 16 = full moon.

CC_i = Cloud cover at hour i.

8 is added as a constant to make all values of MI_i positive.

The porcupines' activity levels, measured as distance moved per night (see p.41), were then correlated with nightly minimum temperature, moonlight intensity and lunar phase on a seasonal basis using Spearman's rank correlation coefficient. Nightly minimum temperature, rather than daily maximum temperature, was used as it showed greater seasonal variation (Fig.14) and as porcupines are nocturnal it was considered to be more relevant. Any influence of the moon on activity, as suggested for H. indica by Alkon & Saltz (1983, 1988a, 1988b), either an endogenous activity rhythm linked to the lunar cycle or an exogenous response to ambient light levels, may thus be determined. Correlations of activity with nightly rainfall were not made due to insufficient data, light rain being infrequently recorded and heavy rain preventing radiotracking.

PRIMARY DATA PROCESSING

The data collected in the field were initially processed using a program written by Dr H.Dott * which utilised the Caddie graphics system (Vector Cad Cam (Pty) Ltd, RSA). This calculated the following values for each location:

1. Position (X and Y coordinates)
2. Time (24 hour clock)
3. Location number (e.g., 1st,2nd,3rd location of night)
4. Time since previous location
5. Distance travelled from previous location (m)
6. Speed of travel from previous location (m/h)

Additionally, the following nightly values were also calculated:

1. Time between first and last locations
2. Total distance travelled (m)
3. Mean nightly speed (m/h = Total distance travelled ÷ Time between first and last locations)

HOME RANGE ANALYSIS

The suitability of the following techniques, commonly used to analyse radiotracking data, were considered; minimum convex polygons, grid cells, probabilistic methods, harmonic means, core convex polygons and cluster analysis.

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Minimum convex polygons

(Dalke & Sime, 1938 in Kenward 1987, Voight & Tinline 1979, Macdonald et al.1980, Kenward 1987, Mykytka & Pelton 1988, Harris et al.1990).

Minimum convex polygons are formed by joining the outermost locations to form the smallest possible convex polygon. By including all recorded locations, some of which may be unusual excursions outside the normal area of activity, this method can greatly overestimate the size of the home range and may include large areas not actually used by the animal. Several methods have been proposed to reduce the inclusion of these unvisited areas but all are somewhat arbitrary and thus not entirely satisfactory. Additionally, no information is given about the intensity of space use within the home range. However, its advantages are that it can be used even if only a small number of locations are available and it is unaffected by the autocorrelation of data. Due to its simplicity it is the only technique that is strictly comparable between studies and therefore its inclusion as one of two or more methods of analysis is useful.

Grid cells

(Siniff & Tester 1965, Adams & Davis 1967, Macdonald et al.1980, Kenward 1987, Saltz & Alkon 1989, Harris et al.1990).

Grid cells may be used to calculate home range sizes although this method generally requires some modification which limits its accuracy and objectivity. However, it is useful for describing the intensity of range use and for the analysis of habitat use and conspecific interactions. The suitability of this method to a particular study depends on the size of the error polygons which determine the size of the grid squares used and thus the accuracy of the analysis. In their simpler forms grid cell analyses have the advantage of being able to be carried out by hand without the necessity for computers.

Probabalistic methods

(Dice & Clarke 1953, in Kenward 1987, Ford & Krumme 1979, Voight & Tinline 1979, Macdonald et al. 1980, Wolton 1985, Kenward 1987, Mykytka & Pelton 1988, Harris et al.1990).

Probabalistic methods attempt to assess an animals probability of occurance at each point in space and thus produce a theoretical home range for an average animal of that species in a uniform environment. The various probabilistic methods all make one or more of the following assumptions:

1. The animals use of space will be normally distributed around a single, centrally placed centre of activity.
2. All locations are independent, i.e., not autocorrelated.

Consequently, most probability circles or ellipses bear little relation to an individuals real pattern of space use and are thus unsuitable for analysing home range size and shape, intensity of space use, habitat use or conspecific interactions.

Harmonic means

(Dixon & Chapman 1980, Wolton 1985, Kenward 1987, Mykytka & Pelton 1988, Harris et al.1990).

Harmonic means use the first inverse moments of locations to estimate activity centres and range use contours. They can identify multinuclear centres of activity and the contours, or "isopleths", can be set to include varying proportions of locations. However, I consider the use of a mathematically derived centre of activity, which in some cases may have little biological significance, and upon which all other calculations are based, to be unsatisfactory. Clusters of locations are not treated seperately and thus isolines may fail to match the real distribution of locations, either being drawn towards concentrations of distant locations or by contouring around large unused areas. Additionally, if the distribution of locations is highly skewed, if there are a large number of outlying locations or if too few locations are available, the home ranges calculated may be highly inaccurate. Despite the above critisisms, this method can provide a useful analysis of some data sets, particularily those comprising a large number of locations. Harmonic means are relatively unaffected by the autocorrelation of data but the use of different algorithms in the various computer programs available make accurate comparisons between studies difficult.

Core convex polygons

(Mohr & Stumpf 1966, Kenward 1987).

Core convex polygons are created by progressively excluding the locations which are furthest from the range centre so producing probability contour polygons. The range centre may be defined as a resting site or some other such focal point, or may be mathematically derived by a variety of methods, none of which necessarily have any biological significance. None of the methods of defining the range centre are particularily satisfactory in most cases, and this method is not suited to the analysis of multinuclear ranges.

Cluster analysis

(Kenward 1987, Harris et al.1990).

Cluster analysis uses hierarchical incremental cluster analysis with a nearest neighbour joining rule to draw contours which include varying proportions of locations. It makes no prior assumptions about the shape of a range or about the distribution of use within a range and clusters are treated seperately. It may therefore be used to analyse multinuclear ranges, those with a skewed distribution of locations or those having a large number of outlying locations. Like the harmonic mean method, cluster analysis is relatively insensitive to autocorrelation of data but also has the disadvantage of different algorithms making comparison between studies difficult.

For the reasons outlined above, cluster analysis was chosen as the main method of home range analysis. Kenward's (1987) "Program 2" was used, with modifications by Dr H.Dott, utilising data produced by the primary data processing program. Not only does cluster analysis provide a satisfactory method of analysing space use patterns but it enables the results to be presented in a clear and easily interpreted manner. The minimum convex polygon method, although of limited value, was also used for the reason of it's simplicity and comparability with other studies.

As Macdonald et al.(1980) pointed out, "...without knowing the answer one cannot predict how appropriate a given estimate will be." Therefore, the contours used to define a home range, core area or territory were not predetermined but were chosen according to which produced the most meaningful analysis of the data. However, to allow comparison between individuals and seasons, the same contours were used for all animals. Range use was therefore classified as follows:

1. Total home range (THR)

Defined by the minimum convex polygon (= 100% cluster). Although often containing large areas not used by the individual, the THR is taken to represent the potential home range of the individual during the specified period and includes exploratory excursions.

2. Normal home range (NHR)

Defined by the 95% contour, i.e., the cluster, or clusters, containing 95% of the locations, the NHR is taken to represent the area used by the individual during the course of it's normal activities.

3. Area of intensive use (AIU)

Defined by the 90% contour, the AIU approximates to the core area of the home range.

Ranges defined by contours below the 90% level often deteriorated into large numbers of small and biologically meaningless clusters. Therefore, even if a cluster below this level appeared to adequately define an individuals range, it was not used as it could not be compared to other individual ranges or to the ranges of the same individual in another month.

For the purpose of home range analysis, individuals have been classified as "natural foragers" (NF) or "crop foragers" (CF) on a monthly basis (Saltz & Alkon 1989). Natural foragers are those animals which foraged exclusively on natural vegetation during any one monthly period. Crop foragers are those which foraged on crops grown on Blindfontein Farm as well as on natural vegetation during any one monthly period. Thus, four categories were used for the purpose of home range analysis:

Natural foragers (winter and summer).

Crop foragers (winter and summer).

Mean home range sizes were calculated for each of these categories and differences in home range sizes between these categories were analysed using the Mann-Whitney U-test.

The four ranges determined by less than 10 nights data were not included in the computations of mean range size as they were considered to underestimate range size compared to estimates based on 10-15 nights data. In order to determine whether the number of nights data, within the range 10-15, was correlated with calculated home range size, Spearman's rank correlation coefficient was used. Insufficient data was available to test for a correlation between these two variables for summer crop foragers.

The relative sizes of total home ranges, normal home ranges and areas of intensive use were also analysed, i.e., the proportion of each total home range occupied by it's respective normal home range (NHR/THR x 100%), and the proportion of each normal home range occupied by it's respective area of intensive use (AIU/NHR x 100%), were calculated. For this analysis individuals were classified into the same four categories as were used for home range size analysis (see above) and differences between categories were analysed using the Mann-Whitney U-test.

Whether or not any of the above range classifications, (THR, NHR or AIU), describe a territory cannot be determined until range overlap, intensity of use of overlapping areas and intraspecific interactions have been considered. The proportion of overlap between the ranges of pair members and between neighbouring ranges were measured using a Quantimet 520 image analyser (Cambridge Instruments, Cambridge, UK) programmed by Dr H.Dott. The size of the overlapping area was expressed as a percentage of each of the overlapping ranges. Eight categories were defined for the purpose of this analysis:

Overlap between the ranges of pair members (winter and summer).

Overlap between the ranges of natural foraging neighbours (winter and summer).

Overlap between the ranges of Henry (M5) and his neighbours (winter and summer).

Overlap between the ranges of crop foraging neighbours (winter and summer).

When the ranges of a natural forager and a crop forager overlapped, this was classified as an overlap between natural foragers as this situation only occurred in areas of natural vegetation. Henry (M5)'s overlaps with the ranges of his neighbours have been treated seperately from other natural foragers as his ranges consistently overlapped much more extensively with his neighbours than was usual for other individuals (see results). Mean range overlaps were calculated for each of these categories and the differences in range overlap between these categories have been analysed using the Mann-Whitney U-test.

Given the accuracy of the radiotracking data, (pp.24 & 29, Tables 1-3), the position of range boundaries were taken to be accurate to approximately 200 m. As a result of this, some range sizes may be under- or overestimated, although inaccuracies are probably small when taken as a proportion of the whole range. As all data were treated in the same manner this was not considered to be a major problem.

ANALYSIS OF TEMPORAL SPACE USE

Not only is spatial overlap important in determining territoriality, but temporal overlap should also be considered. During each nightly radiotracking session the estimated locations and approximate route travelled were plotted for each porcupine, which indicated that encouters between neighbours were rare. In order to quantify these interactions, temporal space use analysis was carried out using a program written by Dr. H.Dott. This measured the distances between individuals at each hourly location using data from the primary data processing programme. Ideally the locations for all individuals should be recorded simultaneously, although in practice this is impossible without the use of automatic tracking stations. Therefore, all locations recorded within 10 minutes of each other were included in the analysis. A shorter time period would have resulted in insufficient data and longer periods would have produced progressively less meaningful results. Taking into account the accuracy of the data, (pp.24 and 29, Tables 1-3), and the fact that locations were recorded at hourly intervals, the results were bracketed into 200 m categories of interindividual distance (IID), i.e., the distance measured between two animals at a given time (Fig.9). An IID of 0-200 m is interpretted as meaning that each animal was probably aware of the prescence of the other in the area and that they may have encountered one another. An IID of 200-400 m is taken to represent a lesser probability of such interactions taking place and at IID's of greater than 400 m it is assumed that no interactions occurred. Due to the time taken to travel between triangulation sites, the probability of recording the locations of two individuals within 10 minutes of each other, decreases the greater the distance between them. Thus, there will be a bias against recording locations in the higher inter-individual distance categories. However, this is not considered to be a problem as it is the possibility of close encounters (IID $\leq$ 400 m) that is important and not the maximum distances between animals.

ANALYSIS OF ACTIVITY PATTERNS

Reeve (1982) stated that nightly distance travelled may be a more useful expression of home range than a conventional area representation, but as sufficient locations were recorded to allow a comprehensive analysis of home range, such an expression was not deemed necessary. However, the distance travelled by an animal during one activity period may be of considerable biological significance and may be closely related to energy demands, particularily for an animal foraging on a dispersed food source which must travel a certain distance to meet its energetic requirements. Nightly distance travelled is therefore a useful measure of activity and allows the comparison of activity levels between individuals, or groups of animals, on a nightly or seasonal basis and enables activity levels to be correlated with environmental variables, such as temperature, rainfall and moonlight (Reeve 1982, Lawson 1986, Kenward 1987, Morris 1988).

Of course, a short distance travelled, may not necessarily be indicative of less activity, but could be caused by intense foraging at a clumped resource. The sample interval between successive locations will greatly affect the estimation of distance travelled, the longer the sample interval the more that the distance travelled will be underestimated (p.21). Ideally, an animal should be continually followed, or at least tracked using a very short sample interval, in order to obtain a precise measurement of distance and route travelled. As Spitz (1989) stated, it is important to realise that the analysis of radiotracking data in terms of movements is "a compromise between the necessity of approximating a valid route and the impossibility of knowing the real one", especially if studying a nocturnal species living in dense vegetation that prevents the validation of the radiotracking data through direct observation. Additionally, each location is in fact an error polygon and even if each location were precisely pinpointed, the exact route between two locations would remain unknown. This source of inaccuracy will be exaggerated if the animal moves in a meandering rather than a linear fashion.

The initial period of trial tracking revealed that porcupines move in a highly irregular manner and therefore measuring the distance between locations recorded at a one hour, or even 30 minute, sample interval will considerably underestimate the true distance travelled and will bear little relation to the real route taken. Thus, analysis of route travelled was not undertaken but "distance travelled per night" and "mean nightly speed", although recognised as not being accurate measurements, were calculated and used as relative measures of activity that allow comparisons of seasonal activity patterns and the correlation of activity with environmental variables. These two values were calculated by the primary data processing program (p.33).

For the purpose of activity pattern analysis, individuals have been classified as natural foragers or crop foragers on a nightly basis. Natural foragers are those which foraged exclusively on natural vegetation during any one nightly activity period. Crop foragers are those which foraged on crops grown on Bindfontein Farm for at least part of a nightly activity period. Therefore, four categories have been used in this analysis:

Natural foragers (winter and summer).

Crop foragers (winter and summer).

Mean distance travelled per night and mean nightly speed were calculated for each of these categories. Differences in these means between the various categories were tested using the Mann-Whitney U-test.

Circadian activity rhythms were analysed using a program written by Dr. H.Dott which plotted mean hourly speed against time, in hourly intervals, throughout the night. Thus, the occurrence and timing of activity peaks, if any, may be identified. Hourly intervals for which there were less than 20 data points were not included in this analysis.

CIRCADIAN RHYTHMS IN CAPTIVE PORCUPINES

Study animals

Two family groups of relatively tame porcupines, from the colony at the University of Pretoria's Experimental Farm, were used in this study. Group A comprised an adult male and female and a subadult male and female (8.5 months old). Group B comprised an adult male and female and a juvenile male (3.5 months old). Each family group was housed in an outdoor concrete enclosure with an area of 3 m^2 and a roofed section which provided shade and shelter from rain. They were maintained on a diet of commercial pellets (Antelope cubes, Epol (Pty) Ltd, Vereeniging, RSA) supplemented with fresh vegetables and with drinking water available ad libitum (Van Aarde 1985d).

Equipment

Body temperatures were measured using intraperitoneally implanted temperature sensitive telemeters.

Receiver: (Yaesu FT290 R2 G Model (144-152 MHz) with whip antenna,
Yaesu Musen Co. Ltd, Tokyo, Japan).

Telemeters with lithium batteries: (Prof. G. van Urk, Dept. of Physics,
Univ. of Potchefstroom for C.H.E.,
Potchefstroom, 2520, South Africa).

Telemeter frequencies: 148.802.5 MHz 149.320.6 MHz
148.924.8 MHz 149.402.0 MHz
149.084.0 MHz 149.525.2 MHz
149.202.0 MHz

Each telemeter, including the battery, was 30 mm long and weighed 20 g. The expected lifespan of the batteries was three months although one was faulty and thus no body temperature data could be collected from the juvenile in group B. The range of the transmitters was about 25 m but was considerably reduced by obstacles such as walls. The telemeters were coated in Paraffin/Elvax (Mini-mitter Co. Inc., Sunriver, USA) and were calibrated in a waterbath at temperatures between 31-42°C. They were sensitive to temperature changes of less than 0.1°C. The signal was audible as a series of clicks at a rate which increased almost linearly with temperature, from approximately 45-125 clicks per minute over the temperature range 31-42°C.

Ambient air temperature (T_a) was measured in the shade using a thermocouple linked to a multi-channel data logger (1200 Series Squirrel, Grant Instruments).

Implantation

The porcupines were caught in a crush box and anaethetised using 140 mg of ketamine hydrochloride and 15 mg of xylazine hydrochloride, with the juvenile receiving half this dose (p.16). A booster injection of 35 mg ketamine hydrochloride was administered to the adult female from group A, and the subadult male from group B required an injection of a respiratory stimulant as described on p.16. Having surgically implanted the telemeters in the abdominal cavity, each porcupine was given a 2 ml injection of a long lasting penecillin antibiotic (Compropen, procaine penecillin G 150 mg/ml & benethamine penecillin 142.5 mg/ml, Millbrow, Johannesburg, RSA). Although, all animals appeared to recover within a few hours of surgery, the adult female from group A died the following night presumably from shock. No infections or other signs of illness were observed in any of the other animals. One week was allowed for recovery before data were collected.

Experimental procedure

Recordings of body temperature were made at hourly intervals over two 72 hour periods, (21-24.09.90 and 29.09-01.10.90), each individual being monitored for a three minute period. Observations of behaviour were made every half hour over the same period and at night observations were made using a red-filtered torch. Behaviour was classified into three categories, resting, feeding and active. Ambient temperature was automatically recorded every hour throughout the experiment.

CHAPTER 3: RESULTS

STUDY ANIMALS

Fourteen adult porcupines, eight male and six female, were caught in the study area, giving a sex ratio of 1.3:1 which was not significantly different from 1:1 (df=1, $X^2=0.143$, $p>0.05$, Chi-squared test), (Table 4). No more than two adult porcupines, one male and one female, were ever captured at any one burrow over a short period of time suggesting that an adult pair is the basic social unit in this area. The locations of the burrows listed in Table 4 are illustrated in Fig.3. Males were recaptured more frequently than females, ($\bar{x}=3.1 \pm 2.3$ times compared to $\bar{x}=1.2 \pm 1.1$ times). This difference was not significant ($U=9$, $p<0.10$, Mann-Whitney U-test). None of the females captured were lactating or in the latter stages of pregnancy and no juveniles or subadults were ever caught.

The mean body weights of males (15.6 ± 1.7 kg, n=8) and females (15.3 ± 0.6 kg, n=6) were not significantly different ($U=19$, $p>0.10$); the mean weight of all animals was 15.4 ± 1.3 kg.

Table 4: Life history variables of porcupines captured and radiotracked at Nylsvley Nature Reserve.

NAME	AGE (Years)	WEIGHT (Kg)	CAPTURES/RECAPTURES		PERIOD TRACKED	OTHER
			Date	Location		
Getafix (M1)	2+	16.5	20.06.89 10.07.89 28.10.89	B9 B8 B9	July'89-June'90 64 nights 728 locations	Movement ceased 27.01.90, burrow excavated, both Getafix & Lady dead, probably ate poisoned bait outside the reserve.
Lady (F1)	2+	16.0	19.05.89 28.10.89	B8 B12	July'89-June'90 67 nights 726 locations	
Batman (M2)	2+	16.5	08.07.89 26.08.89 13.09.89 28.10.89 10.12.89 10.01.90 19.06.90 26.06.90	B11 B11 B11 B6 B11 B11 B11 B11	July'89-June'90 127 nights 1398 locations	Recaptured and damaged collar replaced Jan'89 ,recaptured and collar removed June'90.
Vicki (F2)	2+	14.5	28.08.89	B11	Aug-Nov'89 36 nights 406 locations	Signal lost in storm 26.11.89 not recaptured.
Attilla (M3)	2+	17.0	22.07.89 15.01.90 12.02.90 14.02.90 19.03.90 20.07.90	B5 B5 B5 B5 B5 B5	Nov'89-June'90 81 nights 873 locations	Recaptured and collar removed July'90.
Bodacea (F3)	2+	15.0	26.08.89 29.08.89 30.08.89 25.07.90	B5 B5 B5 B4	Nov'89 12 nights 114 locations	Collar fell off end of Nov'89, collar found, not recaptured until July'90.

Fish (M4)	2+	14.0	07.11.89 22.06.90	B23 B11	Nov'89-June'90 94 nights 976 locations	Recaptured and collar removed June'90.
Wanda (F4)	2+	15.0	11.01.90 12.02.90	B20 B20	March-May'90 30 nights 324 locations	Signal lost on 22.05.90,antenna chewed off. Shot by farmer in maize field 14.06.90.
Henry (M5)	2+	16.0	24.05.89 22.07.89 19.06.90 20.06.90 21.06.90	B9 B9 B20 B20 B20	July'89-June'90 133 nights 1410 locations	Recaptured and collar removed June'90.
Bugeye (M6)	2+	14.0	13.01.90 10.02.90 13.02.90 22.06.90 26.06.90	B20 B22 B22 B22 B22	Jan'90-June'90 67 nights 714 locations	Recaptured and collar removed June'90.
Bimbo (F6)	1.5	15.0	13.07.90	B22	Not captured until end of study and therefore not radiocollared.	
Biggles (M7)	2+	13.0	06.07.89	B4	Inconsistant signal therefore not radiotracked. Collar found intact 2 km north of study area July'90.	
Nelson (M8)	2+	17.5	19.03.90 29.03.90 22.04.90	B19 B19 B19	Antenna chewed off immediately after collar fitted, therefore not radiotracked. Recaptured and collar removed April'90.	
Winnie (F8)	2+	16.0	20.03.90 21.04.90	B19 B19	Faulty battery, therefore not radiotracked. Recaptured and collar removed April'90.	

SPACE USE PATTERNS

Individual space use

Each individual utilised the same general area from month to month as illustrated by Figures 6a-i. The size of each individual's monthly range (THR, NHR, AIU) is given in Appendix 1. Mean home range sizes of natural foragers and crop foragers in both winter and summer are analysed in Tables 5a-d. Table 6 shows that there was no significant correlation between calculated monthly home range areas and the number of nights data per month. Thus, all estimates of home range area based on 10 or more nights data are considered to be reliable measurements of monthly home range.

Natural foragers had significantly larger mean winter ranges than summer ranges. Crop foragers had similar mean range sizes in winter and summer with no significant difference between the two seasons. Crop foragers had larger mean ranges than natural foragers in winter and summer, all differences being significant except for winter AIU.

These seasonal trends in range size are illustrated on a monthly basis in Fig.7. This shows the smaller home range sizes of natural foragers in summer compared to winter, and the larger ranges of crop foragers which show no seasonal pattern.

Each porcupine used several different burrows which were almost always shared with their partner. Burrows were occupied on an irregular basis, a single burrow being occupied for between one and 151 days. Individuals occupied between one and five burrows per month ($\bar{x}$= 2.2 ± 0.9, n=62) and between one and six burrows over the entire study period ($\bar{x}$= 3.6 ± 1.8, n=10).

Table 5: Analyses of differences in mean range sizes (ha ± S.D.):

a. Seasonal differences in the mean range sizes of natural foragers.

b. Seasonal differences in the mean range sizes of crop foragers.

c. Differences in the mean range sizes of natural foragers and crop foragers in winter.

d. Differences in the mean range sizes of natural foragers and crop foragers in summer.

a.

	Natural foragers		Mann-Whitney U-test		
	Winter n=17	Summer n=29	U	z	p
THR	215 ± 75	142 ± 61	104.5	3.243	<0.01 *
NHR	116 ± 35	67 ± 35	67	5.671	<0.01 *
AIU	79 ± 28	40 ± 17	55.5	4.347	<0.01 *

b.

	Crop foragers		Mann-Whitney U-test		
	Winter n=8	Summer n=4	U	z	p
THR	388 ± 118	376 ± 130	14	-	>0.10
NHR	175 ± 58	203 ± 62	14	-	>0.10
AIU	106 ± 35	84 ± 17	10	-	>0.10

c.

	Winter		Mann-Whitney U-test		
	Natural foragers n=17	Crop foragers n=8	U	z	p
THR	215 ± 75	388 ± 118	12	-	<0.02 *
NHR	116 ± 35	175 ± 58	25	-	<0.02 *
AIU	79 ± 28	106 ± 35	38	-	<0.10

d.

	Summer		Mann-Whitney U-test		
	Natural foragers n=29	Crop foragers n=4	U	z	p
THR	142 ± 61	376 ± 130	1	3.144	<0.01 *
NHR	67 ± 35	203 ± 62	0	3.199	<0.01 *
AIU	40 ± 17	84 ± 17	5	2.923	<0.01 *

* Significant difference

Table 6: Home range area (THR, NHR and AIU) correlated with the number of nights data used in the calculation of home range area, using Spearman's rank correlation coefficient (r_s).

	WINTER		SUMMER	
	Natural foragers n=17	Crop foragers n=8	Natural foragers n=29	Crop foragers n=4
THR	$r_s = +0.272$ $p > 0.10$	$r_s = +0.107$ $p > 0.10$	$r_s = +0.279$ $p > 0.10$	-
NHR	$r_s = +0.392$ $p > 0.10$	$r_s = +0.012$ $p > 0.10$	$r_s = +0.219$ $p > 0.10$	-
AIU	$r_s = +0.485$ $p > 0.05$	$r_s = +0.429$ $p > 0.10$	$r_s = +0.300$ $p > 0.10$	-

Figures 6a-i: Individual monthly home ranges for each radiocollared porcupine.

Key to Figures 6a-i:

□ Total home range (THR)

⬚ Normal home range (NHR)

▒ Area of intensive use (AIU)

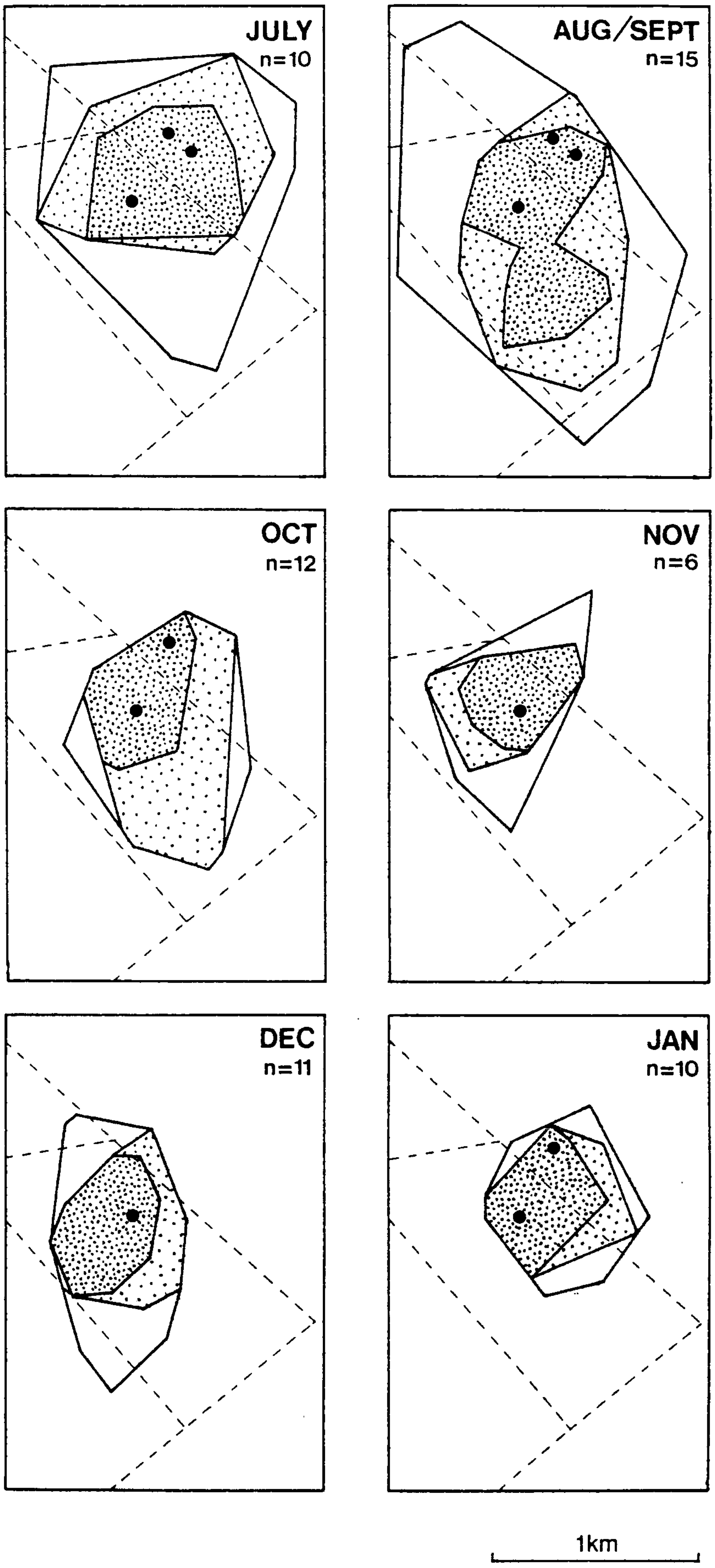
● Burrow

--- Vehicle track

n = Number of nights data

(All maps are aligned such that north is at the top of the page).

Figure 6a: Monthly home range areas of Getafix (M1), July 1989 to Jan. 1990.



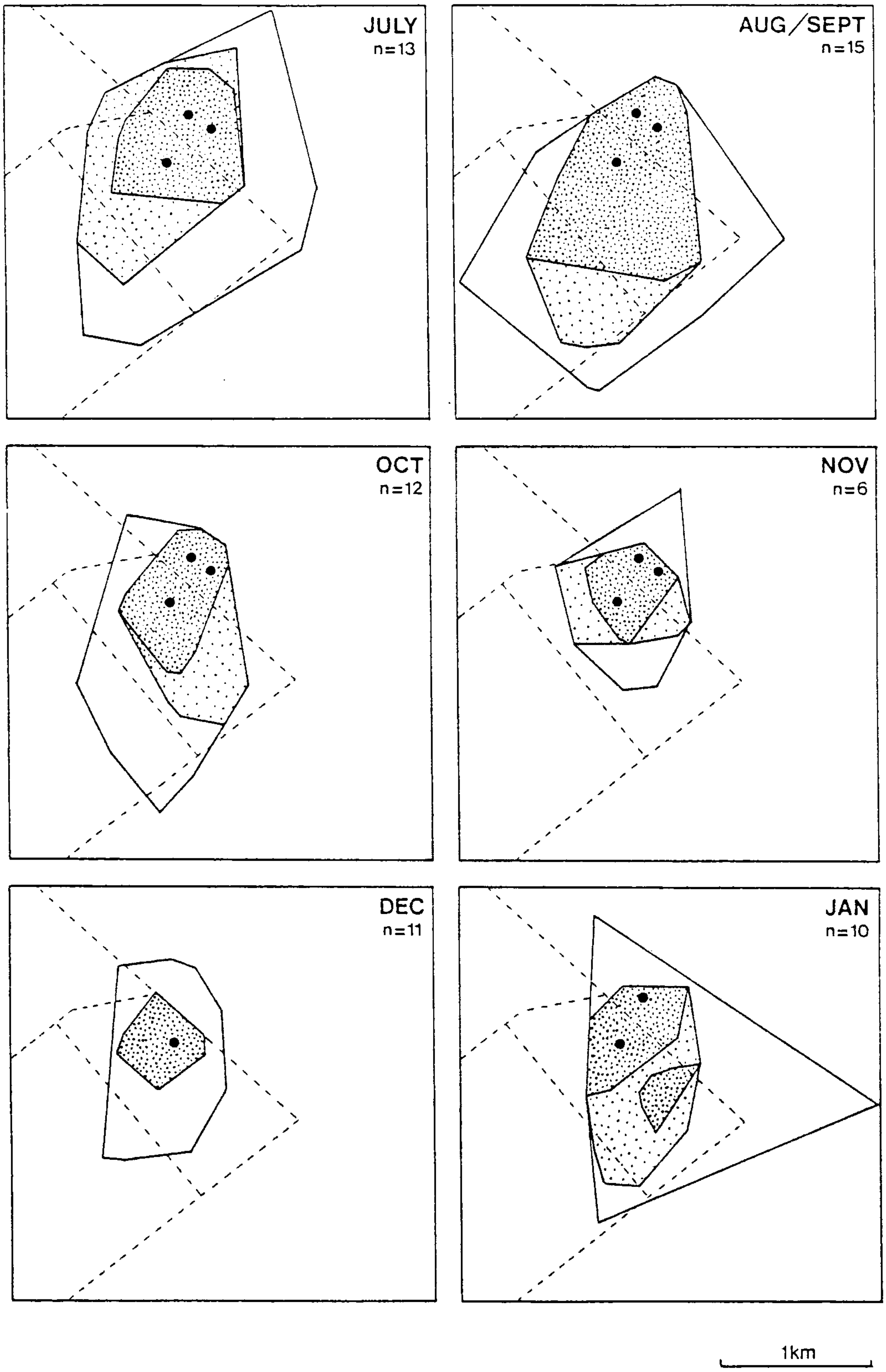
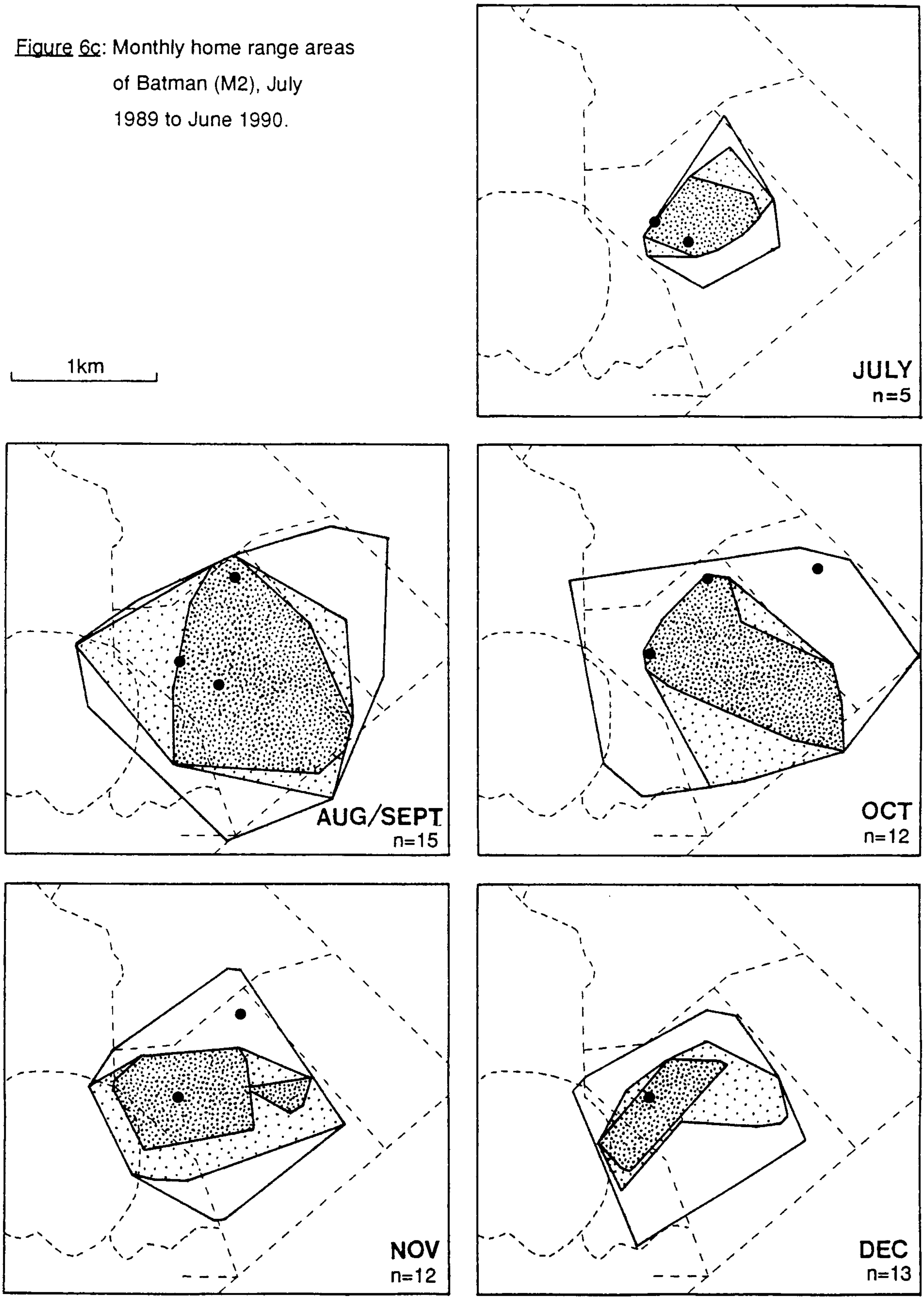


Figure 6b: Monthly home range areas of Lady (F1),

July 1989 to Jan. 1990.

Figure 6c: Monthly home range areas of Batman (M2), July 1989 to June 1990.



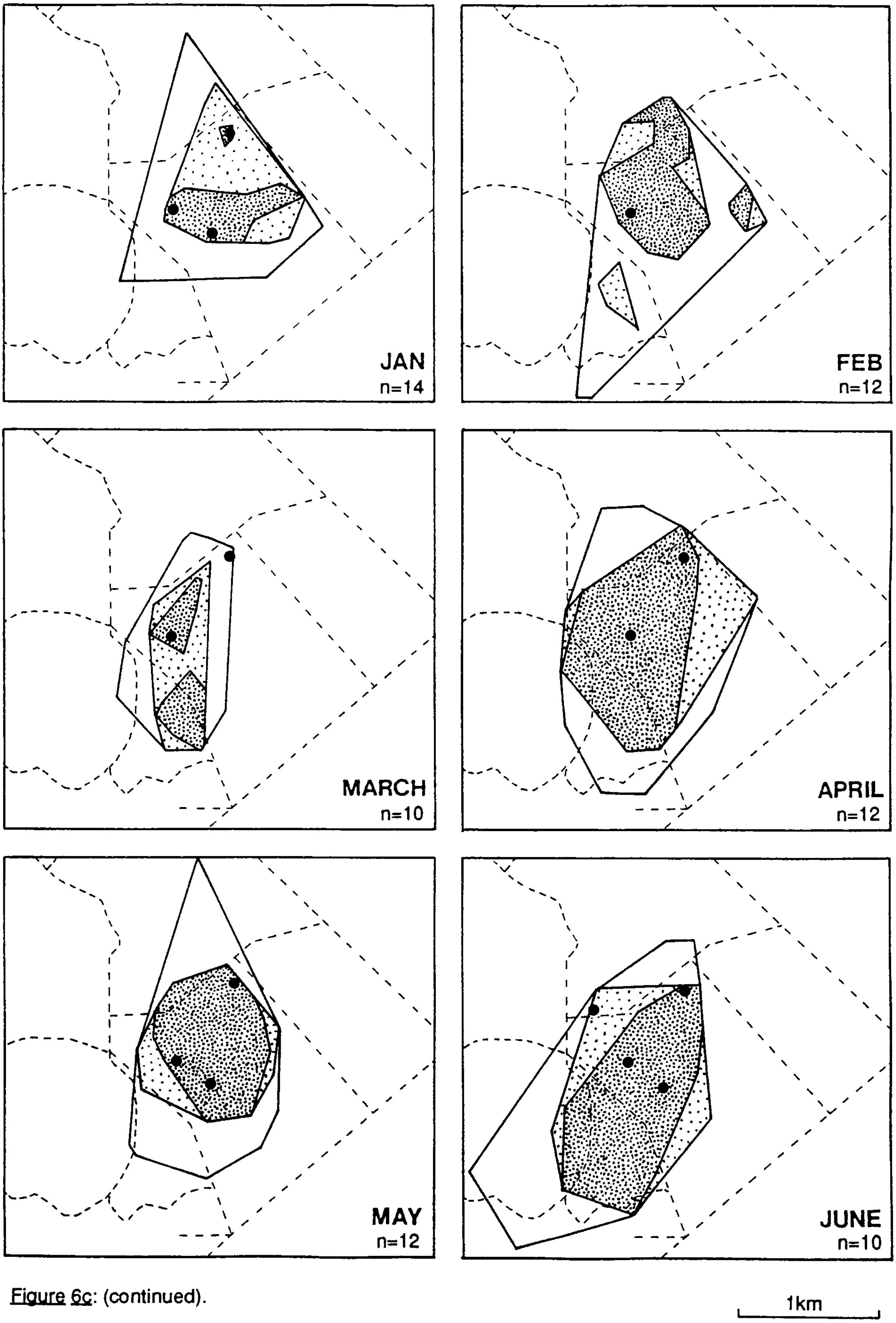
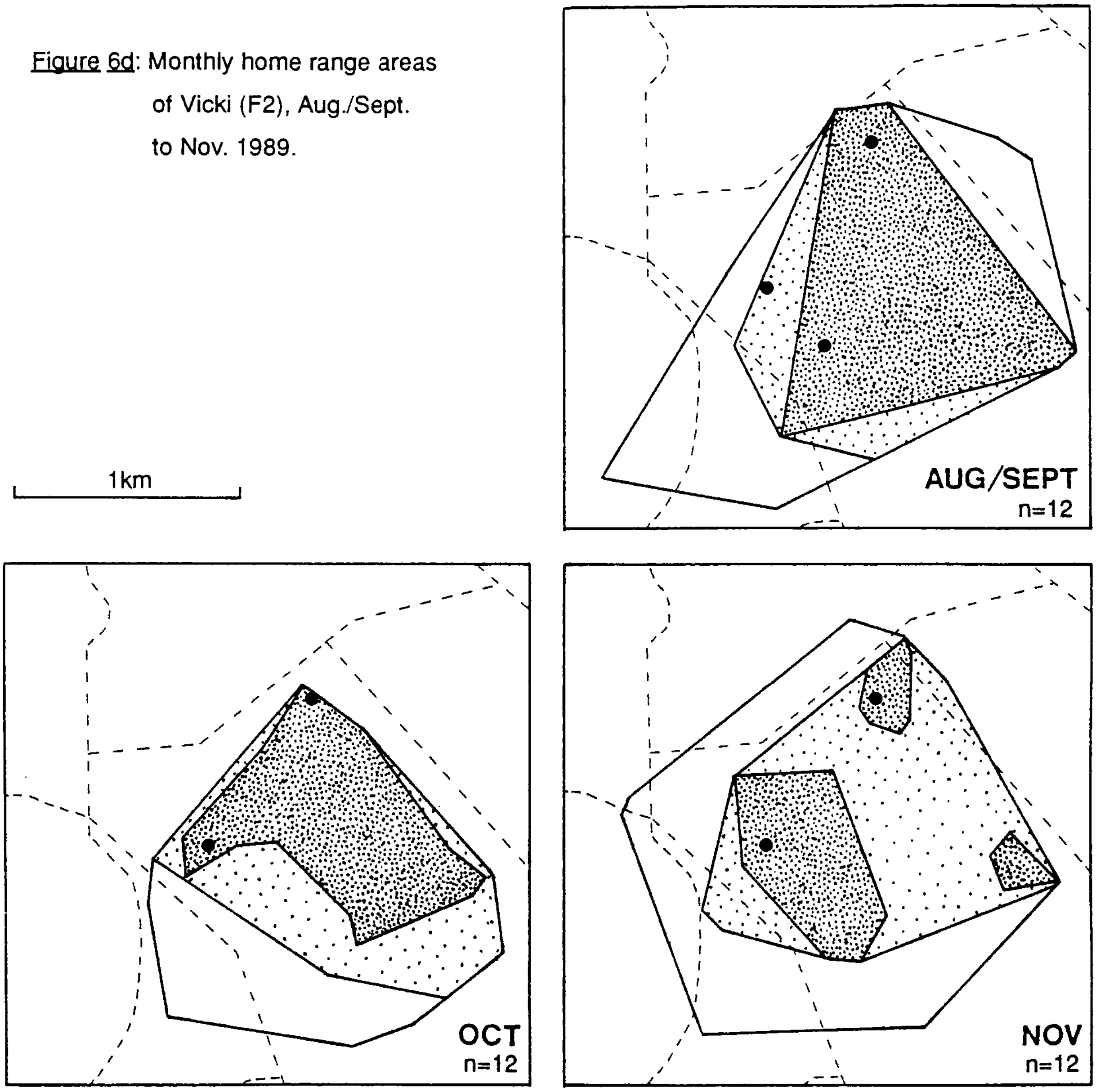


Figure 6c: (continued).

Figure 6d: Monthly home range areas of Vicki (F2), Aug./Sept. to Nov. 1989.



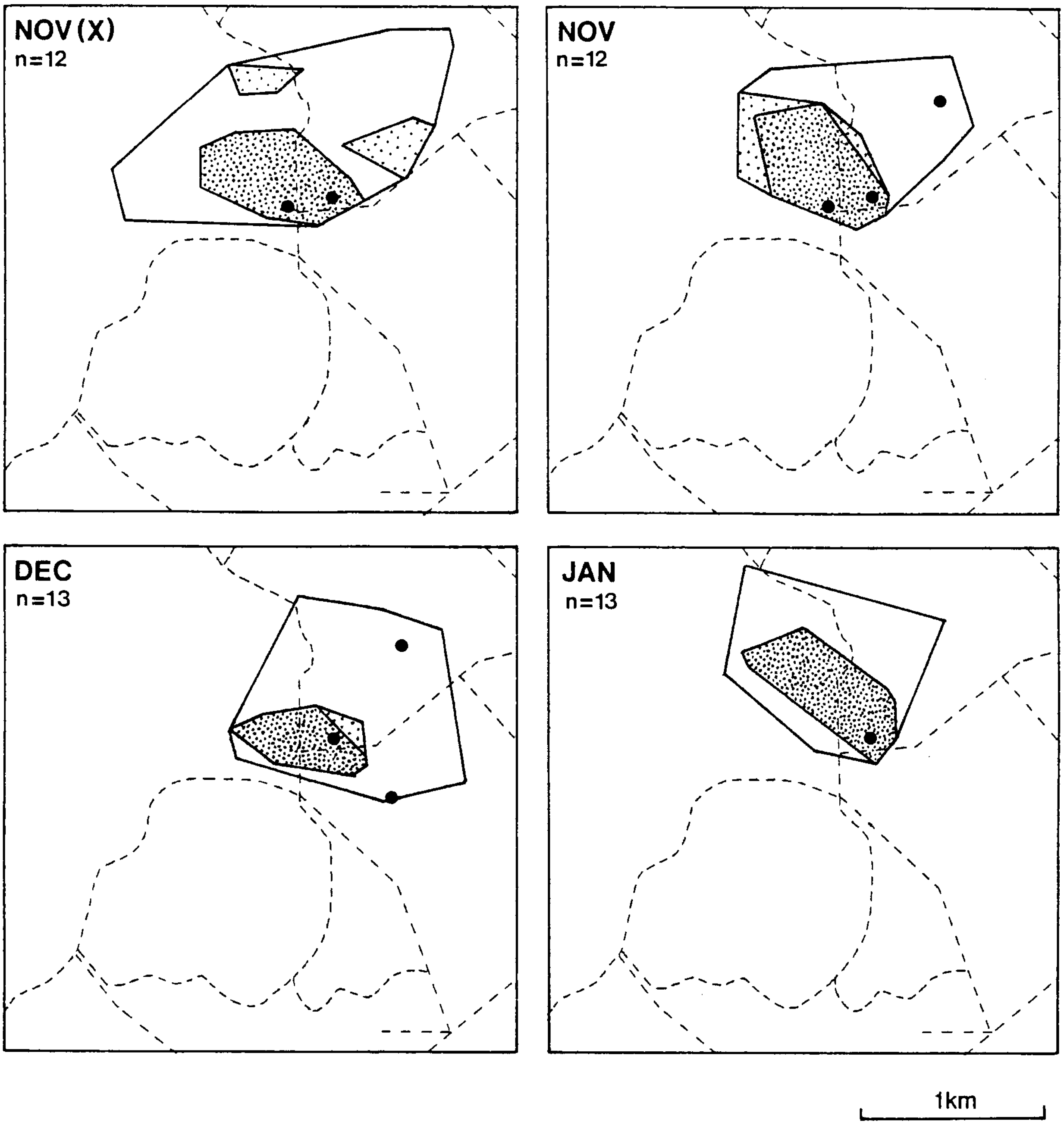


Figure 6e: Monthly home range areas of Bodacea (F3), November 1989 (X) and Attilla (M3), November 1989 to June 1990.

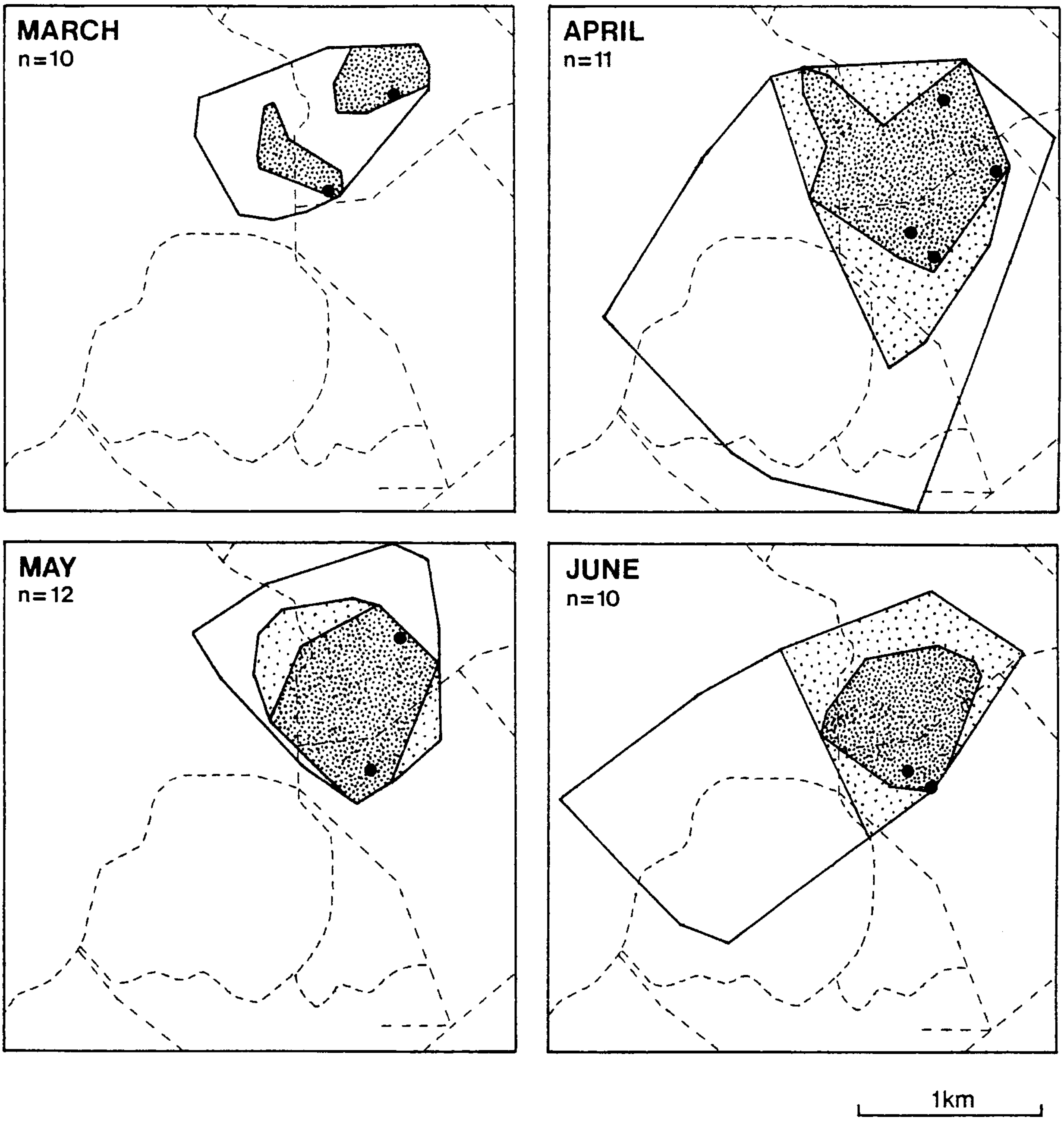


Figure 6e (continued)

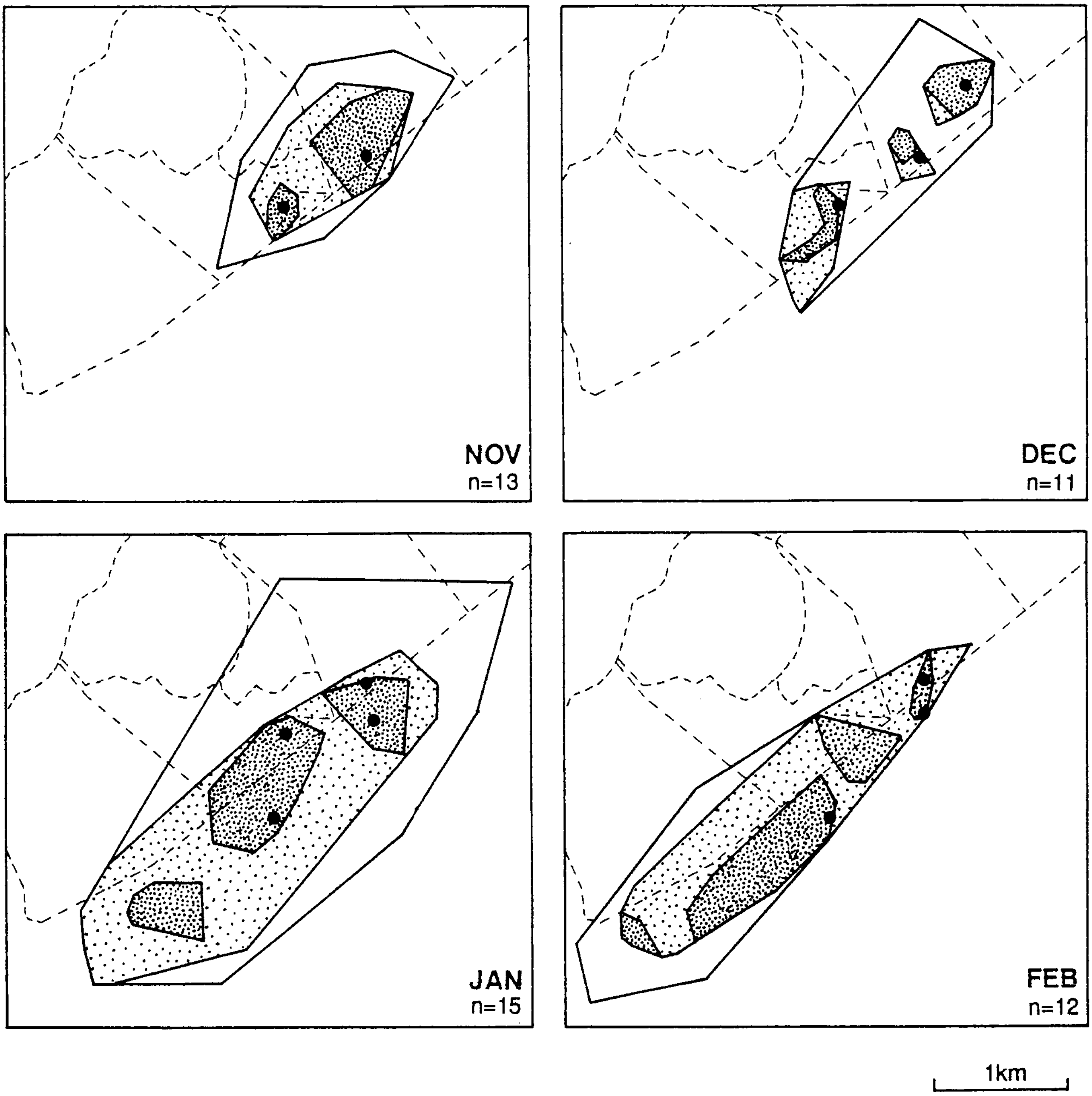
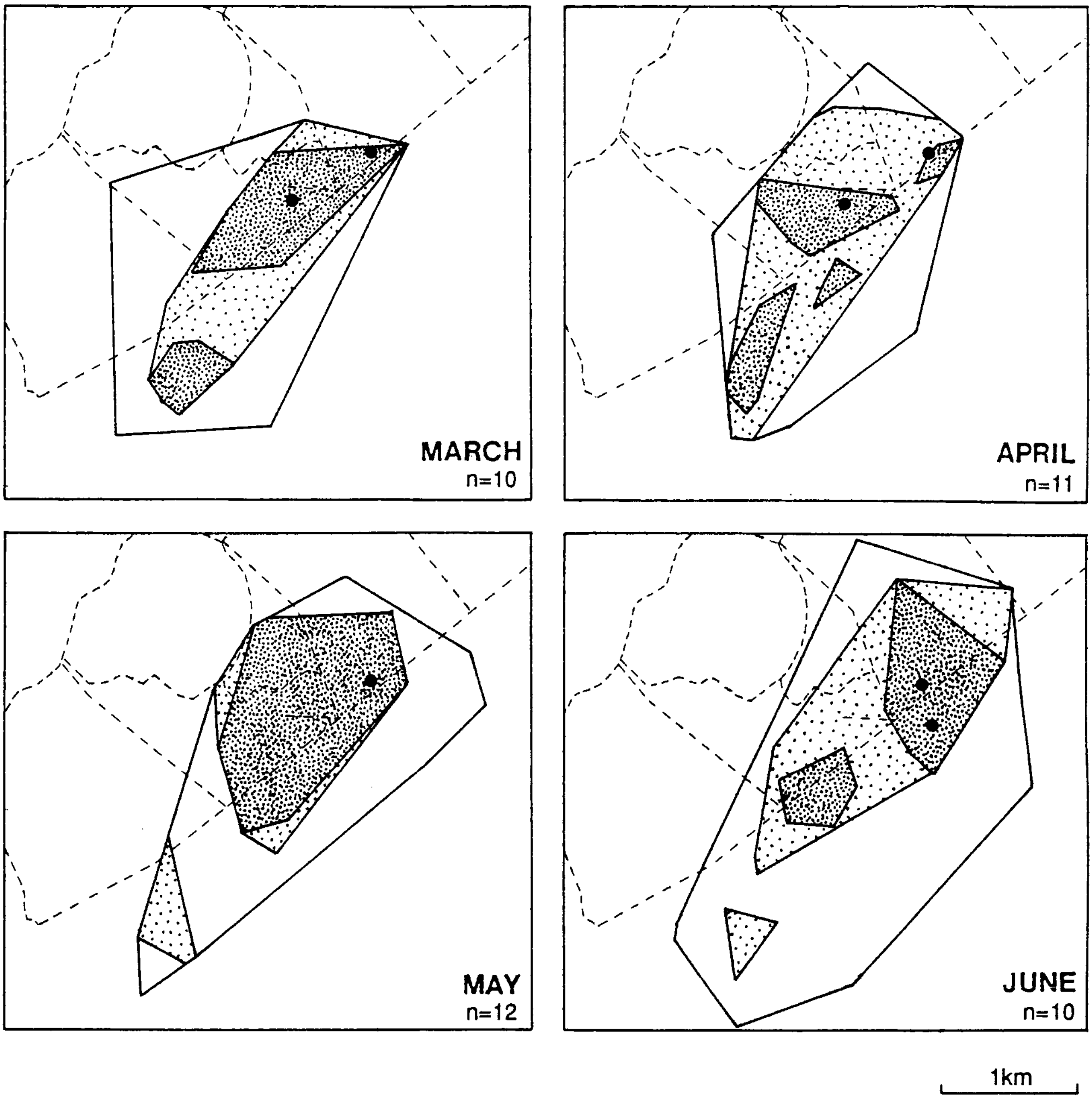


Figure 6f: Monthly home range areas of Fish (M4), November 1989 to June 1990.



<u>Figure 6f</u> (continued)

Figure 6g: Monthly home range areas of Wanda (F4), March to May 1990.

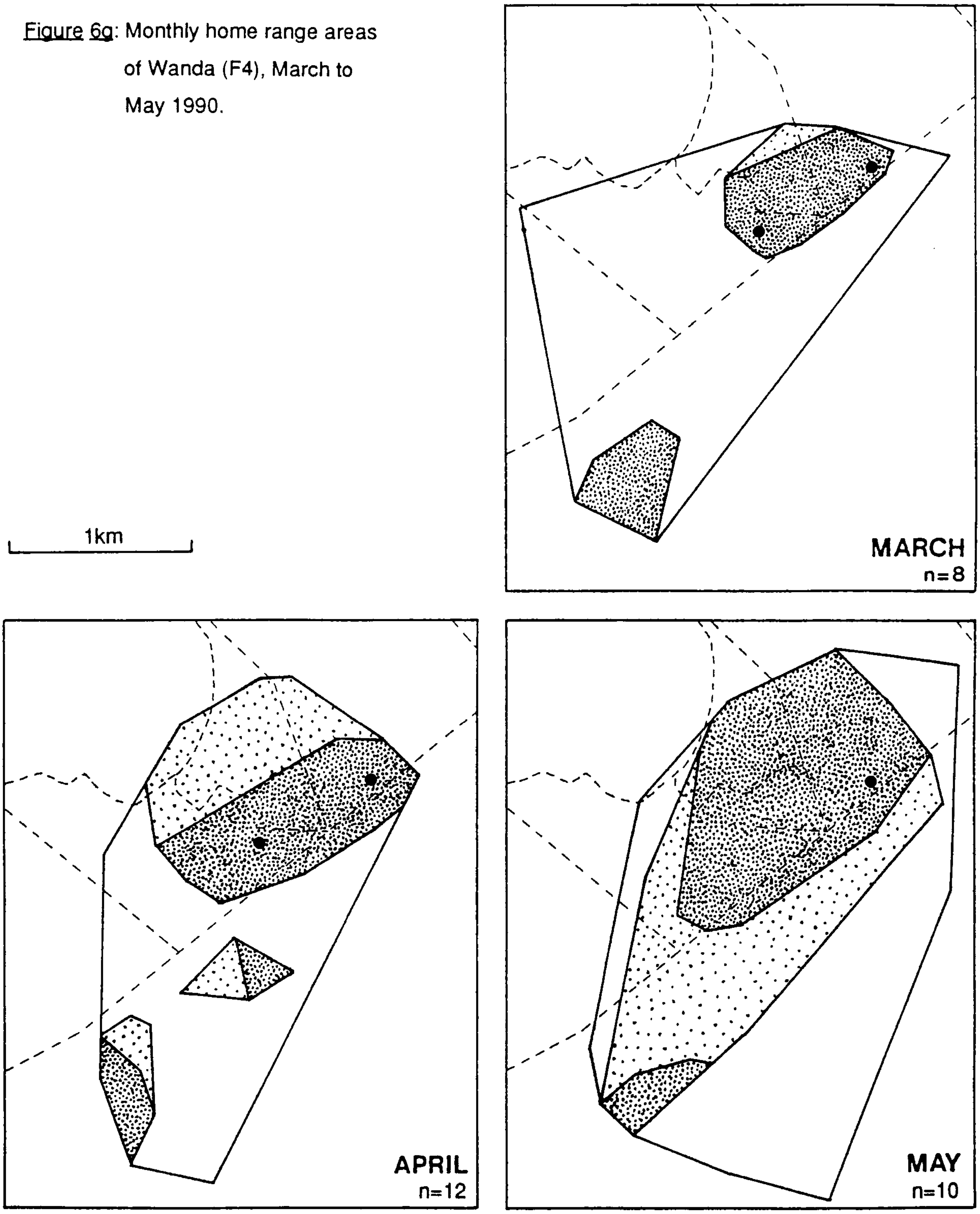
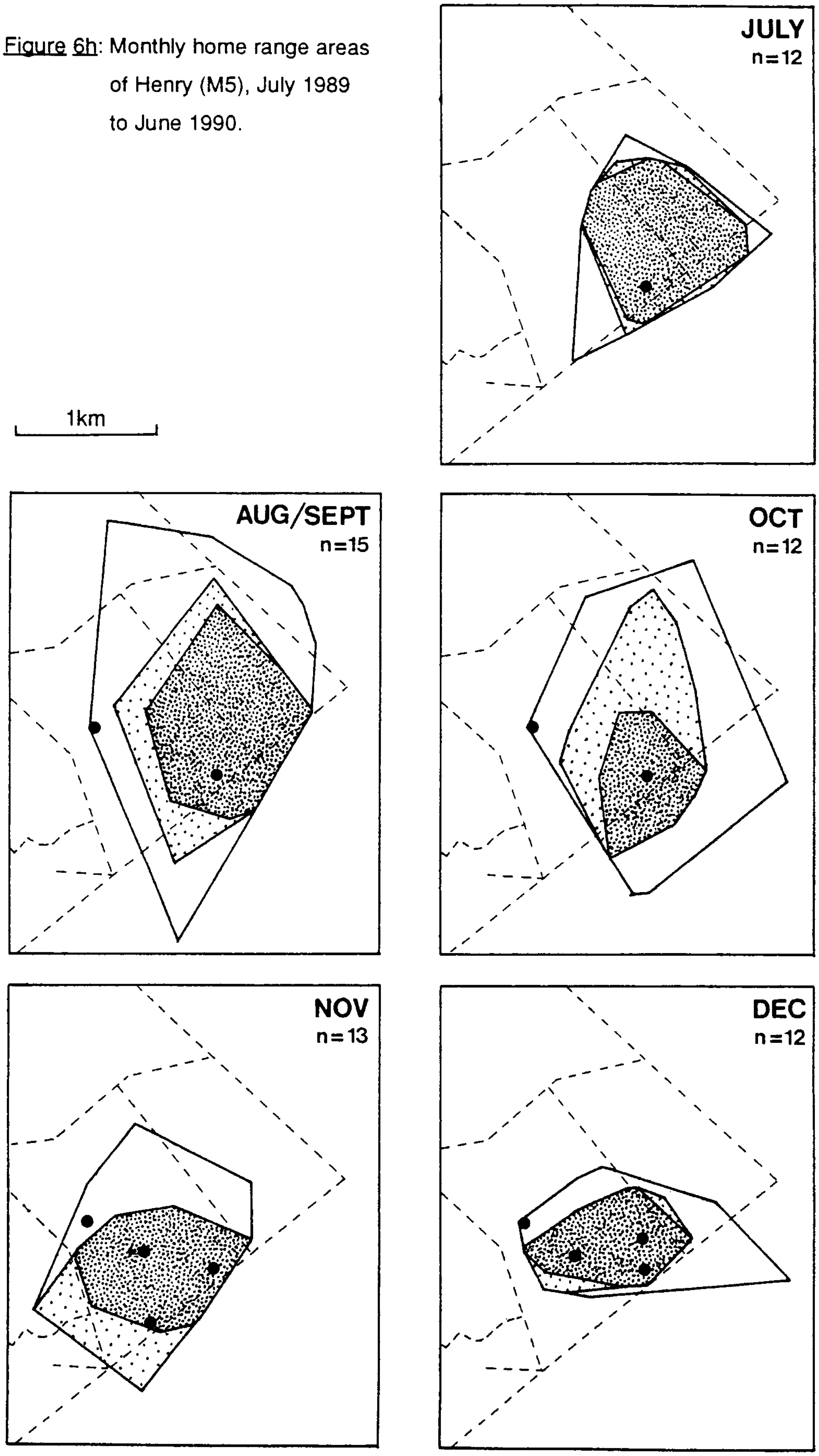


Figure 6h: Monthly home range areas of Henry (M5), July 1989 to June 1990.



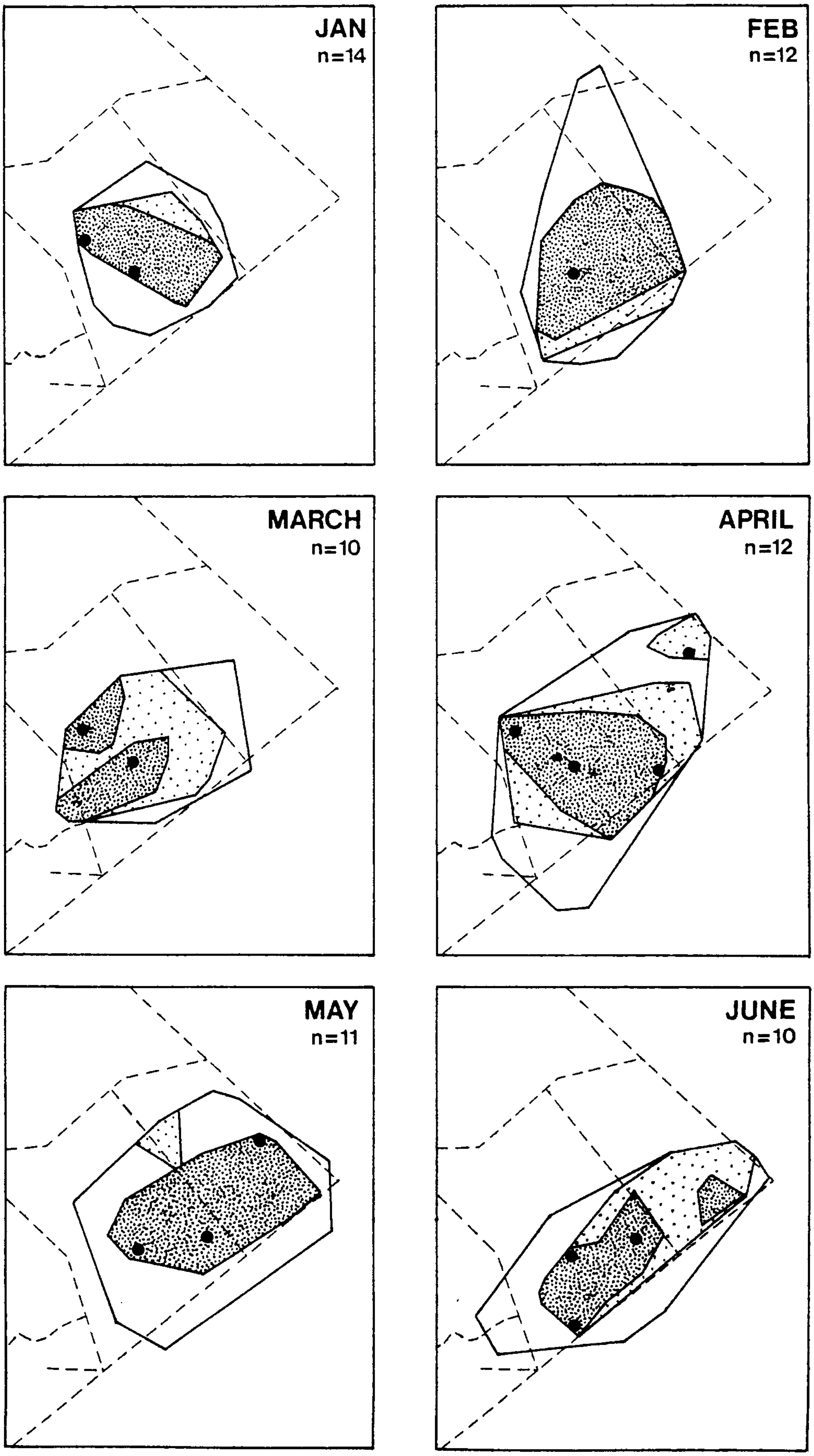


Figure 6h: (continued).

Figure 6i: Monthly home range areas of Bugeye (M6), Jan. to June 1990.

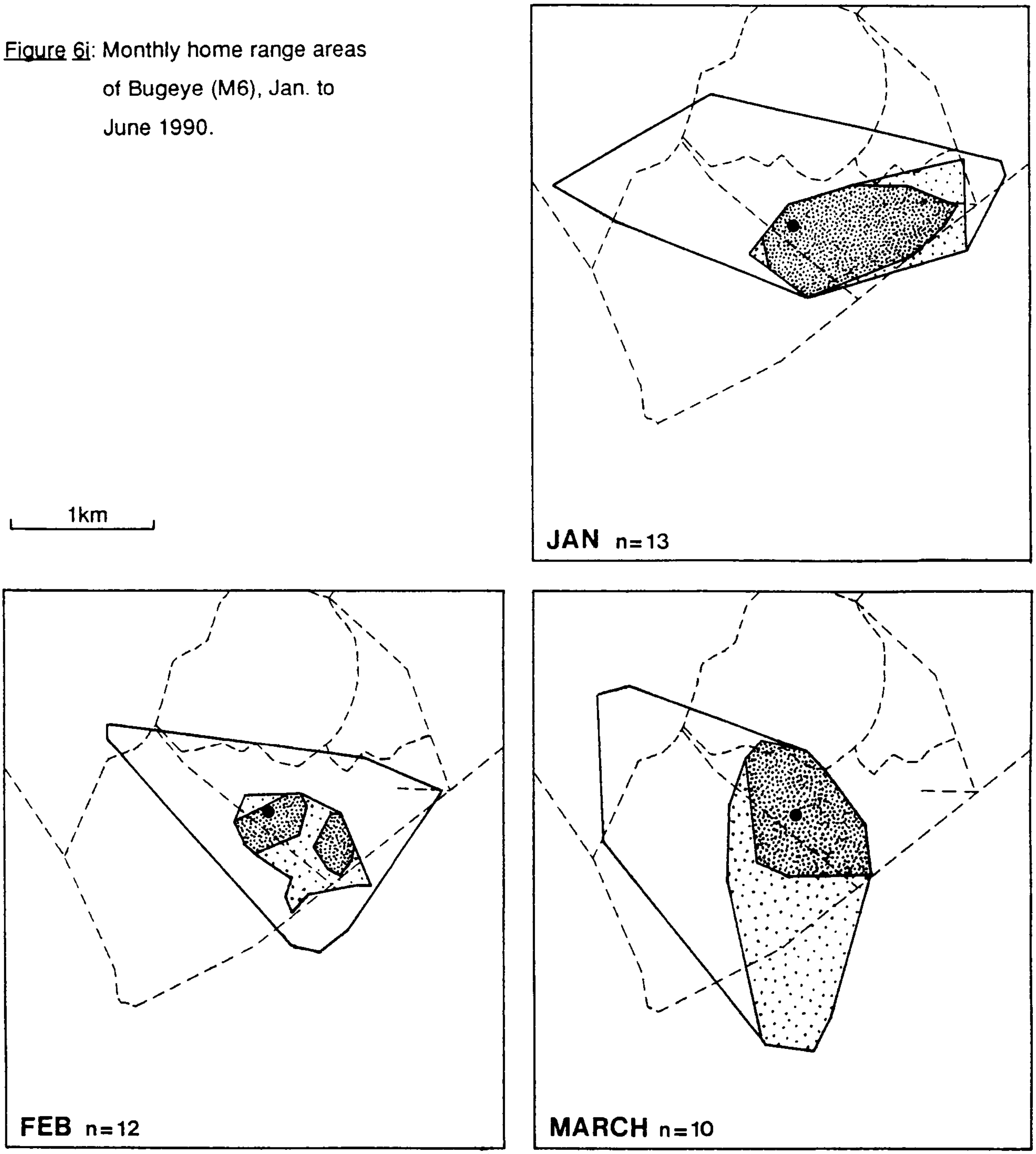
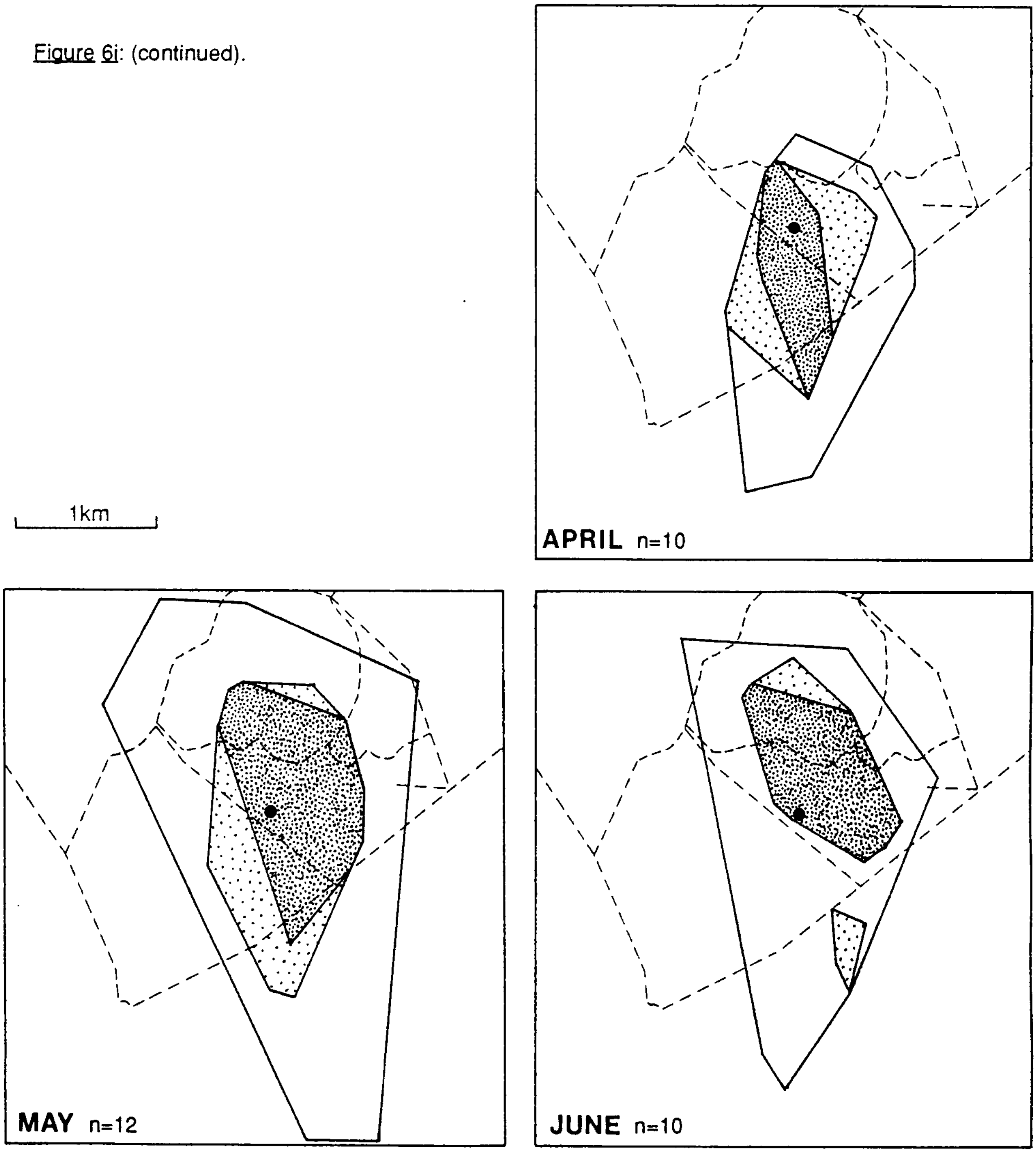


Figure 6i: (continued).



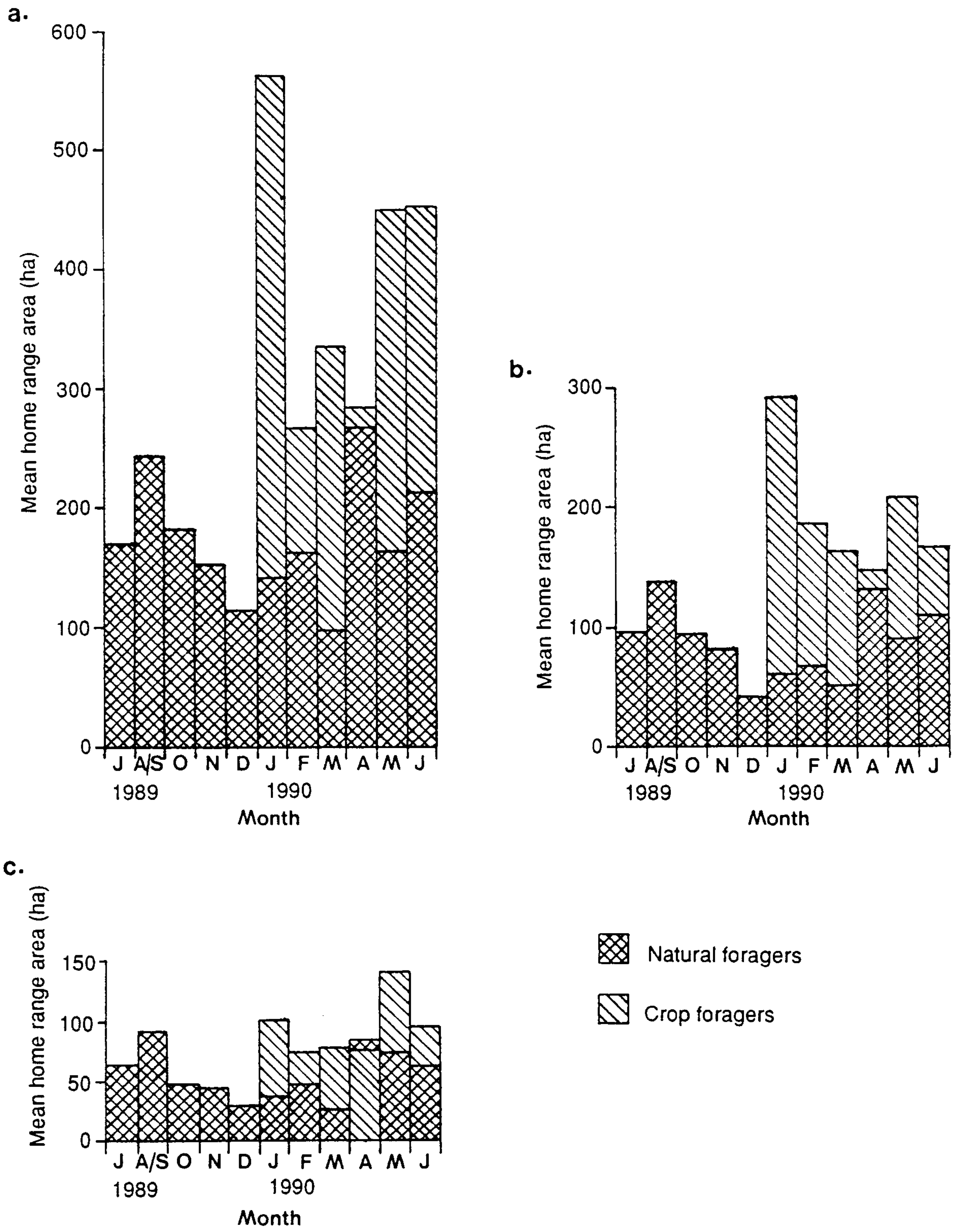


Figure 7: Monthly mean home range sizes: a. Total home range.
b. Normal home range.
c. Area of intensive use.

Relative sizes of total home ranges, normal home ranges and areas of intensive use:

Table 7 shows the mean relative sizes of normal home ranges compared to total home ranges and of areas of intensive use compared to normal home ranges. Table 8 (overpage) analyses the differences in mean relative range sizes between natural foragers and crop foragers, and between seasons for both natural foragers and crop foragers. The difference between winter NF and winter CF (NHR/THR x 100%), although significant, is small and is probably due to the inclusion of large, unused areas in the THR's of winter crop foragers; a fault of the analytical method (minimum convex polygon) and probably of little biological significance. The differences between winter CF and summer CF (AIU/NHR x 100%), and between summer NF and summer CF (AIU/NHR x 100%) may be due to the inclusion of large, unused areas in the NHR's of summer crop foragers and with such a small sample size (n=4) it would perhaps be unwise to attach any great importance to these differences. It is therefore considered reasonable to combine the data to give the following figures:

Mean proportion of THR occupied by NHR (n=58) = 51% (Range = 22-84%)

Mean proportion of NHR occupied by AIU (n=58) = 63% (Range = 32-96%).

Table 7: Mean proportion of total home ranges occupied by normal home ranges (NHR/THR x 100%) and mean proportion of normal home ranges occupied by areas of intensive use (AIU/NHR x 100%).

	WINTER		SUMMER	
	Natural foragers n=17	Crop foragers n=8	Natural foragers n=29	Crop foragers n=4
$\frac{\text{NHR}}{\text{THR}}$ x 100%	56% range=36-66%	46% range=30-61%	49% range=22-84%	55% range=47-70%
$\frac{\text{AIU}}{\text{NHR}}$ x 100%	66% range=39-92%	63% range=36-86%	64% range=32-96%	43% range=40-55%

Table 8: Analyses of differences in mean relative range sizes:

a. Seasonal differences in mean relative range sizes of natural foragers.

b. Seasonal differences in mean relative range sizes of crop foragers.

c. Differences between the mean relative range sizes of natural foragers and crop foragers in winter.

d. Differences between the mean relative range sizes of natural foragers and crop foragers in summer.

a.

	Natural foragers		Mann-Whitney U-test		
	Winter n=17	Summer n=29	U	z	p
$\frac{NHR}{THR} \times 100\%$	56%	49%	169.5	1.75	>0.05
$\frac{AIU}{NHR} \times 100\%$	66%	64%	227	0.44	>0.05

b.

	Crop foragers		Mann-Whitney U-test		
	Winter n=8	Summer n=4	U	z	p
$\frac{NHR}{THR} \times 100\%$	46%	55%	7.5	-	>0.10
$\frac{AIU}{NHR} \times 100\%$	63%	43%	4	-	=0.05 *

c.

	Winter		Mann-Whitney U-test		
	Natural foragers n=17	Crop foragers n=8	U	z	p
$\frac{NHR}{THR} \times 100\%$	56%	46%	31.5	-	<0.05 *
$\frac{AIU}{NHR} \times 100\%$	66%	63%	61.5	-	>0.10

Table 8: (continued).

d.

	Summer		Mann-Whitney U-test		
	Natural foragers n=29	Crop foragers n=4	U	z	p
$\frac{NHR}{THR} \times 100\%$	49%	55%	43.5	0.80	>0.05
$\frac{AIU}{NHR} \times 100\%$	64%	43%	16	2.32	<0.05 *

* Significant difference

Home range overlap

The spatial relationships of pair members and neighbouring animals are illustrated in Figs.8a-k. Pair members occupy similar home range areas and occassionally, quite distinct boundaries may be identified between neighbouring ranges, e.g.:

Between Pairs 1 and 2 (NHR, October 1989, Fig.8c).

Between Pairs 1 and 2 and between Pairs 2 and 3 (THR and NHR, November 1989, Fig.8d).

Between Pair 4 and M2 and M5 (THR and NHR, March 1990, Fig.8h; NHR and AIU, May 1990, Fig.8j).

The mean proportions of home range overlap between pair members and between neighbours (p.39) are given in Table 9 which also examines seasonal differences between range overlap. Pair members, crop foraging neighbours and Henry (M5) and his neighbours show no significant differences in their patterns of range overlap between winter and summer. Natural foraging neighbours however, had significantly higher degrees of range overlap in winter than in summer.

Differences in range overlap between natural foraging neighbours and the the other categories, i.e., pair members, Henry (M5) and his neighbours and crop foraging neighbours, are analysed in Table 10. All of these other categories exhibited significantly greater degrees of range overlap in both winter and summer than did natural foraging neighbours.

Table 9: An analysis of seasonal variation in mean proportions of home range overlap between pair members, between natural foraging neighbours, between Henry (M5) and his neighbours and between crop foraging neighbours, (Mann-Whitney U-test).

		Winter			Summer			Mean overlap (where there is no significant seasonal difference)					
		n	$\bar{x}$	Range	n	$\bar{x}$	Range	n	$\bar{x}$	Range	U	z	p
Pair members	THR	10	75%	47-96%	16	78%	22-100%	26	77%	22-100%	58.0	-	>0.10
	NHR		75%	49-100%		73%	33-100%		74%	33-100%	74.5	-	>0.10
	AIU		73%	38-100%		69%	38-100%		71%	38-100%	70.5	-	>0.10
Natural foraging neighbours	THR	50	18%	0-76%	72	8%	0-73%	-	-	-	1076	3.86	<0.01
	NHR		8%	0-48%		0%	0-2%	-	-	-	1021	4.05	<0.05
	AIU		3%	0-38%		0%	0%	-	-	-	1350	2.44	<0.05
Henry (M5) and neighbours	THR	36	29%	0-79%	44	28%	0-88%	80	28%	0-88%	769	0.22	>0.05
	NHR		18%	0-69%		16%	0-71%		17%	0-71%	777	0.14	>0.05
	AIU		10%	0-51%		8%	0-51%		9%	0-51%	692	0.97	>0.05
Crop foraging neighbours	THR	10	40%	22-52%	8	37%	18-45%	18	39%	18-52%	35.0	-	>0.10
	NHR		16%	6-28%		24%	10-44%		20%	6-44%	23.0	-	>0.10
	AIU		4%	1-11%		7%	0-23%		6%	0-23%	37.0	-	>0.10

Table 10: An analysis of the different degrees of range overlap exhibited by:

a. Natural foraging neighbours and pair members.

b. Natural foraging neighbours and Henry (M5) and his neighbours.

c. Natural foraging neighbours and crop foraging neighbours.

a.

		Natural foraging neighbours			Pair members			Mann-Whitney U-test		
		n	$\bar{x}$	Range	n	$\bar{x}$	Range	U	z	p
Winter	THR	50	18%	0-76%	10	75%	47-96%	1.5	4.94	<0.01*
	NHR		8%	0-48%		75%	49-100%	0.0	4.97	<0.01*
	AIU		3%	0-38%		73%	38-100%	0.5	4.96	<0.01*
Summer	THR	72	8%	0-73%	16	78%	22-100%	17.0	6.05	<0.01*
	NHR		0%	0-2%		73%	33-100%	0.0	6.23	<0.01*
	AIU		0%	0%		69%	38-100%	0.0	6.23	<0.01*

b.

		Natural foraging neighbours			Henry (M5) and neighbours			Mann-Whitney U-test		
		n	$\bar{x}$	Range	n	$\bar{x}$	Range	U	z	p
Winter	THR	50	18%	0-76%	36	29%	0-79%	650	2.22	<0.05*
	NHR		8%	0-48%		18%	0-69%	660	2.10	<0.05*
	AIU		3%	0-38%		10%	0-51%	620	2.57	<0.05*
Summer	THR	72	8%	0-73%	44	28%	0-88%	598	5.61	<0.01*
	NHR		0%	0-2%		16%	0-71%	474	6.32	<0.01*
	AIU		0%	0%		8%	0-51%	986	3.40	<0.01*

c.

		Natural foraging neighbours			Crop foraging neighbours			Mann-Whitney U-test		
		n	$\bar{x}$	Range	n	$\bar{x}$	Range	U	z	p
Winter	THR	50	18%	0-76%	10	40%	22-52%	48.5	4.02	<0.01*
	NHR		8%	0-48%		16%	6-28%	113.5	2.21	<0.05*
	AIU		3%	0-38%		4%	1-11%	101.5	2.99	<0.01*
Summer	THR	72	8%	0-73%	8	37%	18-45%	28.0	3.21	<0.01*
	NHR		0%	0-2%		24%	10-44%	0.0	3.66	<0.01*
	AIU		0%	0%		7%	0-23%	144.0	2.31	<0.05*

* Significant difference

Figures 8a-k: Monthly spatial distributions of radiocollared porcupines illustrating home range overlap.

Key to Figures 8a-k:

—— Range boundary (MALE)

— — Range boundary (FEMALE)

---- Vehicle track

(All maps are aligned such that north is at the top of the page)

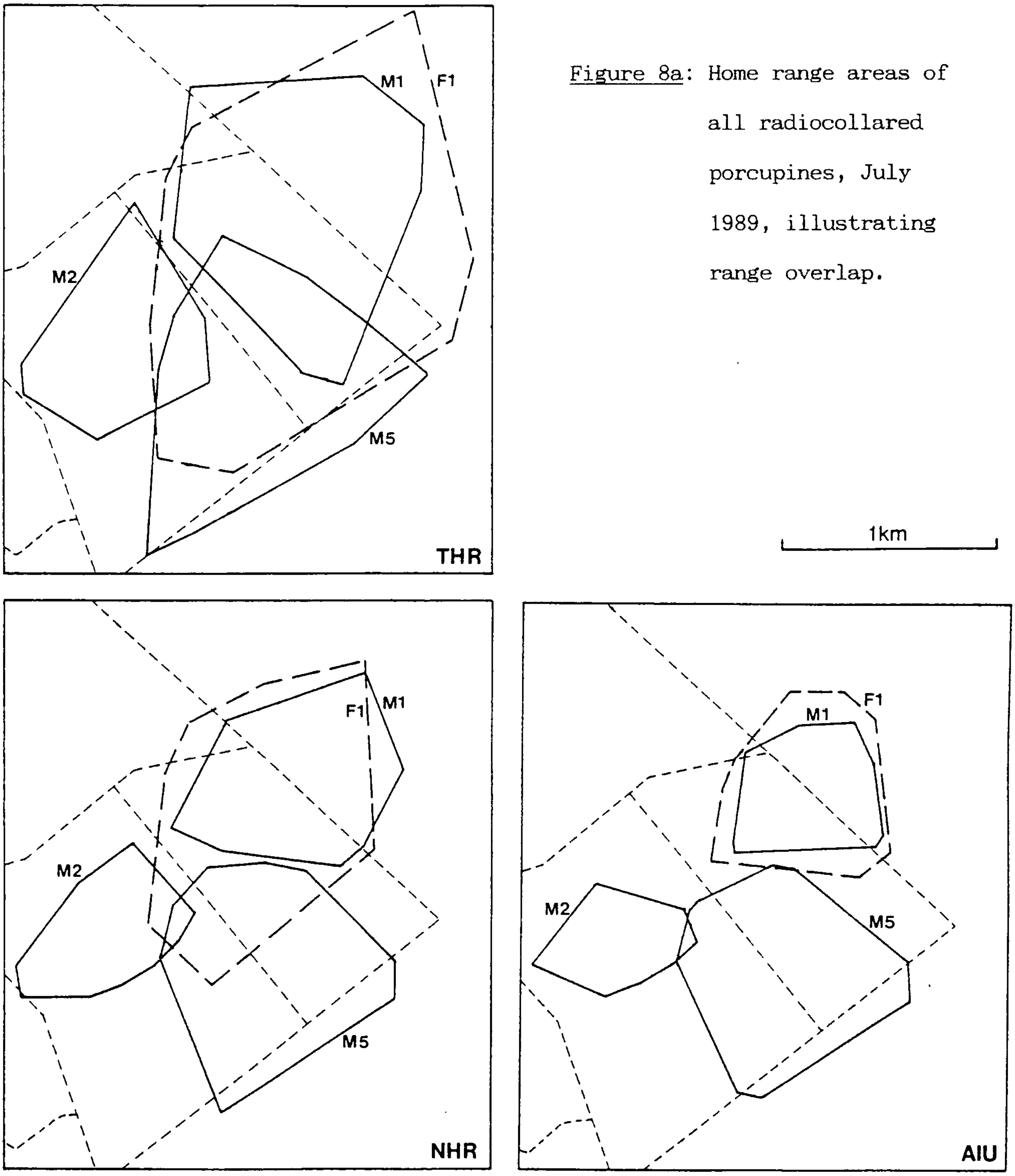


Figure 8a: Home range areas of all radiocollared porcupines, July 1989, illustrating range overlap.

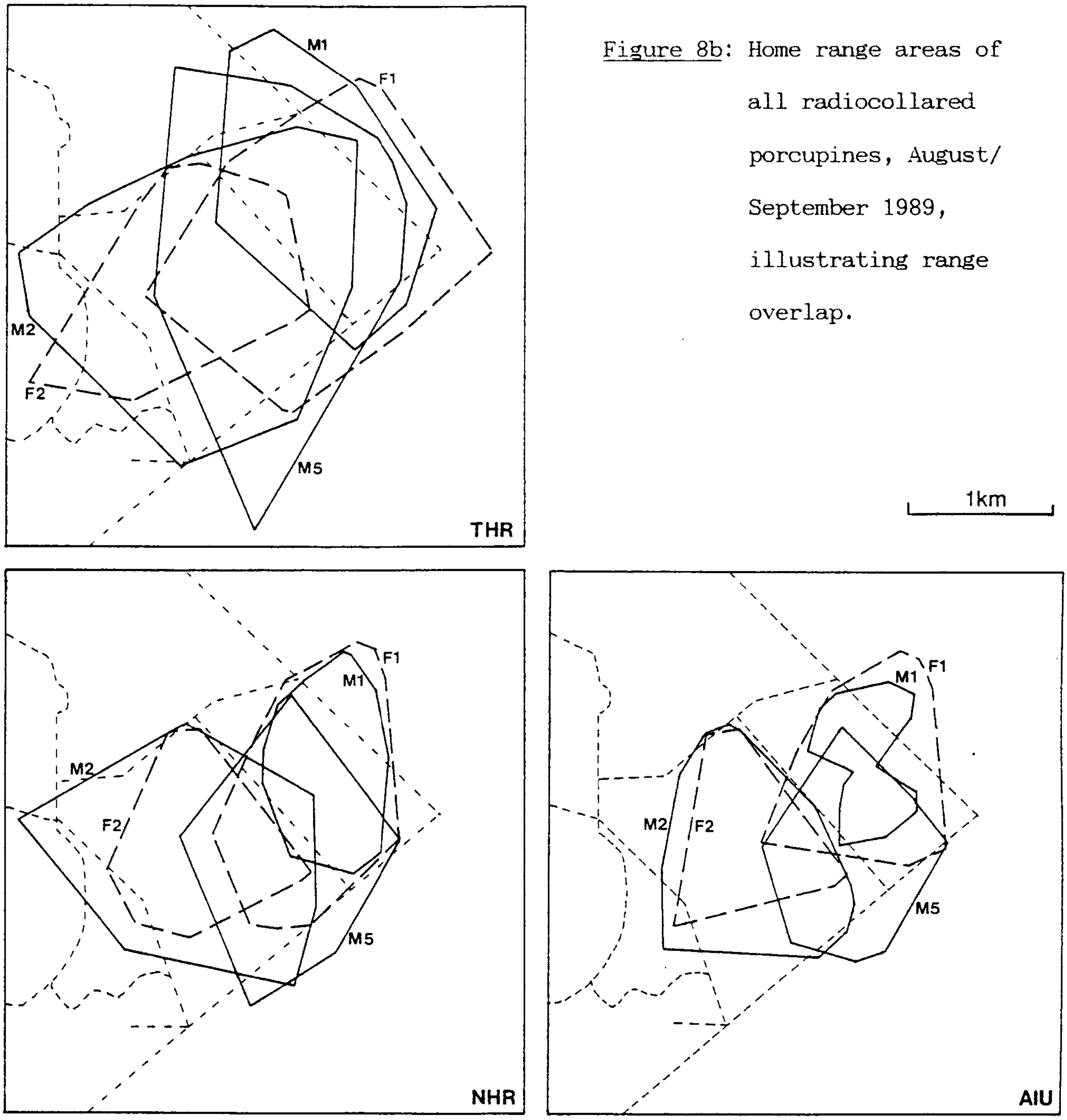


Figure 8b: Home range areas of all radiocollared porcupines, August/ September 1989, illustrating range overlap.

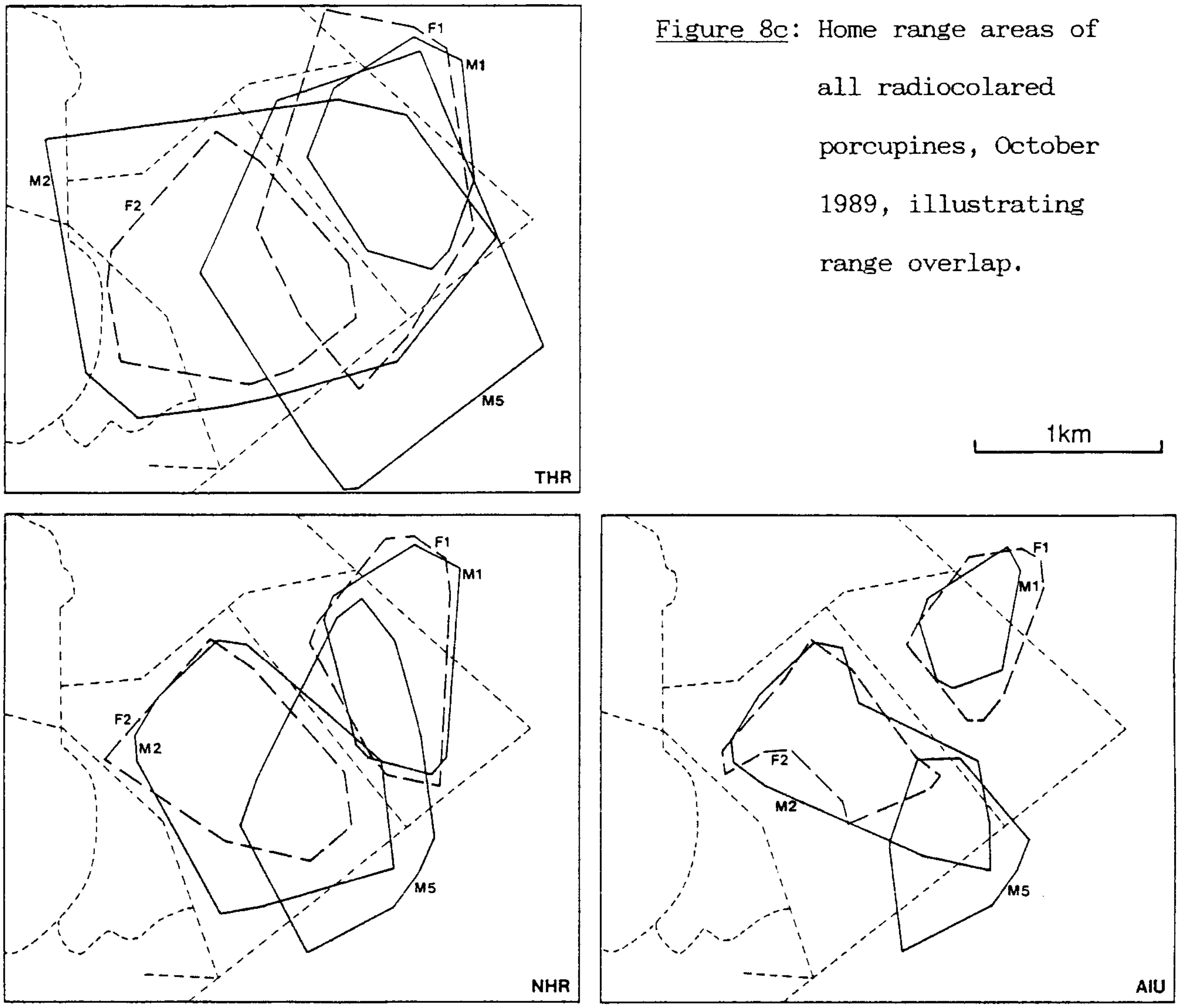


Figure 8c: Home range areas of all radiocolared porcupines, October 1989, illustrating range overlap.

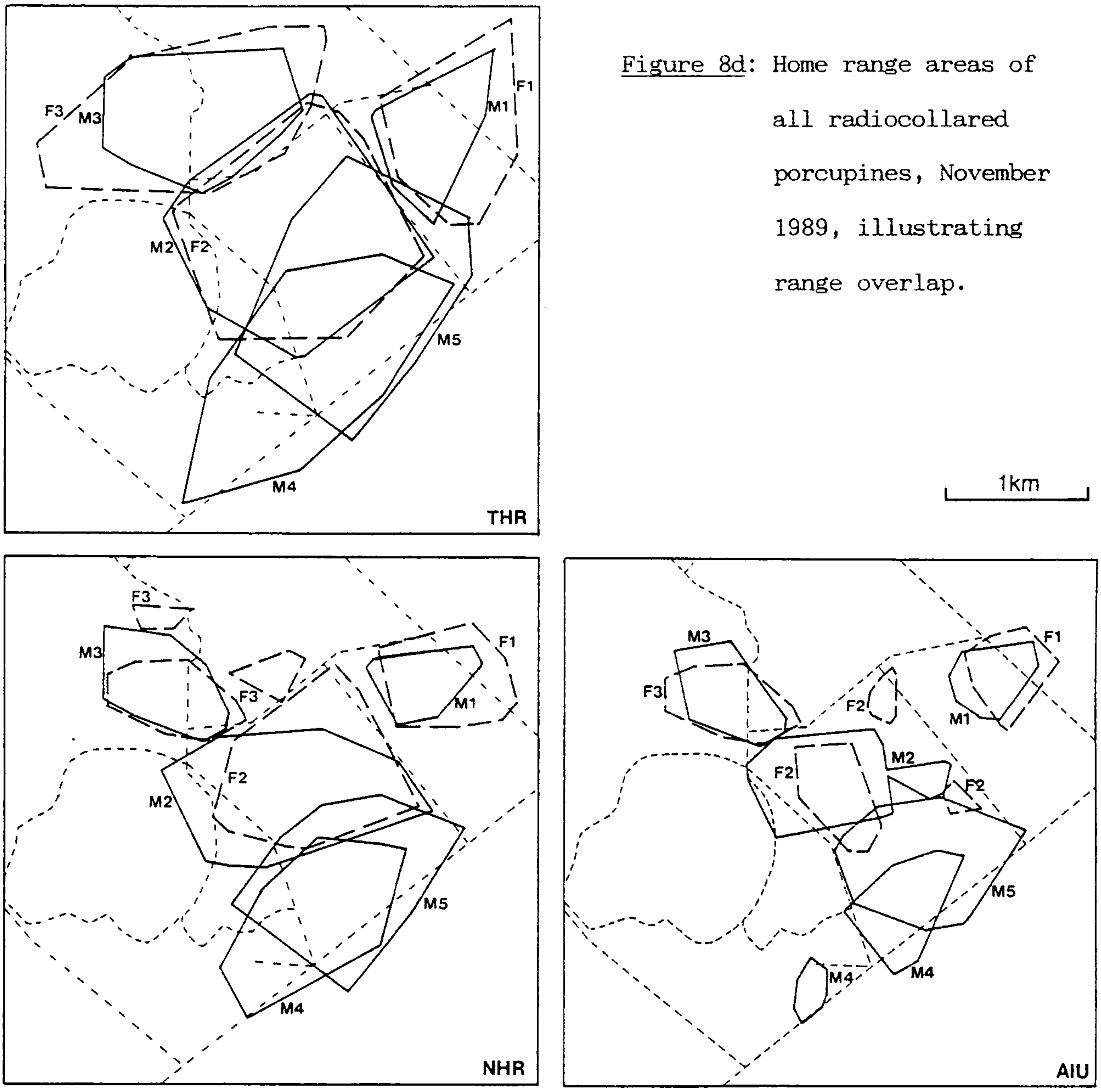


Figure 8d: Home range areas of all radiocollared porcupines, November 1989, illustrating range overlap.

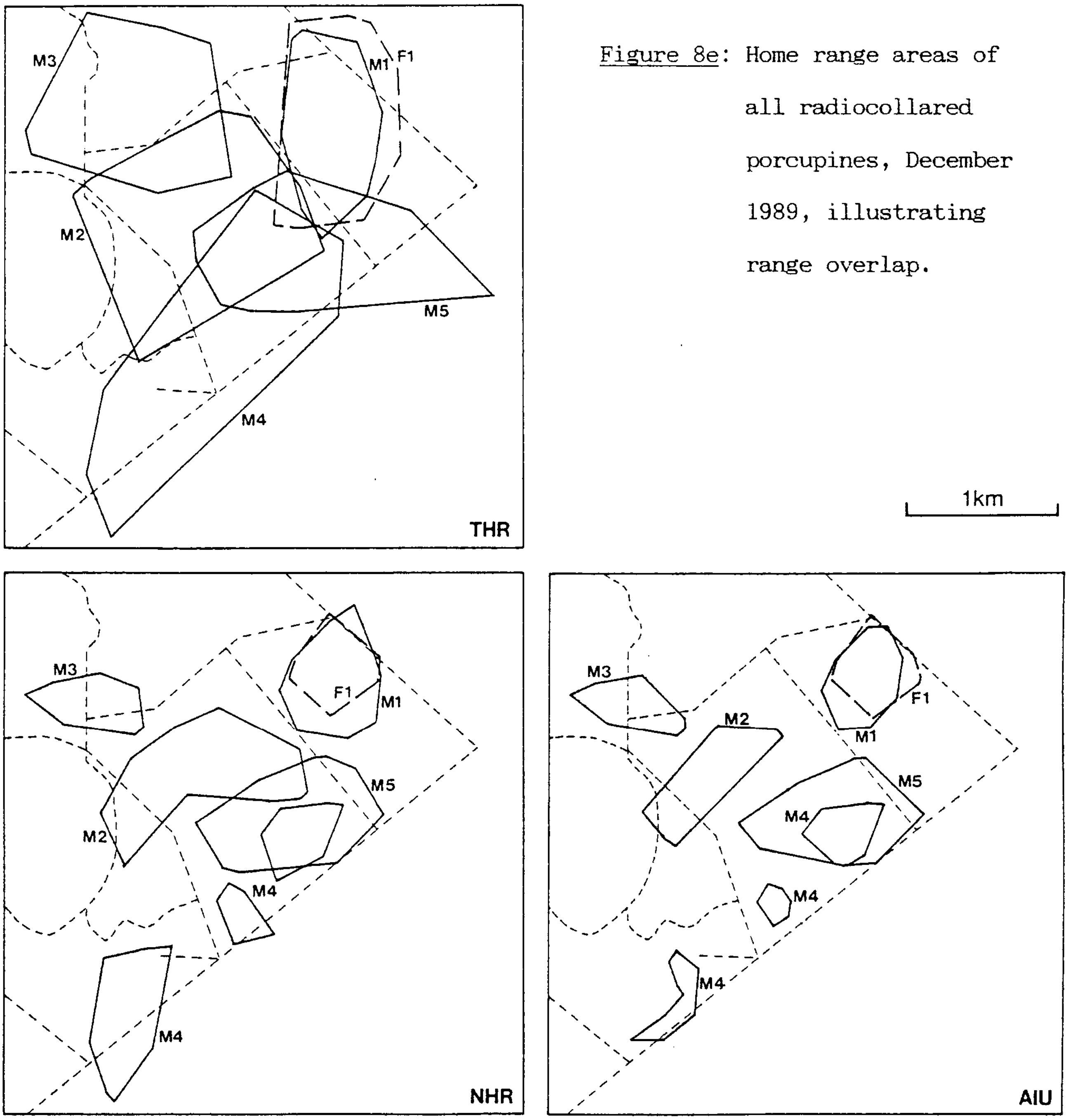


Figure 8e: Home range areas of all radiocollared porcupines, December 1989, illustrating range overlap.

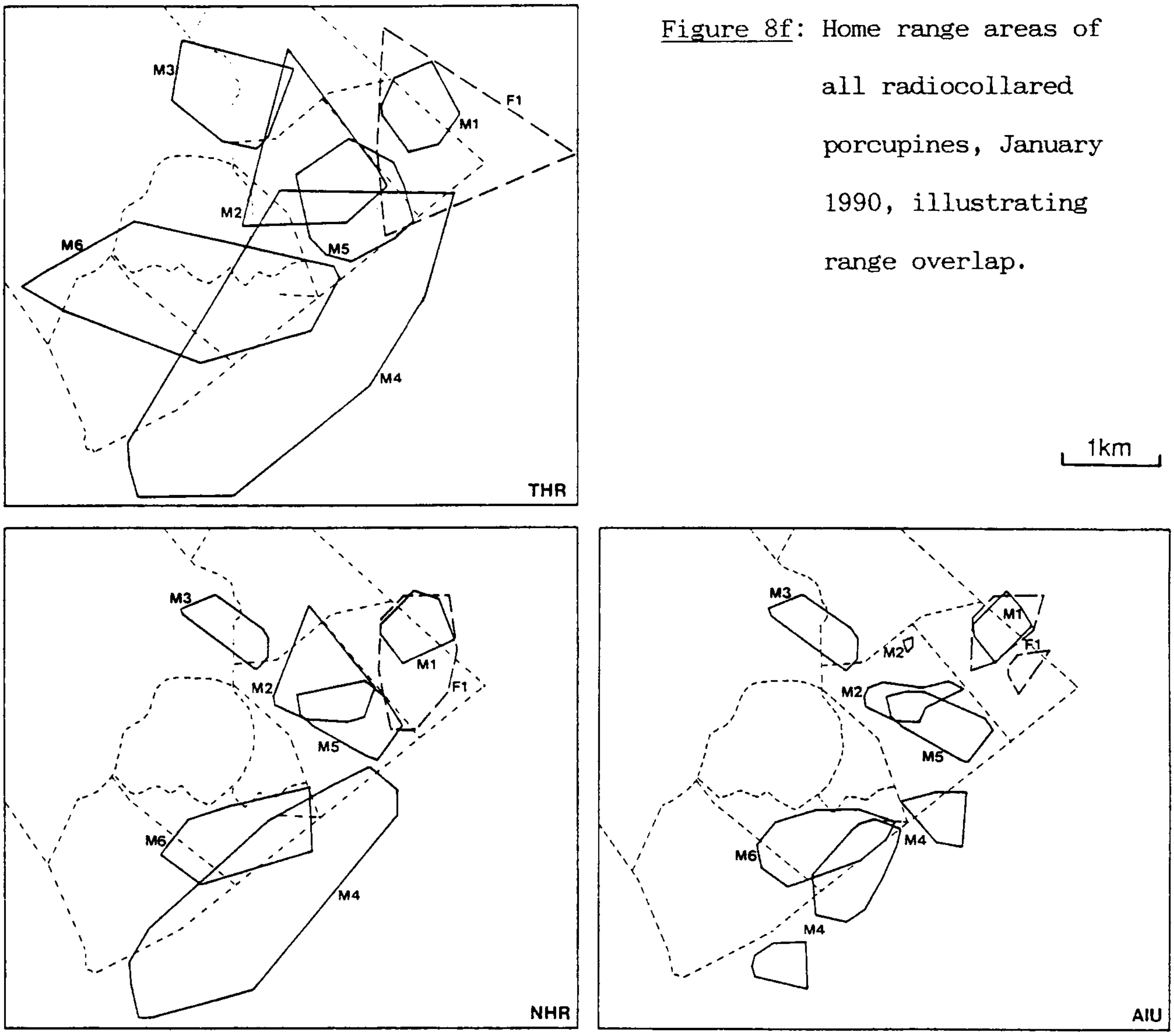


Figure 8f: Home range areas of all radiocollared porcupines, January 1990, illustrating range overlap.

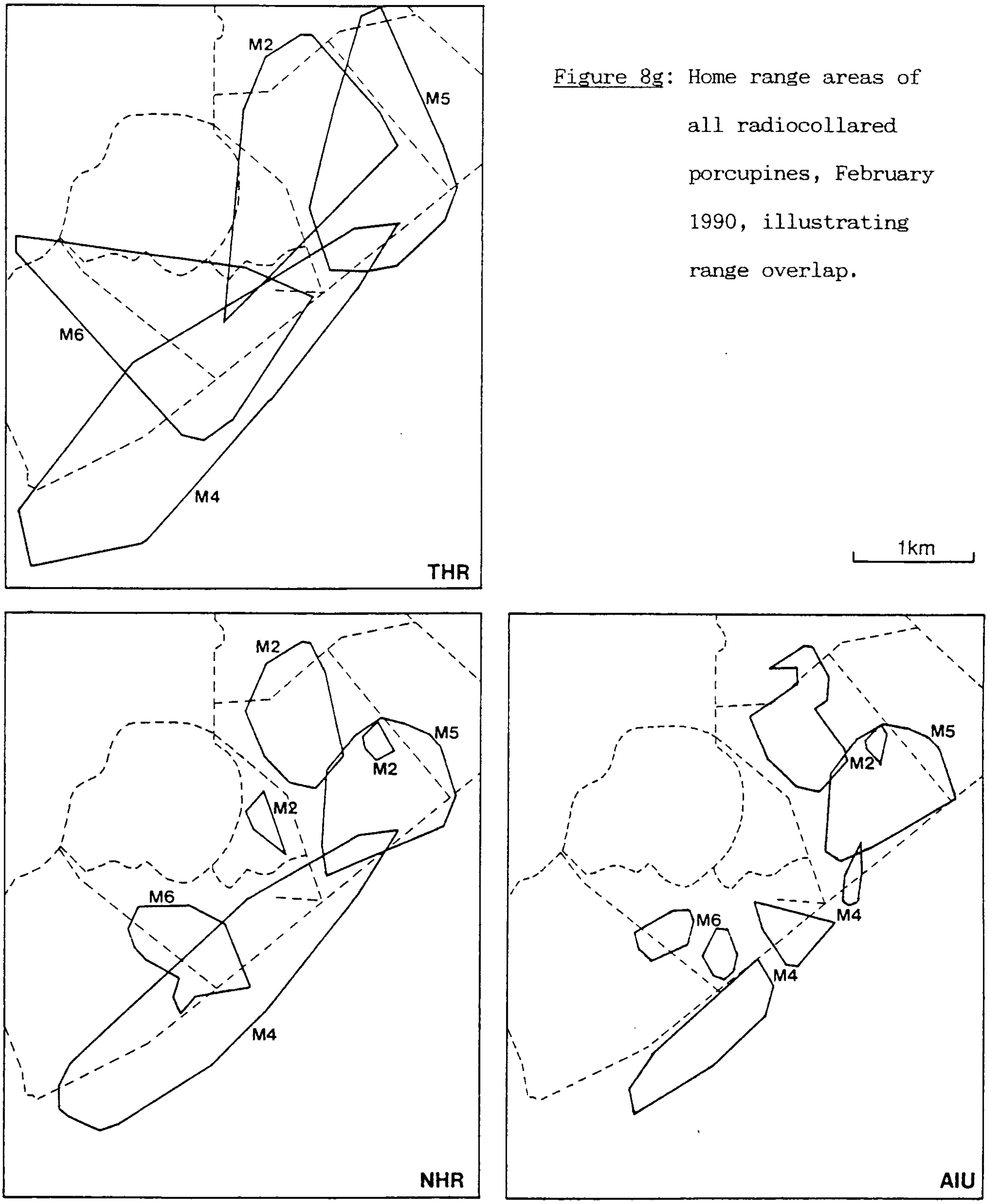


Figure 8g: Home range areas of all radiocollared porcupines, February 1990, illustrating range overlap.

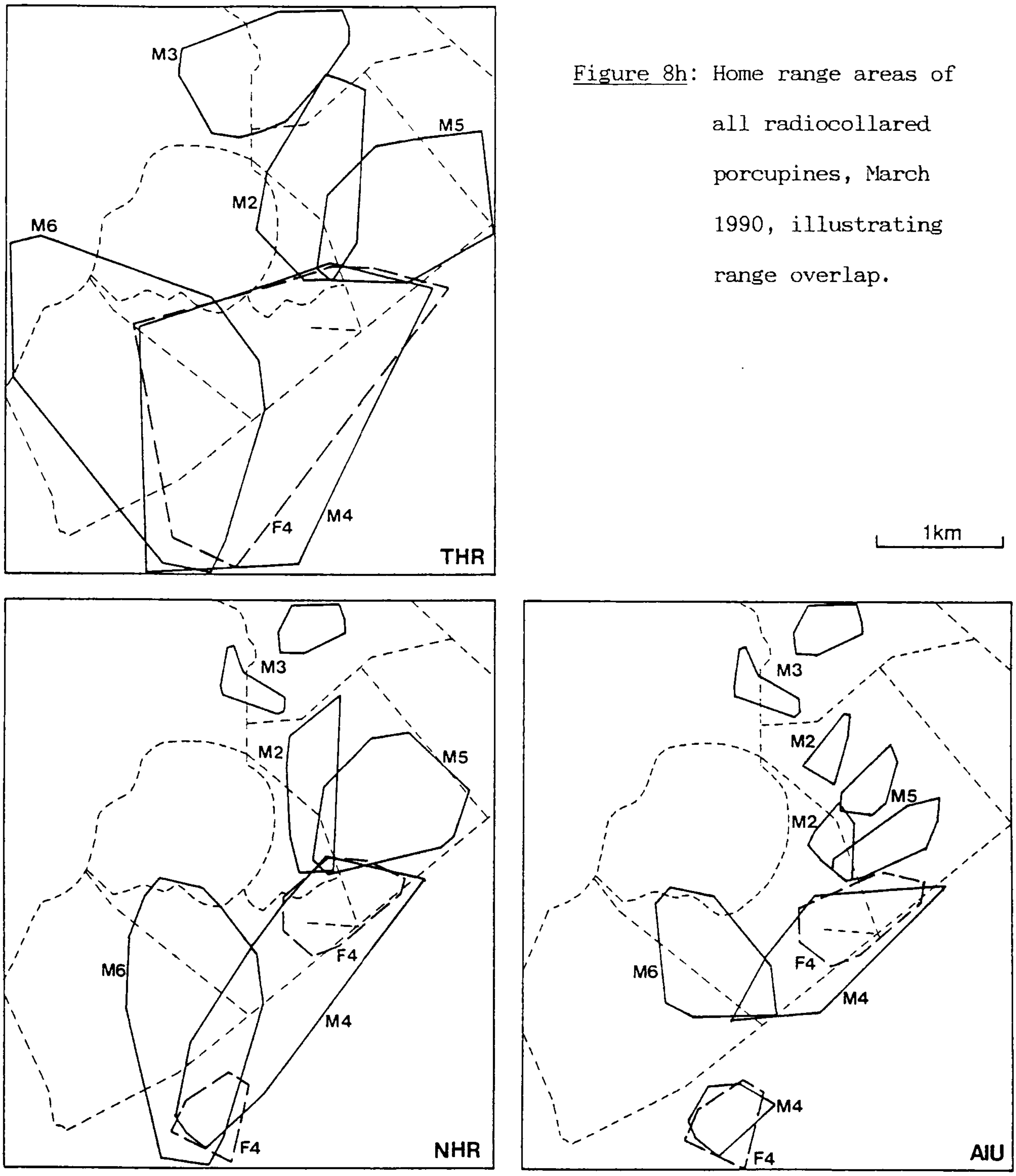


Figure 8h: Home range areas of all radiocollared porcupines, March 1990, illustrating range overlap.

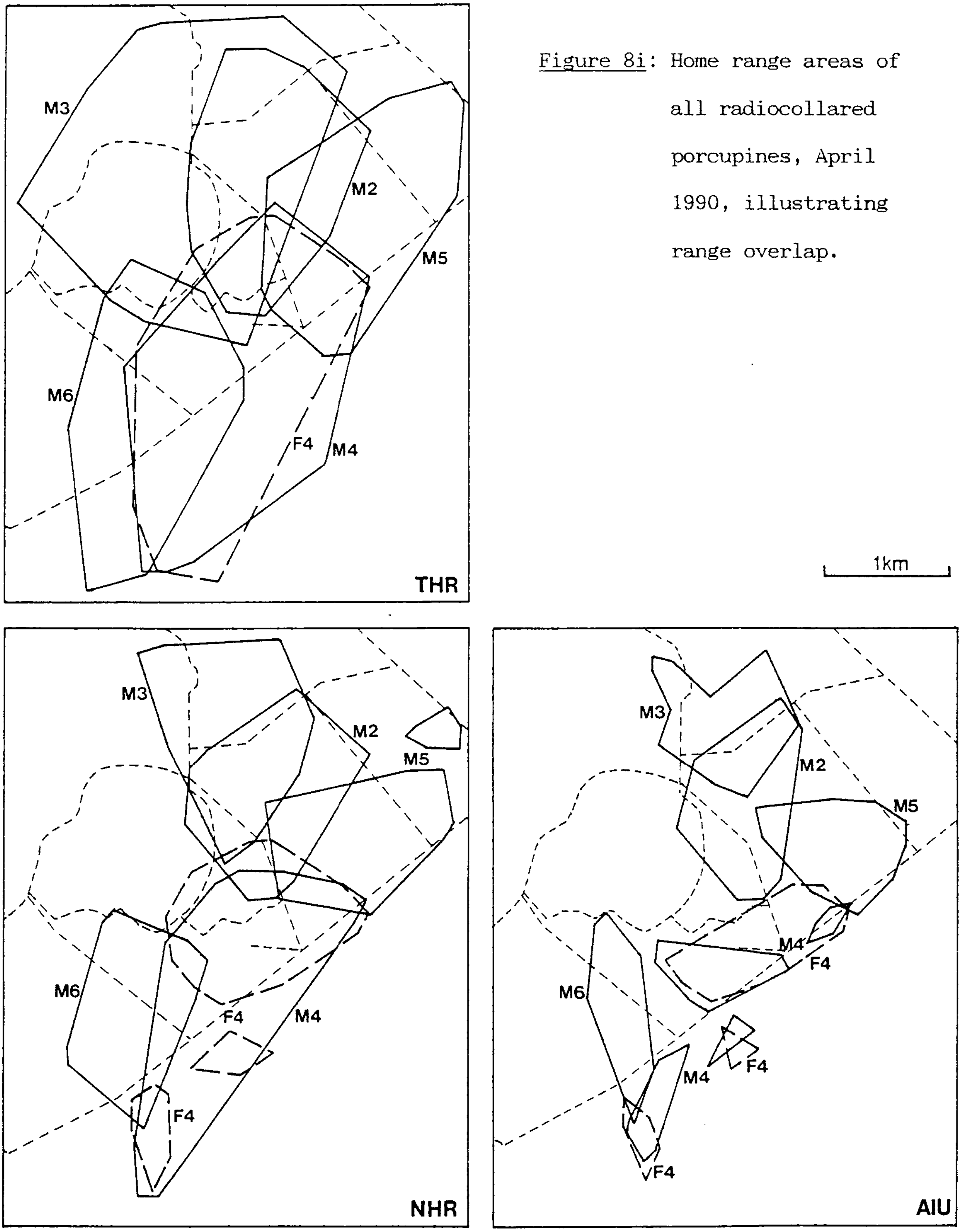


Figure 8i: Home range areas of all radiocollared porcupines, April 1990, illustrating range overlap.

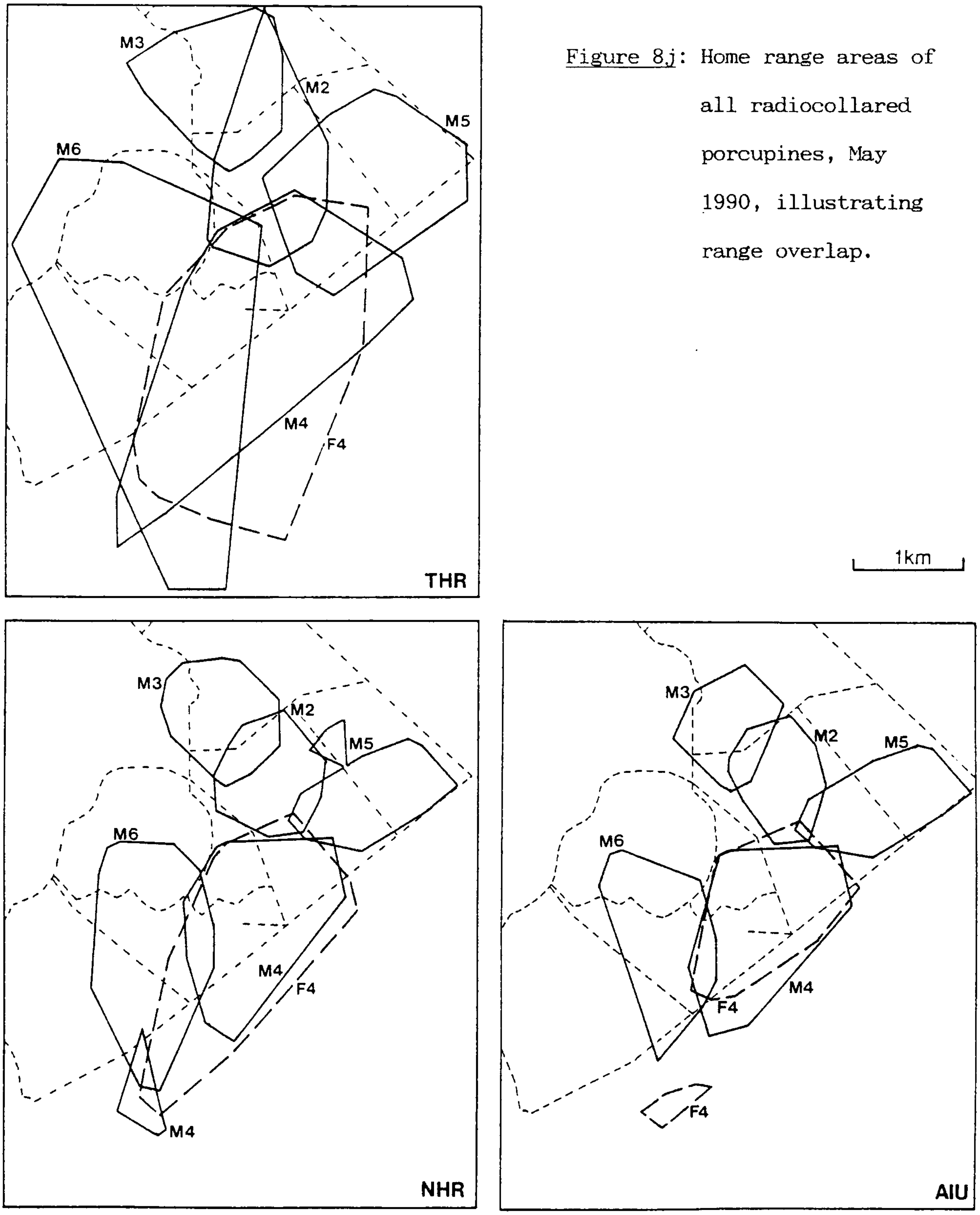


Figure 8j: Home range areas of all radiocollared porcupines, May 1990, illustrating range overlap.

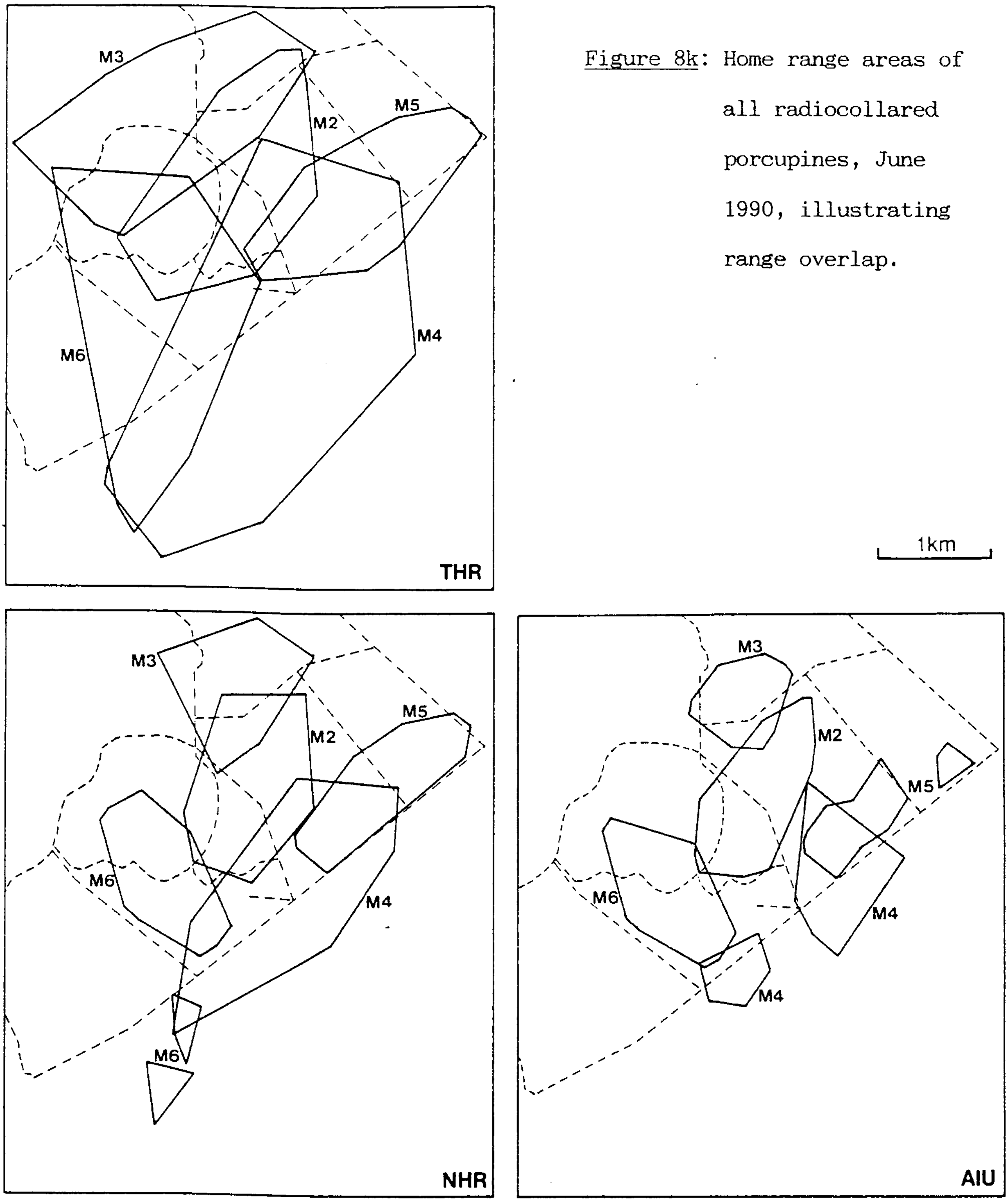


Figure 8k: Home range areas of all radiocollared porcupines, June 1990, illustrating range overlap.

Temporal space use

The observation that encounters between neighbouring porcupines were rare (p.40) was confirmed by the analysis of temporal space use, the results of which are presented in Fig.9.

Pair members spent much of their time roaming in the same general area (inter-individual distance categories 0-200m and 201-400m) (Fig.9a), although they were not necessarily roaming together. From the nightly maps the following observations were made for each pair:

Getafix (M1) & Lady (F1)	They appeared to roam independently of each other, although the estimated routes travelled often crossed, such that several encounters were possible each night.
Batman (M2) & Vicki (F2)	They often followed similar routes for several hours, usually at the beginning of the night, otherwise similar to Pair 1.
Attilla (M3) & Bodacea (F3)	Similar to Pair 1.
Fish (M4) & Wanda (F4)	They usually followed very similar routes for the entire night, presumably roaming together.

Neighbouring individuals rarely encountered one another even when the monthly home range analysis showed considerable overlap between ranges. The frequency of potential interactions between male-female neighbours and between male neighbours were very similar (Figs.9b & c). However, the pattern of seperation between female neighbours (Fig.9d) appears to be different. This difference is probably due to the small sample size and the difficulty in obtaining data in the high IID categories (p.40). However, it is the low frequency of potential close encounters that is important, and in this respect female neighbours are similar to male-female and male neighbours. Note that even if an individual was constantly interacting with it's neighbours, a frequency score of more than 25% in the 0-200 m IID category would not be expected. This is because each individual's range is bordered by about four other ranges; thus if an individual is interacting with one neighbour (or pair of neighbours) it will almost certainly fall in the higher IID categories with respect to it's other three sets of neighbours, such that a maximum of 25% of observations may fall within the 0-200 m IID category. Despite these shortcomings, the observed freqency of close interactions still falls well below this potential 25% level.

Seasonal differences in inter-individual distances were small for both pairs and neighbours despite the lower levels of home range overlap in summer (p.70, Table 9). This reinforces the observation that these overlapping areas are sparsely utilised and do not represent a higher frequency of encounters between the "overlapping" neighbours.

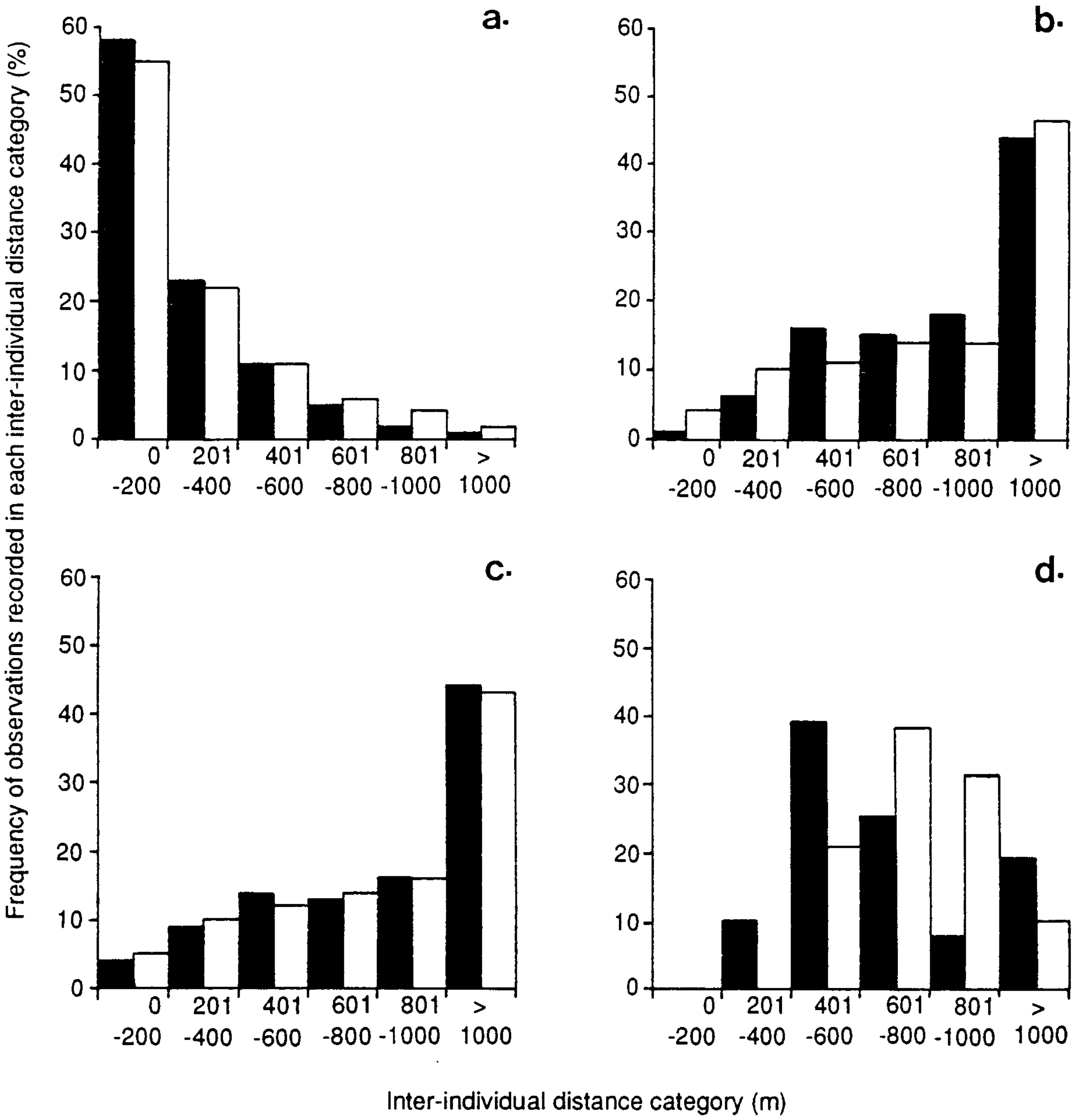


Figure 9: Temporal space use patterns, measured as frequency of observations in each inter-individual distance (IID) category:

a. Inter-individual distances between pair members.

b. Inter-individual distances between male and female neighbours.

c. Inter-individual distances between male neighbours.

d. Inter-individual distances between female neighbours.

■ Summer (October-March) n = a.815, b.649, c.1726, d.71

□ Winter (April-September) n = a.576, b.548, c.1348, d.19

Recorded interactions

Only five interactions between neighbouring individuals were recorded that are worthy of note. These are described below. The interpretation of these interactions is difficult owing to a lack of knowledge concerning the relatedness, if any, of the individuals involved.

1. 27.08.89 (Fig.10). Getafix (M1) and Henry (M5) appeared to encounter one another at about 20:00 hrs (location 3) and thereafter roamed as a pair until approximately 02:00 hrs (location 9) after which they returned to their respective burrows, B8 and B18. No such male-male interaction was ever recorded again and it's significance, if any, is unknown.

2. 14.09.89 (Fig.11). Henry (M5) and Lady (F1) roamed in an apparently irregular manner, possibly encountering one another at about 01:00 hrs (location 8) after which they returned to their respective burrows, B8 and B18. However, they both then moved towards another burrow, B14, which they shared the following day. Neither Henry or Lady had previously been observed to use B14 and it was outside both their previous home range areas. Lady was never recorded to use B14 again and it never fell within any of her subsequent range boundaries. How this interaction was coordinated is unclear as both Henry and Lady returned to their respective burrows, which were over 1 km apart, before converging on B14.

3. 25.09.89. Henry (M5) and Lady (F1) shared the same burrow, B18, during the day but at dusk they seperated and roamed seperately for the rest of the night, returning to their own burrows, B18 and B8, at dawn.

4. 29.09.89 (Fig.12). Batman (M2) and Lady (F1) left their burrows, B6 and B8, at dusk and headed towards an area commonly used by both animals,

possibly encountering one another at about 20:00 hrs (location 3). Each continued to roam seperately but in the same general area, encountering each other again at about 02:00 hrs (location 9). Both animals then headed towards Lady's burrow, B2 or 3, apparently spending approximately two hours together before returning to their respective partners and burrows, B6 & B8.

5. 14-15.06.90. Wanda (F4) was killed by a farmer while foraging in a maize field on Blindfontein Farm on the night of 14.06.90. On the following night her partner, Fish (M4), left the burrow, B20, that they had been using almost exclusively for the previous three months. After returning to the vicinity of this burrow the following morning he moved to another burrow, B24. That same morning, Henry (M5) moved into B20 and stayed there for the remainder of the study. Whether or not this takeover was as the result of an aggressive encounter is not known as a brief interaction is unlikely to have been recorded by the hourly radiotracking sample with it's limited accuracy.

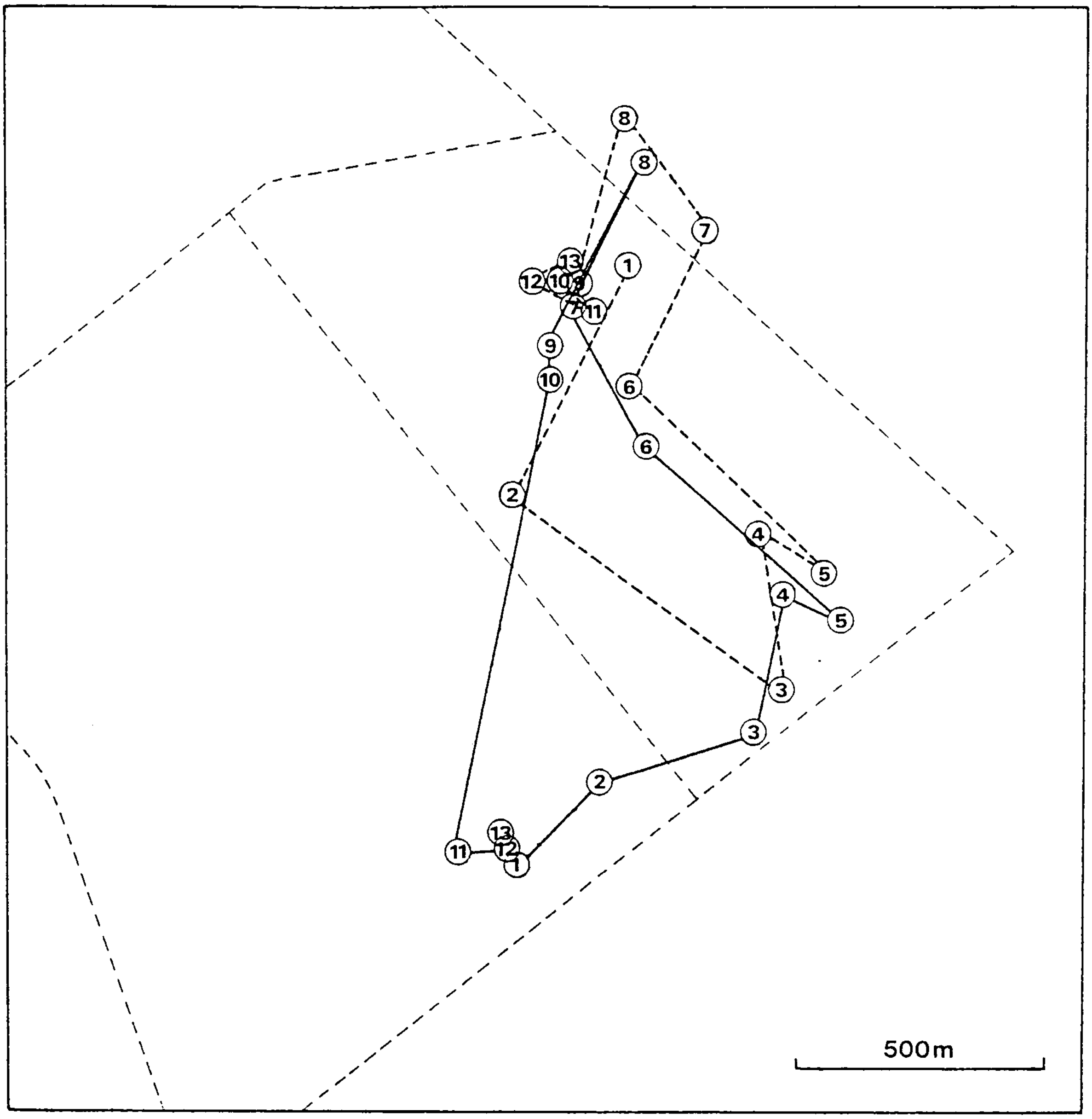


Figure 10: Map of the study area illustrating the encounter between Getafix (M1) and Henry (M5) on 27.08.89.

--ⓧ-- Getafix (M1), hourly locations whereby --①-- is the first location of the night, --②-- the second, etc.

—ⓧ— Henry (M5), hourly locations, as above.

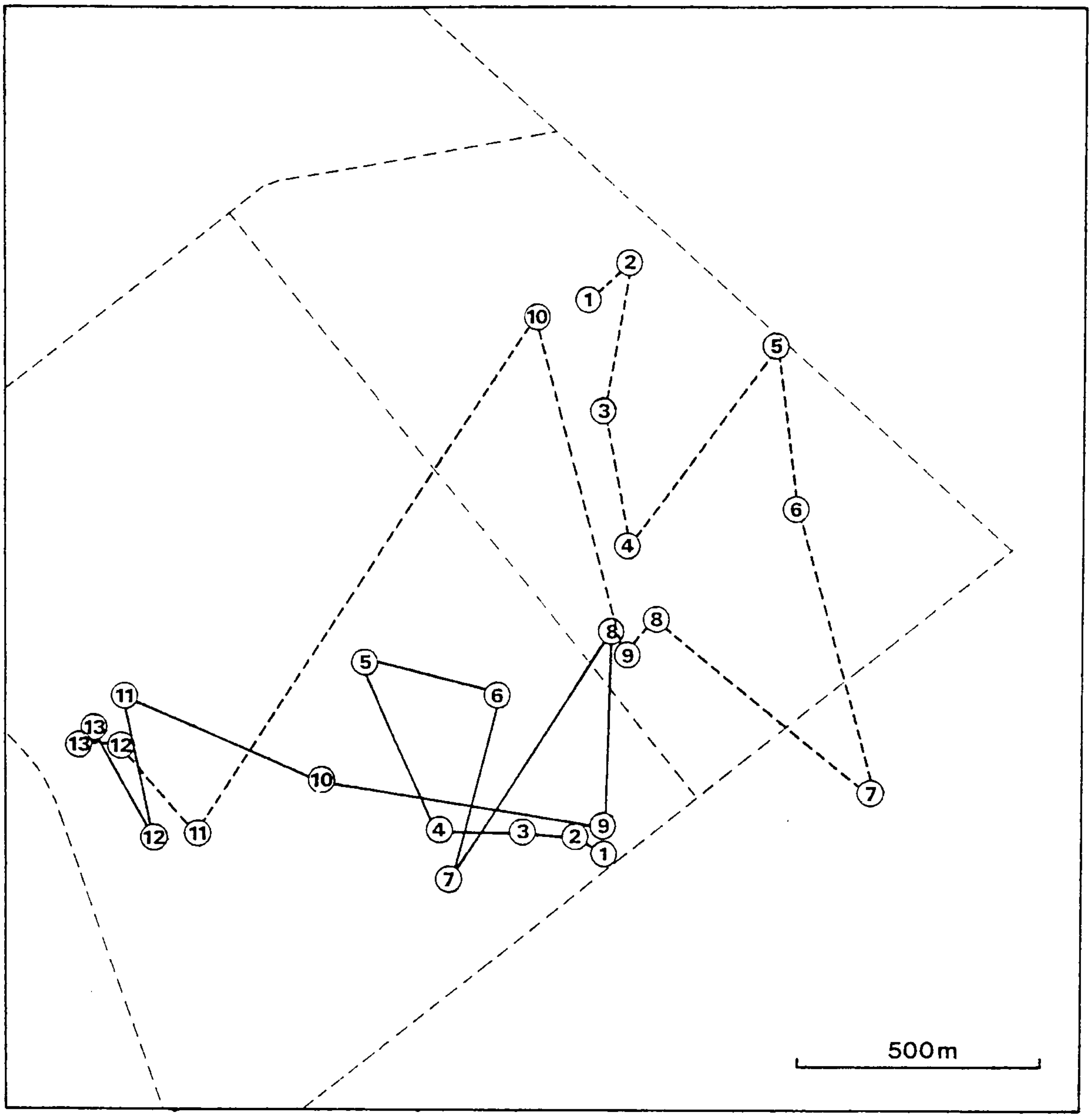
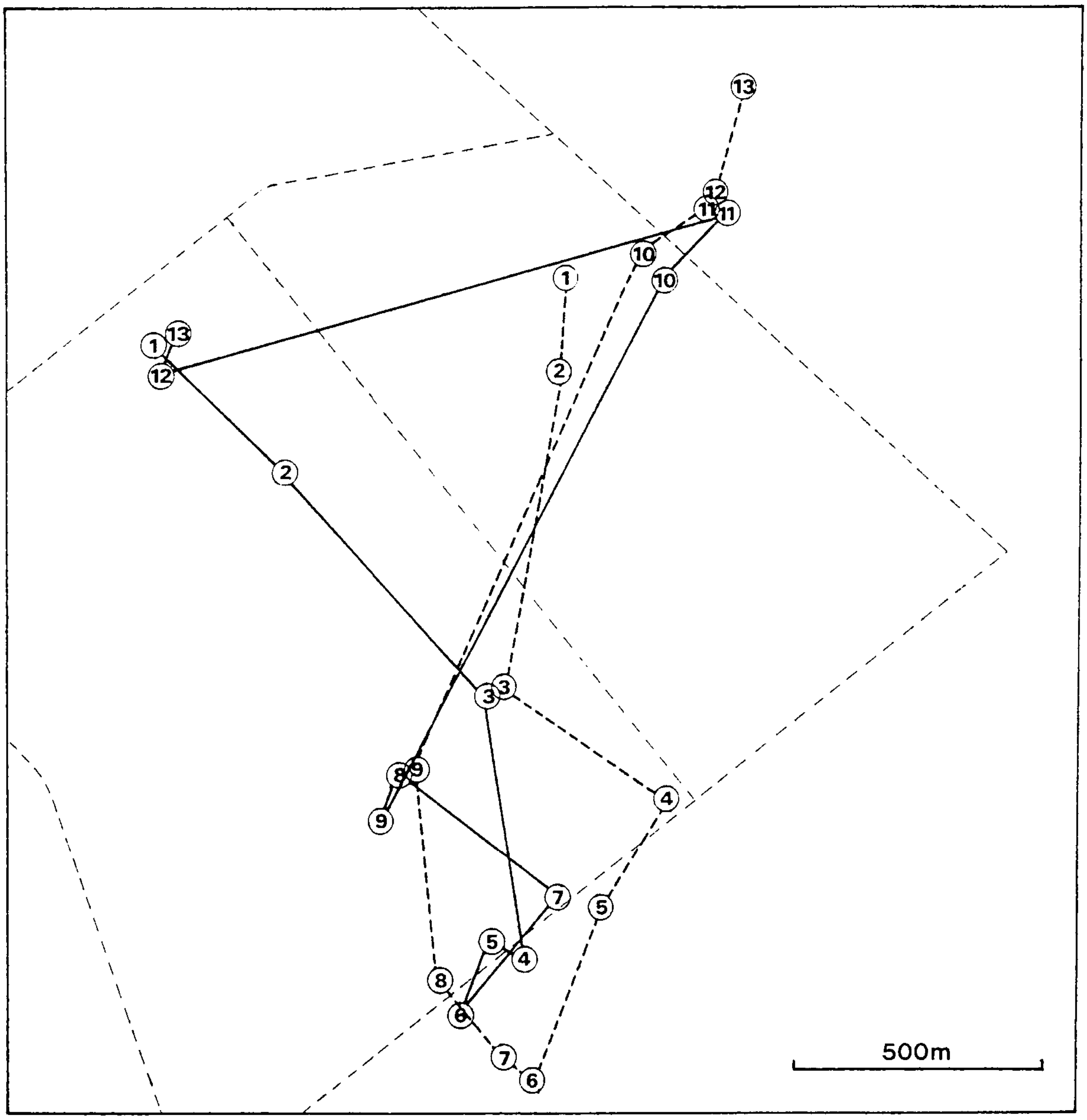


Figure 11: Map of the study area illustrating the encounter between Henry (M5) and Lady (F1) on 14.09.89.

---(X)--- Lady (F1), hourly locations whereby -(1)- is the first location of the night, -(2)- the second, etc.

—(X)— Henry (M5), hourly locations, as above.



<u>Figure 12</u>: Map of the study area illustrating the encounter between Batman (M2) and Lady (F1) on 29.09.89.

---ⓧ--- Lady (F1), hourly locations whereby --①-- is the first location of the night, --②-- the second, etc.

—ⓧ— Batman (M2), hourly locations, as above.

OBSERVATIONS OF PORCUPINES IN THE STUDY AREA

Twenty observations of porcupines on vehicle tracks were made during 153 nights of radiotracking. Nine of these observations were of single juveniles, nine were of single adults and two were of an adult juvenile-pair. Except for three of the juveniles, all of the observed porcupines immediately fled into the bush when illuminated by the vehicles headlights. It was not always possible to see if the porcupines were collared. Sightings occurred throughout the night, the earliest at 17:53 while still light, the latest at 04:01.

Porcupines were observed emerging from their burrows at dusk on 11 occasions. Nine of these observations were of single adults and two were of adult pairs. Although providing no firm data about social organisation, these observations complement the data obtained by capture-recapture and radiotracking, i.e., no more than two adults have been observed to use a burrow at the same time.

On one occasion, in March, emergence occurred at sunset. All other observations were made between 30 minutes and one hour after sunset. Thus, it would appear from these limited observations that emergence normally occurs shortly after sunset.

ACTIVITY PATTERNS

Seasonal activity patterns

The mean distance travelled per night and the mean nightly speed for each animal for each month are given in Appendix 2. Table 11 shows the mean distances travelled per night and the mean nightly speeds for natural foragers and crop foragers in both winter and summer, and analyses the differences between these categories and between the seasons for each category. Seasonal differences are illustrated on a monthly basis in Fig.13.

Table 11 shows that crop foragers were significantly more active than natural foragers in both seasons. Natural foragers were significantly more active in winter than in summer. Crop foragers travelled significantly longer distances per night in winter than in summer, although there was no significant difference between mean nightly speeds in winter and summer.

Fig.13a shows a clear seasonal trend of greater mean distances travelled per night in winter than in summer for both natural foragers and crop foragers. Fig.13b shows a similar trend in mean nightly speed for natural foragers but no seasonal trend for crop foragers.

The maximum and minimum distances travelled and the maximum mean speeds attained are given in table 12. As explained on page, these measurements are probably all underestimates of true distances and speeds travelled.

Table 11: Analyses of differences in mean distance travelled per night (m ± S.D.) and mean nightly speed (m/h ± S.D.):

a. Seasonal differences for natural foragers.

b. Seasonal differences for crop foragers.

c. Differences between natural foragers and crop foragers in winter.

d. Differences between natural foragers and crop foragers in summer.

a.

	Natural foragers		Mann-Whitney U-test		
	Winter n=170	Summer n=236	U	z	p
Mean distance travelled per night	3663 ± 1297	2765 ± 1131	11806	6.65	<0.01 *
Mean nightly speed	291 ± 101	252 ± 98	15458	3.89	<0.01 *

b.

	Crop foragers		Mann-Whitney U-test		
	Winter n=17	Summer n=13	U	z	p
Mean distance travelled per night	6211 ± 991	4962 ± 1695	63	-	=0.05 *
Mean nightly speed	494 ± 81	452 ± 151	80	-	>0.10

c.

	Winter		Mann-Whitney U-test		
	Natural foragers n=170	Crop foragers n=17	U	z	p
Mean distance travelled per night	3663 ± 1297	6211 ± 991	196	5.87	<0.01 *
Mean nightly speed	291 ± 101	494 ± 81	2731.5	5.97	<0.01 *

Table 11: (continued).

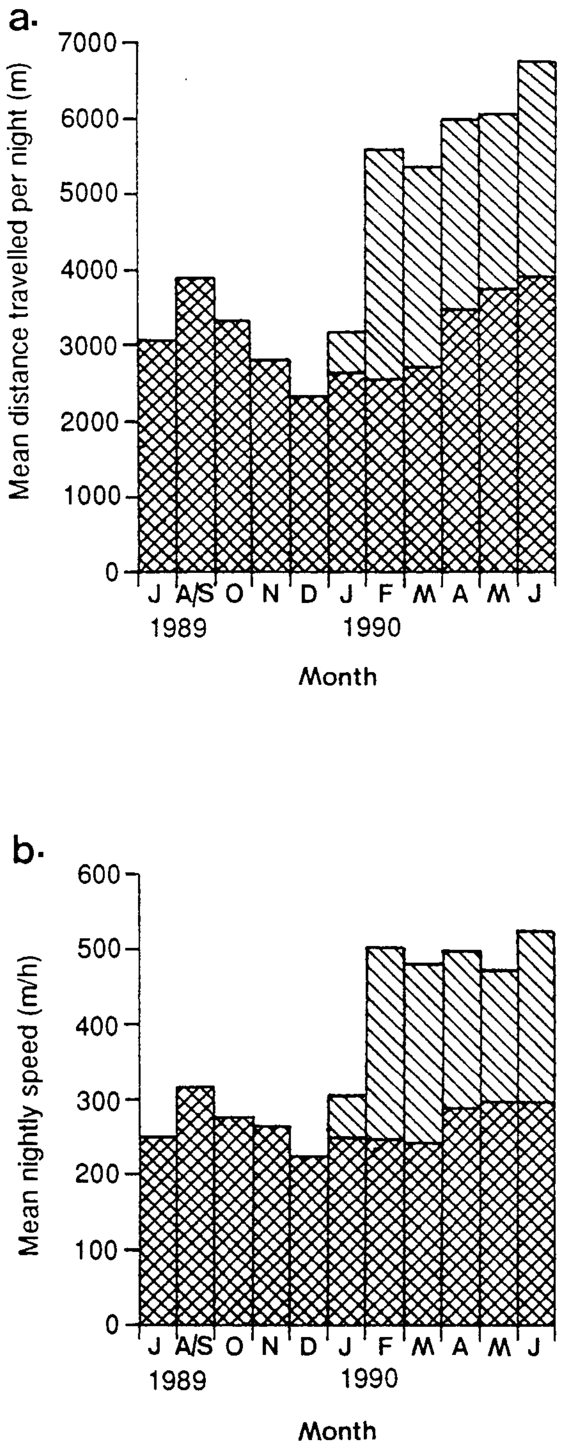
d.

	Summer		Mann-Whitney U-test		
	Natural foragers n=236	Crop foragers n=13	U	z	p
Mean distance travelled per night	2765 ± 1131	4962 ± 1695	390	4.53	<0.01 *
Mean nightly speed	252 ± 98	452 ± 151	2675.5	4.56	<0.01 *

* Significant difference

Table 12: Maximum and minimum distances travelled per night (m) and maximum mean nightly and hourly speeds (m/h).

Maximum distance travelled in one night = 8191 m
Minimum distance travelled in one night = 675 m
Maximum mean speed for one night = 696 m/h
Maximum mean speed for one hour = 2285 m/h



<u>Figure 13</u>: Seasonal changes in activity patterns as suggested by:

a. Mean distance travelled per night during each month.

b. Mean nightly speed during each month.

▩ Natural foragers

▧ Crop foragers

Correlations between activity levels and environmental variables

Total monthly rainfall and mean daily maximum and minimum temperatures for each month are shown in Figure 14. There is an approximate inverse correlation between these climatic variables and activity levels (Fig.13) as well as range size (Fig.7). Thus, months of low activity levels and small range size correspond to months of high rainfall and high temperatures and vica versa.

However, activity levels, as measured by mean distance travelled per night, showed no correlation with minimum temperature throughout most of the year, although in early summer (Oct.-Dec.) a significant negative correlation was observed (Table 13). Unfortunately, due to insufficient data (p.32) it was not possible to test for a direct correlation between rainfall and nightly activity levels.

No correlations were found between nightly activity levels and mean nightly moonlight intensity except in late winter (July-Sept.) when a significant negative correlation was observed. There were no significant correlations between activity levels and nightly moonphase in winter or summer (Table 13).

Table 13: Activity levels (mean distance travelled per night) correlated with minimum nightly temperature, mean nightly moonlight intensity and nightly moonphase using Spearman's rank correlation coefficient (r_s).

	Minimum nightly temperature	Mean nightly moonlight intensity	Nightly moonphase
Late winter (July-Sept.)	$r_s = 0.071$ $p > 0.05$	$r_s = -0.688$ $p < 0.05$ *	$r_s = -0.427$ $p > 0.05$
Early summer (Oct.-Dec.)	$r_s = -0.563$ $p < 0.05$ *	$r_s = 0.159$ $p > 0.05$	$r_s = -0.138$ $p > 0.05$
Late summer (Jan.-March)	$r_s = -0.004$ $p > 0.05$	$r_s = -0.257$ $p > 0.05$	$r_s = -0.159$ $p > 0.05$
Early winter (April-June)	$r_s = 0.045$ $p > 0.05$	$r_s = 0.043$ $p > 0.05$	$r_s = 0.078$ $p > 0.05$

* significant correlation

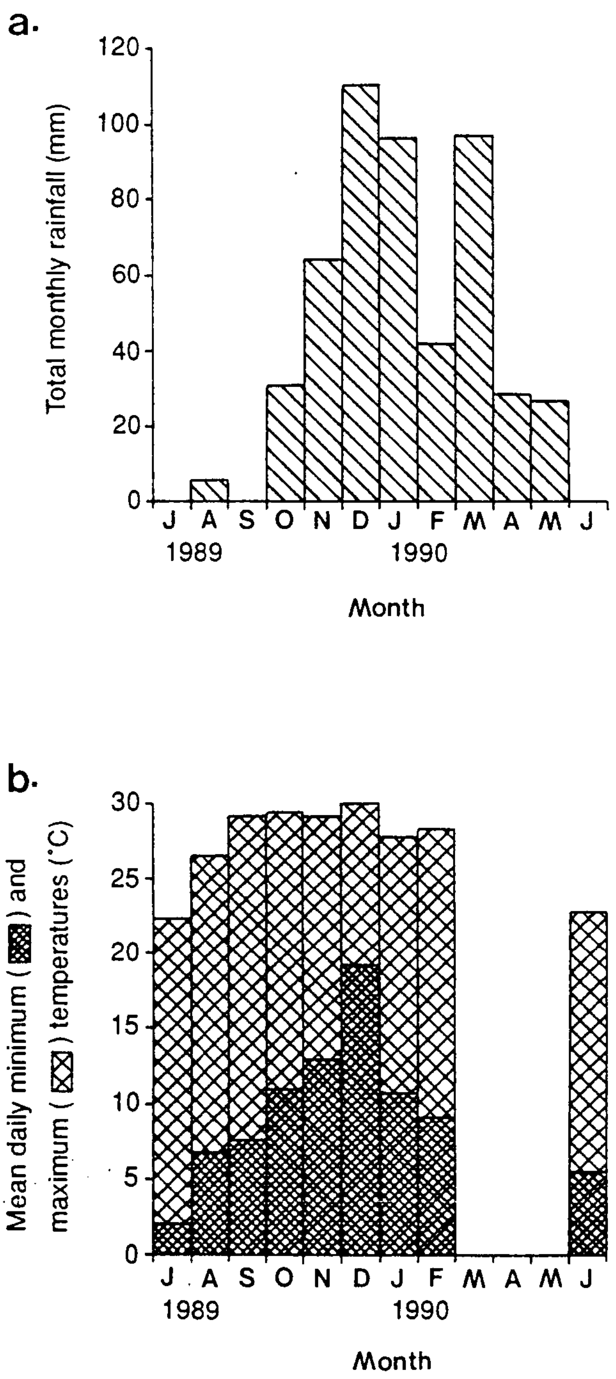


Figure 14: Climatic data for Nylsvley Nature Reserve, July 1989 to June 1990:

a. Total monthly rainfall.

b. Mean daily maximum and minimum temperatures for each month.

Circadian activity rhythms of free ranging porcupines

Activity occurred from dusk to dawn throughout the year (Fig.15), thus the active period was longer in winter than in summer. However, it was not possible to accurately determine when an individual departed from or returned to it's burrow due to the limited accuracy of the radiotracking technique (pp.24 and 29, Tables 1-3). Signals were often inconsistent when a porcupine was in it's burrow such that movement may sometimes be recorded for an animal that was actually stationary. Thus, the length of the active periods recorded in figure 16 may sometimes be overestimated by approximately an hour at the beginning and end of the night, particularily in summer. Generally activity was greatest shortly after dusk, i.e., between 19:00 and 22:00, gradually decreasing towards dawn. In some months, July, August/September, February, March and June, a second, smaller peak occurred shortly before dawn, i.e., between 02:00 and 05:00, thus activity patterns may sometimes exhibit slight bimodality.

Circadian rhythms of captive porcupines

The behavioural circadian rhythms of the captive porcupines (Fig.16a) corresponded closely to the activity circadian rhythms observed in free ranging animals (Fig.15) with a peak in activity shortly after dusk gradually declining towards dawn. The increase in activity about 16:00 was due to food being placed in the cages at this time.

The body temperature circadian rhythm also exhibited a similar pattern, peaking at about 21:00 and remaining fairly stable until 03:00 after which a steady decline occurred, minimum T_b being recorded around midday (Fig.16b).

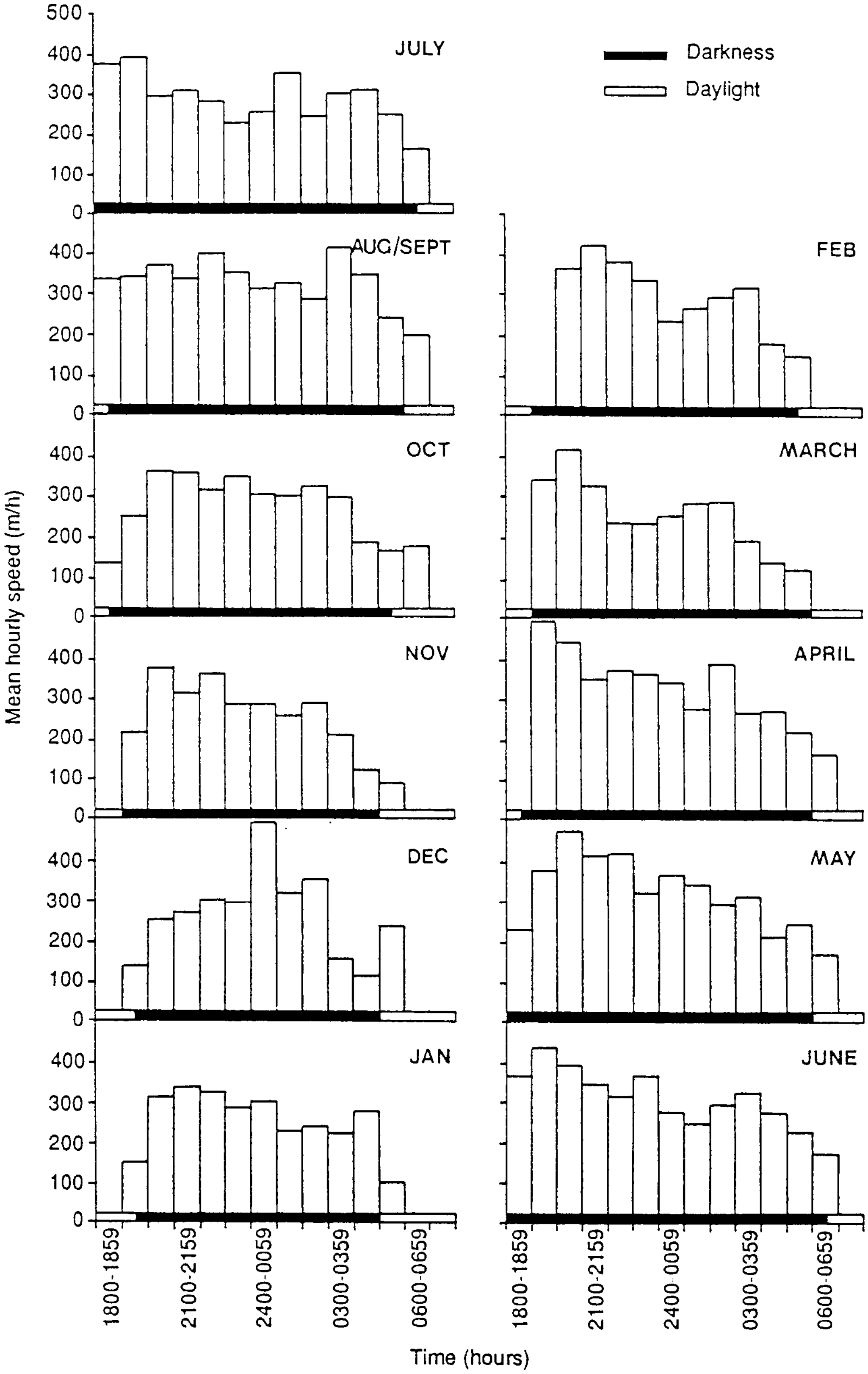


Figure 15: Monthly activity circadian rhythms of free ranging porcupines showing hourly activity levels (mean hourly speed, m/h) from dusk to dawn.

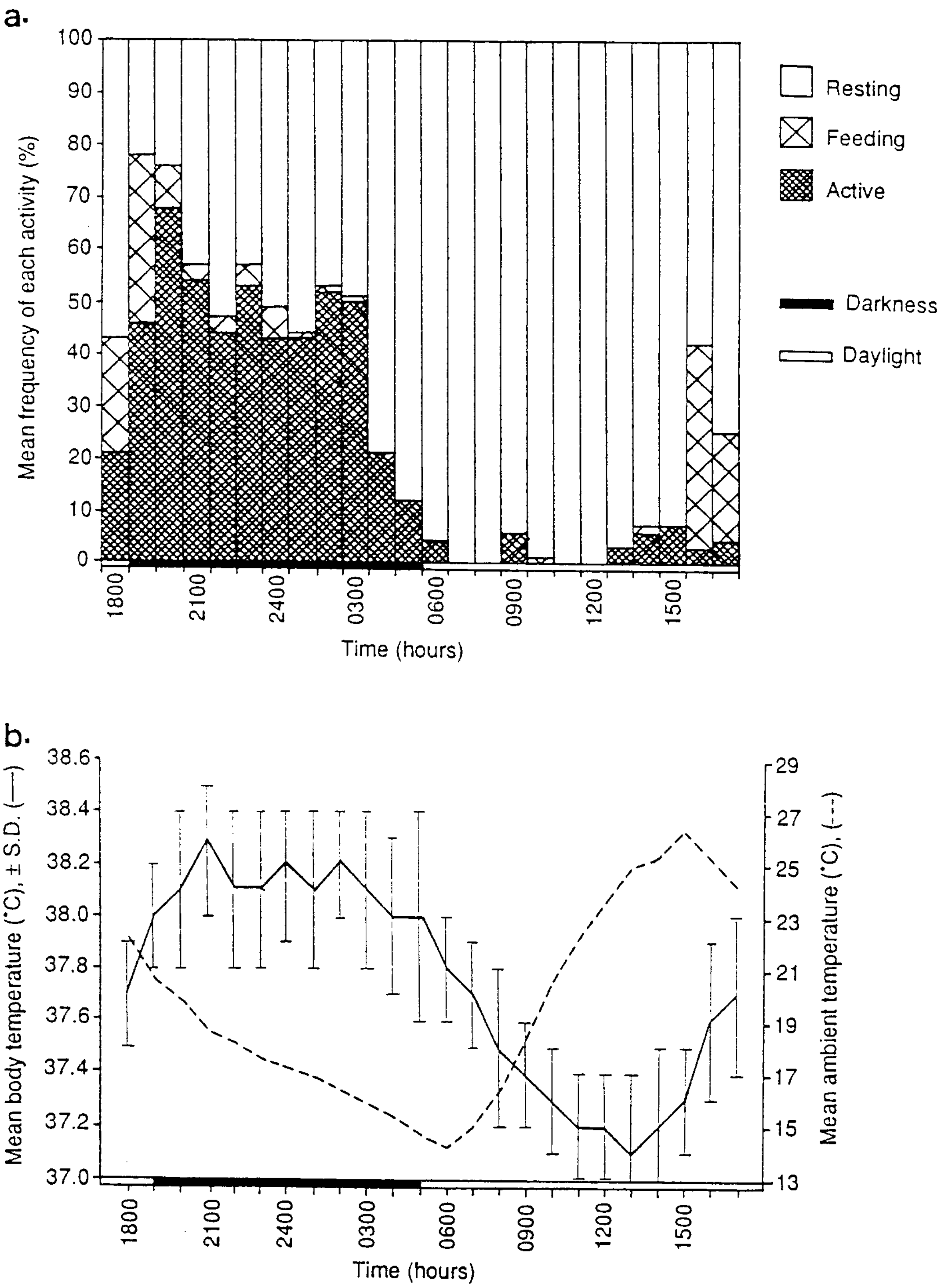


Figure 16: Circadian activity rhythms of captive porcupines monitored for two 72 hour periods, 21-24 Sept. and 29 Sept.- 1 Oct. 1990:

a. Behavioural circadian rhythms.

b. Body temperature circadian rhythms (vertical bars represent one standard deviation of the mean).

CHAPTER 4:DISCUSSION

SOCIAL ORGANISATION

Capture-recapture data (p.46) and observations of porcupines emerging from their burrows (p.94) suggest that adult porcupines live in pairs. Juveniles were never caught, probably due to their wariness in entering traps, although in a seperate study at Nylsvley a very young juvenile was caught in a small carnivore trap three nights in succession (pers.obs.). However, juveniles were seen in the study area (p.94) and are assumed to live with their parents as a family group. There is no evidence of more than two adults cohabiting, thus, extended family groups are thought not to occur in this area.

Radiotracking confirmed that an adult pair forms the basic social unit in the Cape porcupine. These pairs appear to be temporally stable as all four pairs studied remained together for the duration of the period for which both pair members were radiotracked: Pair 1 (seven months), Pair 2 (three months), Pair 3 (one month) and Pair 4 (three months). Pair members normally shared burrows and utilized similar home range areas with an average overlap of about 75% (Table 9). Thus, the monogamous pair bond described for captive animals (Morris & Van Aarde 1985) also appears to exist in free-ranging Cape porcupines. Monogamy has also been suggested for captive crested porcupines (Pigozzi 1987) and for captive Indian crested porcupines (Sever & Mendelssohn 1988b) and is therefore possibly a uniform feature of most natural populations of _Hystrix_ spp.. The only individual studied that did not appear to have a partner was Henry (M5). Henry was radiotracked for the entire study period during which time no potential partner was caught despite an intensive trapping effort in his home range area. Additionally, he exhibited significantly different "territorial" behaviour from other natural foragers as will be discussed later (p.126). It is therefore suggested that Henry was a single male.

The family groups as proposed above appear to be typical of the social organisation suggested by several previous authors (Shortridge 1934, Smithers 1971, Kingdon 1974). Shortridge(1934), Kingdon (1974) and Van Aarde (pers.comm.) have all observed much larger groups (p.4) but as the age structure, sex ratio and temporal stability of these groups are unknown their significance is therefore uncertain. However, Van Aarde (1987a) trapped both adults and juveniles in the the Orange Free State and identified two extended family groups each consisting of an adult pair, two subadults and two juveniles. Thus, the Cape porcupine appears to have a variable social organisation. Such variation is also apparent in different populations of the Indian crested porcupine which lives in family groups on the coastal plain of Israel (Sever 1985, Sever & Mendelssohn 1988a) and in extended family groups in the Negev desert (Saltz & Alkon 1989). As Banks (1977) stated, "There is increasing evidence that the social structure of a species with a wide geographic distribution may vary considerably depending on the ecological conditions in different parts of its range.".

Thus, although the monogamous pair-bond appears to be a uniform feature of the social organisation of Hystrix spp., group size, i.e., a family or extended family group, appears to be variable. Two questions are therefore apparent:

1. Why are porcupines monogamous ?
2. What dictates whether porcupines live in family or extended family groups?

Monogamy is relatively rare amongst mammals with less than 3% of species monogamous compared to over 90% of birds (Kleiman 1977). The primary reason for this disparity is the provision of milk by female mammals for their offspring. Male mammals can therefore make a relatively small contribution to the rearing of their offspring such that the best way for them to increase their reproductive success is to mate with as many females as possible rather than to invest in paternal care. Thus, polygyny would be expected to be the favoured mammalian mating system and is in fact the most common. Why then should any male mammal become monogamous ? A male should not choose to be monogamous and should only become so if he is prevented from mating with more than one female, i.e, monogamy occurs by default (Mock & Fujioka 1990). This could occur in the following circumstances:

If females are widely dispersed due to the pattern of resource dispersion and are either polyoestrus or have synchronized oestrus, a male may only be able to ensure "exclusive" access to a single female. Thus, female dispersion may be determined by resource dispersion whereas male distribution may be determined by female distribution (Macdonald 1983). In such a situation, it is probable that a male may best increase his reproductive success by guaranteeing "exclusive" matings with a single female rather than by only mating promiscuously with several females who may already have been mated a number of times by different males. However, if a male can guarantee "exclusive" access to a single female, while at the same time mating promiscuously with one or more other females, he may further increase his reproductive success (Richardson 1987). Thus, promiscuity may be a common phenomenon amongst "monogamous" mammals and will be discussed in more detail later. However, if females are dispersed but have a single, short oestrus that is not synchronized, a dominant male may be able to mate "exclusively" with several females in succession as in the stoat (Mustela erminea), (Sandell 1986). Thus, female dispersal alone need not result in monogamy.

If a male is forced to mate "exclusively" with a single female, as proposed above, the only way that he can then increase his reproductive success, apart from becoming promiscuous, is to invest in the survival of his offspring by performing paternal care. A monogamous situation is probably a prerequisite for the development of anything but the most superficial paternal care. Thus, paternal care is unlikely to be the primary cause of a male mammal staying with a single female (Elwood 1983), but will result from his inability to mate with more than one female. Paternal care may be direct, e.g., the provision of food, protection from predators (or conspecifics), thermoregulatory benefits from huddling (newborn young may be ectothermic), grooming and "teaching" social and foraging skills. Alternatively it may be indirect, e.g., provisioning the mother with food during lactation, nest or burrow construction and resource defence (Elwood 1983). There is little experimental evidence for the beneficial effects of paternal care except for thermoregulatory benefits demonstrated in a few species of captive rodents (Elwood 1983). However, as paternal care is exhibited to some degree by most monogamous species there is presumably some benefit in terms of offspring survival, albeit minor. The low juvenile mortality rate recorded for porcupines (Van Aarde 1987a) may be at least partially due to paternal care. In contrast, paternal care is generally rare or inconsistent in non-monogamous mammals (Kleiman 1977). Due to the difficulties of quantifying paternal care or it's benefits, it's importance has not been demonstrated in free-ranging animals.

Paternal care is most likely to be important in species with altrical young, as is the case with most monogamous species which also have low neonate weights and small litter sizes, the exceptions being monogamous primates, cetaceans and hystricomorph rodents whose offspring are precocial (Kleiman 1977, Zeveloff & Boyce 1980). However, although porcupines have precocial young these are small relative to maternal body weight when compared to other species of hystricomorphs (Van Aarde 1985a), and may therefore stand to gain thermoregulatory benefits from paternal huddling. Juvenile porcupines usually huddle between both parents when resting (Gosling 1980, Grant 1984). Additionally, both parents groom their offspring and both, particularily the male, behave aggressively towards any conspecific which approaches their young (Grant 1984). Juvenile porcupines up to the age of about six months are accompanied by one or both parents while foraging (Shortridge 1934, Santini 1979, Van Aarde 1987a). This probably serves to protect the juveniles from predators (and possibly conspecifics) and also to familiarise them with their home range and food species. Van Aarde (1987a) noted that in all cases where a juvenile was accompanied by a single parent it was always the male that was present. If the male looks after the offspring it may allow the female to forage more efficiently which could be important if she is to satisfy the high energetic demands of lactation. Small rodents have been recorded to increase their energy intake by 50-150% while lactating, although the North American porcupine (Erethizon dorsatum) only exhibited an increase of 17%, considerably less than that expected for an animal weighing 4-8 kg (Farrell & Christian 1987). Unfortunately, no comparable data is available for Hystrix spp.. In the monogamous bat-eared fox (Otocyon megalotis) and aardwolf (Proteles cristatus) the male has been recorded to stay at the den to guard the cubs, at the expense of his own feeding requirements, while the female forages (Malcolm 1986, Richardson 1987). In the present study only two of the 11 juveniles sighted were with adults (p.94), some were probably six months of age or older but some were almost certainly younger. This apparent lack of adult accompaniment could possibly be due to locally reduced predation pressure, due to the virtual absence of large carnivores in the area (p.12). However, predators are also scarce in the area of the Orange Free State where Van Aarde (1987a) observed that juveniles were always accompanied by one or both parents. Male porcupines have not been recorded to provision either their offspring or mate with food, although the remains of maize cobs around some burrows in the study area (pers.obs.) and reports of food hoarding in burrows (Van Aarde pers.comm.) suggest that food is sometimes carried back to the burrow by foraging animals. Monogamy is the commonest mating-system amongst canids and in this group provision of food to the offspring by both parents is an important feature (Mock & Fujioka 1990).

Not only may paternal care increase the reproductive success of the male, and female, but the resulting interactions between the male and female may strengthen the monogamous pair-bond. Van Aarde (1985b) observed that female

Cape porcupines require the physical presence of a male to initiate and maintain cyclic ovarian activity and this has also been recorded in another hystricomorph rodent, the cuis (Galea musteloides), (Weir 1970 in Van Aarde 1985b). Additionally, a female must experience between three and seven sterile cycles before conceiving (Van Aarde 1985b), thus a male must be "continually" present for a considerable period for conception to occur. As with paternal care this phenomenon may strengthen the pair-bond but was probably not a causative factor in the evolution of monogamy as such a reproductive system would be unlikely to evolve in anything but an existing monogamous mating system.

An alternative reason for a male to live with a female would be to benefit from some of the advantages associated with group living, e.g., improved predator detection, anti-predator defence, increased foraging or hunting efficiency, resource sharing and defence, thermoregulatory benefits through huddling or increased offspring survival (which may come about as a result of one or more of the other factors). Could such a mutually beneficial association lead to the formation of a monogamous mating system ? If it were advantageous for a species to live in groups for any of the above reasons and resource dispersion allowed the formation of groups, a male could theoretically ensure access to, and defend, several females at once. If circumstances allow the monopolisation of several females by a single male, a polygynous mating system is most likely to result. Indeed, polygyny is the commonest mating system amongst mammals and is the most likely outcome of mammals aggregating together to share the benefits of group living. Polygyny could also evolve if females are dispersed, but not over such a wide area that a male cannot defend and thus gain exclusive mating access to more than one female. Thus, a number of mammalian species exhibit single female territories with a larger male territory overlapping several females, e.g., several species of Muridae such as the wood mouse (Apodemus sylvaticus), (Wolton 1985) and many species of carnivores (Kruuk & Macdonald 1985).

It is therefore most likely that monogamy will evolve in a species in which the females have a dispersed distribution and are polyoestrus or exhibit synchronized oestrus. However, once a monogamous mating system has developed pair members may subsequently derive one or more benefits from group living (including increased offspring survival as a result of paternal care). Thus, the advantages of group living should reinforce but not cause monogamy and when such advantages exist a pair-bond should be established. If it is uneconomic or disadvantageous to live in a group, perhaps due to the dispersed nature of resources or an increased risk of predation, a pair-bond may not necessarily develop and the monogamous "pair" may live seperately, although sometimes sharing the same territory, only coming together to mate, e.g., several species of small ungulates such as the common duiker and grysbok (Raphicerus spp.) (Jarman 1974).

Koenig (1981) identified two types of groups, "competitive" and "cooperative". Competitive groups are those forced together by resource aggregation with a resulting decrease in individual "fitness" as group size increases due to competition for resources. Cooperative groups form in order to benefit from an advantage associated with group living resulting in an increase in individual "fitness" as group size increases (up to an "optimum" group size). However, within a competitive group, behaviour which mitigates the costs and realizes the potential benefits of group living should evolve (Cowan 1987) such that most existing groups, whatever their origin, will probably exhibit some cooperative characteristics. Thus, a monogamous pair brought together as a result of resource dispersion or reproductive necessity should adapt their behaviour in order to live cooperatively.

How could a larger group evolve from a monogamous pair ? This is most likely to occur as a result of offspring remaining with their parents, therefore most groups containing a monogamous pair will probably be largely composed of closely related individuals. If a single generation of offspring stay with their parents beyond the age of weaning this is known as a family group. An extended family group comprises a monogamous pair with two or more generations of offspring (Elwood 1983). The development of a family group from a monogamous pair is fairly straightforward, the immature offspring simply remaining with their parents as they are dependent on parental care or the security of their natal territory. If a species exhibits delayed maturity of the young then an extended family group may simply form if one years offspring have not matured and dispersed before the parents have produced their next litter. Thus, porcupines which mature at approximately one year of age (Van Aarde 1985b, Van Aarde & Skinner 1986a) are often found in family groups and beavers (Castor spp.) which mature at two years of age usually live in extended family groups (Svendson 1980, Patenaude 1982, 1984, Pfeifer 1982, Busher, Warner & Jenkins 1983, Busher 1987). Delayed maturity is considered to be a primary factor in the evolution of sociality and group living in several genera (Cynomys, Marmota and Spermophilus) of North American ground squirrels (Armitage 1981, Rayor 1988). Alternatively, an extended family group may result from the delayed dispersal of mature offspring. If the parents are monogamous, the offsprings reproduction may be suppressed while they remain in their natal group. The adult male may suppress the reproductive activities of his sons in order to ensure exclusive mating within the group thereby maximizing his own reproductive success. The adult female may suppress the reproductive activities of her daughters to ensure that her own reproductive success is not compromised by competition between her offspring and those of her daughters. How is such reproductive suppression effected ? Social behaviour may evolve to decrease reproductive competition within a group (Alexander 1974) and this often takes the form of a social dominance hierarchy which limits reproduction to the adult pair. Thus, the dominant adult male may act aggressively towards subordinate male group members when his mate is in oestrus as Kruuk (1989) observed in captive European badgers. The dominant female may suppress reproduction in subordinate females in a number of ways. She may act aggressively towards them to prevent mating taking place or may kill their newborn offspring. Alternatively, reproduction in subordinate females may be physiologically suppressed by urinary chemosignals or primer pheremones which may delay puberty, suppress oestrus or ovulation, or block embryo implantation (Faulkes, Abbott & Jarvis 1990, Van Aarde & Van Wyk 1991). In the case of the Cape porcupine, subordinate females have been observed to copulate within their natal group and thus their reproduction is not behaviourally supressed. Van Aarde & Van Wyk (1991) have proposed that cyclic progesterone secretion in subordinate females is affected, although not totally inhibited, thus preventing them conceiving. However, the mechanism by which this occurs is not understood. No observations have been made of behavioural suppression amongst male porcupines so it is not known if subordinate males ever sire offspring within their natal group. Although intragroup aggression may be common in some species, it does not usually escalate to serious fighting due to the stability imposed by the social dominance hierarchy (Hodgdon & Larson 1973).

In some species subordinate males may mate promiscuously with females from neighbouring groups and in particularly favourable environmental circumstances, e.g., high food abundance, one or more of the subordinate females may reproduce (if the factor causing their reproductive suppression can be turned off, e.g., reduced aggression by the dominant female). Both of these phenomena have been observed in the European badger (Cheeseman, Cresswell, Harris & Mallinson 1988, Evans, Macdonald & Cheeseman 1989, Kruuk 1989) and the latter in the beaver (Busher et al. 1983). Thus, subordinate animals may ensure their own survival by remaining in their natal group but may still be able to reproduce, albeit to a limited extent. Obviously if the risks of dispersing are not too great a mature offspring should leave it's natal group voluntarily in order to increase it's reproductive success. The decision to disperse will therefore be based upon parental aggression and the relative reproductive opportunities and survival probabilities as a disperser or non-disperser.

Amongst Hystrix spp. the strength of the pair-bond between existing pairs and the reproductive suppression of subordinate females probably result in subordinate males having little chance of mating within their natal group, or with a neighbouring adult female. Due to the non-flexible nature of female reproductive suppression, i.e., it is not behavioural suppression and therefore cannot be turned on and off, subordinate female porcupines will have no chance of reproducing within their natal group. It is therefore hypothesised that porcupines must disperse and find their own mate in order to reproduce as suggested by Van Aarde (1987c).

Why therefore, should the mature offspring of Hystrix spp. remain in their natal group ? In many cases they may be unable to disperse, particularily in territorial species, due to lack of unoccupied areas (Van Aarde 1987c). Therefore, although not able to reproduce within their natal group, mature offspring may avoid dispersion as it could decrease their survival potential through aggression from territory holders and subsequent lack of access to resources such as food and shelter, which would be compounded by decreased foraging efficiency in an unfamiliar area. Dispersion will therefore be influenced by population density in combination with resource abundance. For example, Woollard & Harris (1990) recorded increased mortality rates among dispersing red foxes (Vulpes vulpes) compared to non-dispersers. Additionally, if delayed maturation has caused a species to live in groups, activities such as predator detection and pack hunting, which are enhanced by, or require a minimal group size, may consequently evolve to maximize the potential benefits of group living. In some species a beneficial consequence of group living may come to assume increased importance during the evolution of the species and as Bertram (1987) stated, "... the relative strengths of different selection pressures probably change as the species evolves". Within such a group, complex social behaviour can evolve to maximize the benefits and minimize the costs of group living (Alexander 1974). In the case of North American ground squirrels (Armitage 1981, Rayor 1988) and dwarf mongooses (Helogale parvula) (Rasa 1972) extended family groups benefit from enhanced predator detection, and in the case of African wild dogs (Lycaon pictus) (Kruuk 1972) and wolves (Canis lupus) (Mech 1970 in Andelt 1985) the extended family group increases its foraging efficiency by cooperative hunting. In species such as these, an individuals survival outwith the group will be reduced as it's survival has become dependent on activities requiring the cooperation of conspecifics.

If there are advantages to group living for the species concerned, as previously described, parents should tolerate the continued presence of at least some of their offspring, depending on optimum group size, beyond the age of sexual maturity. In some species, e.g., marmosets (Callitrichidae), jackals (Canis spp.), dwarf mongooses and beavers (Kleiman 1977, Patenaude 1982 & 1984), mature juveniles may help in the rearing of their younger siblings. However, the importance of these "helpers" is difficult to determine. Even if no direct benefit exists for the parents, they will increase their reproductive success, if, by allowing their offspring to remain in the group, the offsprings chances of survival are increased. However if prevailing environmental conditions, e.g., limited food abundance, are such that the presence of mature offspring is detrimental to the survival of the parents and immature offspring, the parents will no longer tolerate these subadults who must then disperse. Von Schantz (1984a) described such a situation for red foxes in Sweden whereby a decrease in food availability led to a decline in the reproductive output of the dominant females. This was followed by the dispersion of the subadults and a subsequent increase in the reproductive output of the dominant females despite no improvement in food abundance. In this case, resource consumption by the subadults presumably outweighed their usefulness as helpers.

Do porcupines benefit from the presence of the other group members ? Although porcupines live in groups, the present study and that of Van Aarde (1987a) indicate that they usually forage alone. However, Sever & Mendelsshon

(1988b) observed that pairs foraged together, rarely seperated by more than three meters.

The solitary foraging behaviour of the Cape porcupines in the present study indicates that defence from predators is probably not a benefit of group living in this species. Where porcupines have been observed to forage in pairs (Sever & Mendelssohn 1988a) this is unlikely to be a local response to high predation pressure due to the absence of potential predators. Additionally, Ferguson (1987) reported that there was very little cooperation between group members during aggressive encounters with conspecifics and therefore intra-group cooperation in anti-predator defence seems unlikely.

Increased foraging efficiency cannot be a benefit of group living in a species which forages alone and even where pairs forage together the nature of the food precludes cooperative foraging. It is possible that information about rich food patches could be communicated to other group members although there is no evidence for this. Kruuk (1989) demonstrated experimentally that captive badgers could increase their foraging efficiency in such a manner but like porcupines they forage alone in the wild.

The habit of huddling when resting suggests that porcupines may gain thermoregulatory benefits from group living. Van Aarde (unpublished) compared burrow temperatures and outside ambient temperatures in the Orange Free State. In summer, ambient temperatures varied between 15 and 42°C whereas burrow temperatures remained between 20 and 24°C. In winter, ambient temperatures varied between -3 and 15°C and burrow temperatures remained between 11 and 16°C. The temperature in an occupied burrow may be several degrees higher. Therefore, although the burrow provides a fairly constant environment, in winter burrow temperatures may still be below the porcupine's thermoneutral zone of approximately 24-27°C (Haim et al.1990). Therefore, in some parts of their range porcupines may save energy by huddling while resting in burrows. Where porcupines shelter in crevices and small caves on rocky hills, which provide less insulation than burrows, thermoregulatory huddling may assume increased importance.

Associated with the close proximity of group members when resting, is allogrooming behaviour which is performed by all but very young juveniles (Grant 1984, pers.obs.). Not only does allogrooming remove parasites but it may also help to strengthen social bonds between group members. Extensive grooming was observed on a number of occasions when an individual was returned to it's group after being removed for several hours, suggesting a social function of this behaviour (pers.obs.).

Resource defence, i.e., the defence of a territory containing food resources and resting sites, can theoretically be enhanced by additional group members. If both pair members help to defend a territory this could be a benefit of pair formation, and if mature offspring also defend their natal territory this could benefit the whole group. Territorial defence may also function as a mate guarding mechanism (Davies 1987, Richardson 1987) in species in which promiscuous matings may occur. Territorial behaviour and mate guarding in porcupines will be discussed in more detail later.

Therefore, although not the primary reason for pair formation, adult porcupines may potentially benefit from living as a pair in terms of thermoregulation, grooming and resource defence. Mature offspring may gain similar benefits through remaining in their natal group. Immature offspring obviously benefit from group membership as their survival is dependent on parental care although they themselves do not contribute to the wellbeing of the group. Thermoregulatory benefits and grooming are unlikely to be important enough to cause mature offspring to stay in their natal group at the expense of the opportunity to reproduce. Whether or not mature offspring benefit from living in a defended territory will depend on the availability of vacant territories in the surrounding area. If there is a vacant territory they will gain little from staying in their natal group but if no territory is available they have a lot to gain in terms of access to resources. The presence of subadult helpers in their natal group may benefit the parental pair and immature offspring in terms of thermoregulation, grooming and resource defence but the benefits may be minor relative to the amount of resources consumed.

In view of the lack of reproductive opportunities within their natal group and the independence of mature offspring in terms of anti-predator defence and foraging, they should disperse as soon as possible.

Thus, whether porcupines live in family or extended family groups will primarily depend on the opportunities available to mature offspring to disperse. Dispersal requires the availability of a suitable area in which to live, which is dependent on population density (Van Aarde 1987c) and resource abundance. Thus, where environmental conditions are favourable, porcupines should voluntarily leave their natal group as soon as they are sexually mature resulting in a social organisation characterised by family groups. If environmental conditions are not so favourable and opportunities to disperse are consequently more limited, extended family groups may result. Therefore, in relatively fertile areas such as Nylsvley and the coastal plain of Israel, porcupines live in family groups whereas in more arid areas such as the Negev desert, extended family groups have been recorded. However, the occurrence of extended family groups in the Orange Free State cannot be explained in terms of limited food abundance, as although it is a semi-arid area, it is rich in plant species consumed by porcupines (Van Aarde pers.comm.). In this case, it appears that high population densities alone restrict the dispersion of subadults (Van Aarde pers.comm.). It is possible that the extensive hunting of porcupines in the agricultural areas surrounding Nylsvley (De Villiers pers.comm.) has created artificially low population densities, thus enabling offspring to disperse to vacant territories as soon as they are mature.

On the coastal plain of Israel, Sever & Mendelssohn (1988b) recorded a number of non-territorial single males. Despite the apparent lack of vacant territories for these individuals they were presumably able to disperse from their natal group due to an adequate abundance of food and shelter. Such dispersal presumably increased their chances of locating vacant territories immature offspring in terms of thermoregulation, grooming and resource defence but the benefits may be minor relative to the amount of resources consumed.

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A strong pair bond and the possible importance of paternal care probably limit the propensity for extra-pair matings in porcupines and mate guarding, territorial or otherwise, restricts the number of opportunities for promiscuity. In the present study only three potential extra-pair matings were recorded in 153 nights of radiotracking (Interactions 2,3 and 4, p.89), suggesting that promiscuity was uncommon in the study population. However, without knowing the relatedness, if any, of the porcupines involved, the suggestion that these interactions were sexual must remain speculative. As promiscuity in monogamous species is very much an opportunistic phenomenum this observation should not be extrapolated to other porcupine populations where environmental circumstances may increase or restrict such opportunities.

SPACE USE

Individual space use patterns (Figs.6a-i) indicate that the same general area is used by an individual from month to month and that activity appears to be concentrated in a relatively small area of the total home range. Normal home ranges, i.e, 95% of locations, occupied on average 51% of the total home range area (p.68). Areas of intensive use, i.e., 90% of locations, occupied on average 63% of the normal home range or 32% of the total home range area. It is therefore clear that porcupines do not utilise their home range area evenly, the majority of locations being recorded in approximately one third of the total potentially available area. Why should an animal concentrate its activities in such a manner ? By confining foraging to as small an area as possible, foraging costs may be minimised by reducing time and energy spent travelling and by increasing foraging efficiency through familiarity with the environment. If it is beneficial for the individual or group to have exclusive access to the area in which they live, i.e., if territorial behaviour is required to defend resources such as food, shelter and mates (Elseth & Baumgardner 1981), the smaller the area, the easier it is to defend economically.

To what extent are the observed home ranges exclusive? Figures 8a-k and Table 9 show the extent of overlap between neighbouring ranges. The following discussion will deal solely with natural foragers as Henry (M5) and crop foragers showed significantly different patterns of range overlap (p.71, Table 10). Natural foragers showed significant differences in seasonal range use and overlap. In winter mean overlap of total home ranges was fairly extensive at 18% whereas mean overlap of areas of intensive use was very small at 3%. Thus, in winter natural foragers utilise a relatively small exclusive area within a much larger non-exclusive area. In summer, normal home ranges (and therefore also areas of intensive use) were almost completely exclusive although total home ranges still exhibited a small degree of overlap (8%). As the majority of overlap in both seasons involves only the total home range, i.e., only 5% of recorded locations, these areas of overlap do not appear to be intensively used. Additionally, temporal space use analysis (Fig.9) indicates that neighbouring individuals, regardless of sex or season, rarely come into contact with one another. Such a pattern of space use, i.e., a small, exclusive, intensively used area within a larger, non-exclusive, sparsely utilised area, suggests that porcupines may be territorial. The exclusive area may be defended with the non-exclusive area serving as a "buffer zone" between neighbours. However, as can be seen from Figs.6a-i, the area of intensive use and normal home ranges, as well as the total home ranges, do not always occupy exactly the same position from month to month, although they do usually occupy the same general area. A large, sparsely utilised zone surrounding the area of intensive use may therefore allow an individual to shift it's centre of activity in response to temporary changes in local resource availability. Thus, if territorial defence does occur the territorial boundaries do not appear to be permenant or rigidly defined.

As previously discussed (p.9), territoriality is as much a behavioural as a spatial phenomenon. Do porcupines therefore exhibit any behavioural traits associated with territoriality ? In captivity Cape porcupines have been observed to scent mark their enclosures (Morris & Van Aarde 1985) and both adults and subadults were observed to behave aggressively towards members of other groups (Grant 1984, Ferguson 1987). No sex-specific differences were noted with respect to scent marking although males were reported to be generally more aggressive than females. De Villiers (pers.comm.) recorded the frequency of scent marking acts (urination, defecation and perineal dragging) for two hand-reared subadult porcupines, one male and one female, leash walked in a one hectare enclosure in the Nylsvley study area. The male performed a mean of 14.9 scent marking acts per hour compared to 1.8 by the female, with no significant seasonal difference. However, nothing is known about the frequency or distribution of scent marking in free-ranging porcupines or about the longevity and "active radius" of the scent marks themselves. Scent marking allows animals to determine if they have entered the territory of another individual and to identify the territory owner if encountered. A territory owner should behave more aggressively than an intruder in such an encounter as it has the most to lose and a serious fight would be too costly to an intruder which may have relatively little to gain. In experiments with captive porcupines Ferguson (1987) demonstrated that "territory holders" behaved significantly more aggressively than "intruders" in conspecific encounters. Scent marking therefore warns an intruder that it is trespassing and so enables it to avoid conflict with an aggressive territory holder by backing down from a potential clash and withdrawing from the territory. Overlapping buffer zones surrounding a territory probably allow greater indirect communication, e.g., scent marking, between neighbours so enhancing individual territorial integrity (Brown & Orians 1970, King 1975). Thus, "although territories may be vigorously defended when the occassion demands, fights over possession of a territory are in fact, quite rare" (Gorman 1990).

Temporal space use patterns (Fig.9) indicate that neighbours rarely encounter one another. Additionally, maps of the approximate route travelled by each porcupine during nightly radiotracking sessions did not reveal any apparent boundary patrolling behaviour such as has been recorded for male African brush-tailed porcupines (<u>Atherurus africanus</u>), (Emmons 1983). Thus, direct intergroup aggression probably does not play an important role in territoriality. These very limited observations suggest that porcupines can potentially defend a territory, with scent marking being the most important method. These data also suggest that males may play a more important role than females in territorial maintenance and that subadults could potentially help to defend a territory. Interaction 5 (p.90), when Henry (M5) appeared to displace Fish (M4) from his burrow immediately following the death of Fish's partner, Wanda (F4), suggests that the pair-bond may be an important factor in territorial maintenance. Either the pair can defend their territory better than a single animal against an aggressive neighbour (even if the neighbour is single, as in this case), or the stability of the pair-bond may provide the incentive to maintain a territory.

Familiarity between neighbouring animals may reduce aggressive interactions between them. Thus, a known neighbour might not be perceived as a threat whereas a strange conspecific may be considered threatening and therefore attacked. Communications between neighbours, e.g., through scent marking allows mutual avoidance, decreased aggression and consequently reduced costs of territorial defence. Such familiarity between neighbours could also occur as a result of relatedness between the individuals involved. Randall (1989) demonstrated decreased aggression between familiar neighbours in territorial banner-tailed kangeroo rats (Dipodomys spectabilis).

Scent marking by porcupines may thus allow mutual avoidance by familiar neighbours within a "loose" territorial framework as previously described. Such a system reduces costly intraspecific aggression while allowing pairs to maintain a fairly exclusive "territory" at relatively little expense. It would presumably be uneconomic to defend a completely exclusive territory as the potential benefits are unlikely to be sufficient to counteract the high cost of such defence (Brown 1964, in Carpenter 1987).

Although scent marking is used to make up for the inability of an animal to constantly patrol it's entire range, it is probably not effective enough to guarantee complete territorial integrity unless it is performed very extensively and at considerable cost. It is therefore common for many species of mammals to have undefended, strongly overlapping home ranges, or in this case loosely defended, partially overlapping ranges. Birds are often more territorial than mammals due to their greater mobility which allows for rapid and more economically viable responses to territorial violation (Brown & Orians 1970).

The seasonal difference observed in range overlap, i.e., significantly less overlap in summer than in winter, is probably primarily due to changes in range size resulting from seasonal fluctuations in resource abundance as will be discussed below.

Crop foragers overlapped each others ranges to a significantly greater extent than natural foragers (Table 10) and showed no significant seasonal variation (Table 9). Overlap between total home ranges was considerable at 39% and even areas of intensive use had a mean overlap of 6%. Both the increased degree and aseasonality of range overlap in crop foragers is probably attributable to the presence of an artificial resource concentration, i.e., crops of maize and watermelons. It is probable that this resource is sufficiently abundant such that it is unnecessary and therefore uneconomic to defend it. Thus, normal territorial behaviour breaks down in the area around the resource, resulting in increased range overlap. Artificial food supplies have been known to cause unnatural aggregations of normally territorial animals of several species, e.g., golden jackals (<u>Canis aureus</u>) attracted to rubbish tips in Israel (Macdonald 1983).

Henry (M5), although a natural forager, exhibited significantly greater, aseasonal, range overlap with his neighbours than did other natural foragers (Table 10). Total home range overlap was 28% and area of intensive use overlap was relatively high at 9% (Table 9). This apparent difference in territoriality is thought to be due to Henry being a single, young male. Possibly there was insufficient space and he was unable to maintain an exclusive territory, again suggesting that a pair may be able to defend a territory more effectively than a single animal. Alternatively he actively trespassed on neighbouring territories in search of a mate or extra-pair copulations, as was perhaps recorded in Interactions 2 and 3 (p.89).

What determines the size of a territory ? The distribution of resources, primarily food, is probably the most important determinant of territory size in many species, variations in resorce dispersion probably accounting for the considerable intraspecific variability in territoriality and social organisation sometimes observed (Brown & Orians 1970, Macdonald 1983, Kruuk &

Macdonald 1985, Carr & Macdonald 1986, Davies 1987). A territory must encompass a sufficient area to provide the territory holder with access to sufficient resources for it's survival. If resources are widely dispersed a larger territory will result than if resources are concentrated in a small area. If resource abundance and dispersion vary temporally, the territory defended must either vary in size to accomadate changes in resource availability or must be of sufficient size to contain adequate resources when they are at their least abundant.

Where the "territory holder" is a group rather than an individual and resources are evenly dispersed, territory size may increase proportionally to group size, however, when resources are unevenly or patchily distributed group size and territory size may be less closely correlated or even completely unrelated (Macdonald 1983, 1984, Carr & Macdonald 1986). The Resource Defence Hypothesis (RDH), (Macdonald 1983, 1984, Carr & Macdonald 1986) describes how this later situation could occur if resources are patchily dispersed in such a way that the area necessary to sustain a single individual could support several additional animals. For example, if an individuals territory must contain several different habitat types but these habitats are not evenly dispersed, the minimum area containing a sufficient portion of each habitat may be a highly convoluted shape. Such an area would have a high perimeter to area ratio, thus, a larger area with a similar perimeter length could be defended at no extra cost and such an area may contain sufficient resources to support extra individuals. If these extra animals are the territory holders offspring, such a system would allow the parents to increase the survival of their offspring at no cost to themselves. Presumably additional animals would only be tolerated by the territory holder if resources remained sufficiently abundant, a drop in resource abundance may result in the expulsion of these extra animals. Thus, the RDH suggests that territory size is determined by resource dispersion whereas group size is determined by resource abundance within the territory. The RDH can therefore only operate in an environment in which resources are both spatially and temporally heterogeneous.

Subsequently, an increase in group size may be beneficial to the territory holder(s) and extra animals, e.g., more economical territorial defence, improved foraging/hunting efficiency, improved predaror defence or perhaps thermoregulatory benefits. Thus, resource dispersion may set the limits of group and territory size within which other combinations of selective pressures operate (Macdonald 1983). Therefore, in some instances group territoriality may be a function of resource distribution and the functional advantages of group living, if any, may be secondary (Carr & Macdonald 1986). Such a situation has been suggested for the European badger which, although it lives in well defined group territories, appears to gain little direct benefit from group membership (Kruuk & Parish 1982,Kruuk 1989). Of course, as previously discussed (p.114), these secondary functional advantages of group living may assume increased importance after their conception such that the species becomes dependent on group living for it's survival. Since most observed patterns of social organisation, behaviour and space use are probably a result of a complex series of evolutionary changes it becomes very difficult, when viewing a species in its present context, to distinguish between the causes and consequences of group living and territoriality.

Kruuk & Macdonald (1985) proposed that territorial animals can also be viewed as "expansionists" or "contractors". Expansionists increase their territory size in tandem with an increase in group size. A species should only behave as an expansionist if there is a significant advantage to group living such that an increase in group size is favoured so necessitating a larger territory. Conversely, contractors maintain the smallest economically defensible area. If resource abundance increased within this minimal area a contracter should theoretically reduce the size of the territory. Alternatively however, these additional resources may allow extra animals, e.g., the territory holders offspring, to stay in the territory. Von Schantz

(1984b) proposed the Constant Territory Size Hypothesis (CTSH) whereby an animal living in an environment with fluctuating resource levels should maintain a constant territory size. The CTSH suggests that it is more costly to continually adjust territorial boundaries in response to changes in resource abundance than it is to maintain a constant territory size. Territory size is therefore determined by the area necessary to support the territory holder during periods of minimum resource availability. During periods of resource abundance the defence of such an area may become uneconomic although it may allow for increased litter sizes, increased neonate weights or improved survival of mature offspring permitted to remain in the natal territory. When resources become scarce these extra individuals are expelled from, or perhaps voluntarily leave, the territory as Von Schantz (1984a) described for red foxes (p.115).

It is possible that territory size may change in response to long term environmental changes whereas group size may be used as a more flexible response to short term fluctuations in resource availability.

What determines territory size in porcupines ? As can be seen from Tables 5 and 6 there are considerable variations in range size measured for porcupines in the study area. Natural foragers had significantly larger ranges in winter than in summer whereas crop foragers had similarly sized ranges in both seasons. Thus, in the study area natural foraging porcupines do not appear to maintain a constant territory size throughout the year. It is hypothesized that food abundance in summer makes resource defence unnecessary and consequently uneconomical. Thus, range size decreases in summer resulting in largely exclusive ranges (p.71, Table 9), exclusivity resulting from range shrinkage rather than increased territorial defence. Alternatively, these exclusive summer ranges may result from increased territorial defence as a form of mate guarding during the summer breeding season. However, the lack of seasonality in the range size of crop foragers suggests that food abundance rather than mate guarding is the primary factor determining range size.

This is not to say that mate guarding is not a factor that influences territoriality in porcupines. The only evidence of possible direct mate guarding recorded during the present study, i.e., accompanying a mate while foraging, was for the crop foraging pair, Fish (M4) and Wanda (F4), (p.86). This behaviour corresponded to relatively high degrees of range overlap that may have precluded mate guarding through territorial integrity. Thus, normal levels of territorial behaviour in natural foraging porcupines may be sufficient to prevent extra-pair copulations from occurring.

Conversely, scarcity of food in winter forces animals to forage over a wider area resulting in larger, less exclusive ranges although the largely exclusive areas of intensive use suggest that territorial maintenance is practised in winter. Seasonal fluctuations in the range sizes of natural foragers (Fig.7) exhibit increases and decreases that are approximately inversely correlated with seasonal climatic factors (Fig.15), i.e., small range size corresponds to periods of high rainfall and temperature. Assuming that plant productivity is positively correlated with such environmental variables, this inverse correlation supports the theory that range size in natural foraging porcupines is related to resource abundance. Thus, natural foragers in the study area appear to behave as seasonal contractors rather than behaving according to the CTSH. It is thought that the study area was relatively spatially homogeneous with respect to plant species eaten by porcupines (De Villiers pers.comm.) such that the RDH would not be expected to operate. Thus, the minimum area required to support a pair will not support additional animals so favouring family rather than extended family groups. In the Negev desert resources were observed to be more patchily dispersed and subject to considerable seasonal and annual fluctuations (Saltz & Alkon 1989) which may explain the occurance of extended family groups in the area in accordance with the RDH.

Further evidence to suggest that porcupines in the study area behave as contractors rather than as expansionists is the lack of observed range expansion by Batman (M2) and Henry (M5) in response to the death of their neighbours Getafix (M1) and Lady (F1) at the end of January 1990. Henry did eventually shift his range into part of their old range but not until May 1990 when winter range expansion was taking place (Figs.8a-k). Cheeseman et al. (1988) noted similar contractionism in European badgers following the removal of neighbouring clans.

Saltz & Alkon (1989) also recorded that the range size of crop foragers showed little seasonal variation compared to natural foragers. In the present study crop foragers had significantly larger ranges than natural foragers in both seasons, except for areas of intensive use in winter (Table 5). However, as already discussed on p.126, crop foragers had significantly greater overlap with their neighbours than did natural foragers. Thus, the size of area defended by crop foragers may not have been very different from that defended by natural foragers, hence the lack of significant difference between natural and crop foragers with respect to the size of winter areas of intensive use. In both the Negev desert and on the coastal plain of Israel, range sizes of crop foragers were also different to those of natural foragers although in this case they were smaller rather than larger. The size of a crop foragers range will depend largely on the distance of the crops from the porcupines burrow and also on the relative importance of natural vegetation to the crop forager. Range sizes of crop foragers should therefore be expected to vary widely but should always be relatively aseasonal compared to natural foragers as long as crop availability is also aseasonal. Absolute range sizes cannot be compared between the different studies due to the different analytical methods used and the different time periods for which the ranges were measured.

ACTIVITY PATTERNS

Using distance travelled per night and mean nightly speed as measures of activity, Table 11 and Fig.13 show that activity levels exhibit similar trends to those shown by range size. Thus, natural foragers are significantly more active in winter than in summer. The increase in distance travelled per night in winter is probably due to both the longer nightly period of activity, corresponding to longer hours of darkness (Fig.15), as well as to the increased speed of travel (Table 11). Crop foragers travelled significantly further per night in winter than in summer although there was no significant seasonal difference in mean nightly speed. Thus, the increase in distance travelled per night in winter is largely due to the longer hours of activity (Fig.15) rather than to an increase in the speed of travel.

These results are consistent with the hypothesis that range size is linked to food abundance. Thus, it is hypothesised that in winter greater distances are travelled for a longer active period in order to forage on less abundant and more widely dispersed food resources. In summer the converse situation exists. The lack of correlation between minimum nightly temperature and activity levels, in early and late winter and in late summer, (Table 13) supports the hypothesis that it is food abundance rather than a direct effect of ambient climatic conditions which determines seasonal activity levels. However, in early summer activity levels were negatively correlated with minimum nightly temperature, i.e., porcupines were less active on warmer nights. This correlation is attributed to the occurrence of a few very warm, humid nights in December when porcupines may have avoided activity and possible heat stress. December was the hottest month of the year (Fig.14) and during one nightly radiotracking session (16.12.89) the ambient temperature did not drop below 26°C.

Neither ambient moonlight or moonphase appeared to affect activity levels except in late winter when activity levels were negatively correlated with ambient moonight (Table 13). Reduced activity on moonlit nights has however been recorded for H.indica (Alkon & Saltz 1983, 1988a, 1988b, Sever 1985) and H.cristata (Pigozzi & Patterson in press). The threat of predation has been suggested as the cause of this moonlight avoidance behaviour despite the virtual absence of predators, except man, in the respective study areas. The observed behaviour may however be vestigial. A correlation between moonlight avoidance and predator avoidance has also been proposed for a variety of mammalian species, e.g., banner-tailed kangeroo rats and Frenso kangeroo rats (D.nitratoides), deermice (Peromyscus maniculatus) and African brush-tailed porcupines (Lockard & Owings 1973, 1974, Clarke 1983, Emmons 1983). The lack of large predators, including man, in the present study area (p.12) may therefore account for the absence of moonlight avoidance behaviour in the study population. Additionally, the long grass which occurs throughout the study area, and in most similar savanna ecosystems, provides cover from visually orientated predators which would otherwise benefit from moonlight. In late winter when activity levels and ambient moonlight were negatively correlated, i.e., less activity occurred on bright moonlit nights, cover from vegetation was reduced due to winter die-off and burning (pers.obs.). Such cover from visually orientated predators is not present to the same extent in the areas in which moonlight avoidance has been recorded for porcupines. It is therefore suggested that the presence or absence of cover will affect an animals response to moonlight. The lack of correlation between activity levels and moonphase suggests that porcupines do not have an endogenous activity rhythm linked to the lunar cycle.

The circadian rhythms observed in both free-ranging and captive porcupines (Figs. 15 & 16) together with the observations of porcupines emerging from their burrows after sunset (p.93) suggest that porcupines are completely nocturnal with little crepuscular activity. The highest activity levels occurred shortly after dusk with a gradual decline in activity between midnight and dawn. In some months (p.102, Fig.15) activity levels increased slightly a few hours before dawn indicating slight bimodality.

Unlike many smaller species of rodents which have several short active periods per night, between which they return to their burrows or nest (Ashby 1972), porcupines at Nylsvley have only a single nightly period of activity. A single, long activity period may be possible due to the larger body size and subsequent increased thermoregulatory ability of the porcupine, which frees it from the need to interupt it's foraging in order to return to the warmth of the burrow.

The length of the active period approximately corresponded to the number of hours of darkness and may in fact have been slightly shorter particularly in summer. It is hypothesised that longer activity was required in winter in order to forage for scarce and widely dispersed food items to enable the porcupines to simply satisfy their normal energetic demands. The greater energetic costs of this increased foraging activity, together with low ambient temperatures, would lead to even higher energetic demands thus further necessitating an increase in foraging activity.

CONCLUSION

The Cape porcupines studied at Nylsvley are thought to live in family groups comprising a monogamous adult pair with their immature offspring. One young bachelor male was also identified. Pairs appeared to be temporally stable for the duration of the study period. Pair members usually shared burrows, up to six, and utilised similar home range areas with an average overlap of approximately 75%.

It is hypothesised that monogamy evolved in porcupines due to the inability of males to guarantee "exclusive" mating access to more than one female. Once monogamy has been established, paternal care may become important, thus reinforcing the pair-bond and perpetuating the monogamous mating system.

There are also several secondary advantages associated with living in pairs, that result from, but do not cause monogamy. Apart from increased offspring survival as a result of greater parental care, these advantages probably include thermoregulatory benefits and more efficient territorial defence. Territorial defence not only allows "exclusive" access to food and other resources, but it is hypothesised that it may also have a mate guarding function by deterring potentially promiscuous neighbours. Few potential extra-pair matings were recorded, and it is suggested that cuckoldry may be uncommon amongst porcupines as a result of the strong pair-bond and territorial mate guarding.

The social organisation of porcupines does however, exhibit geographical variation, with both family and extended family groups being recorded. Considerable numbers of single males have also been recorded in some areas. Whether or not a family or extended family group develops, depends upon the opportunities available to sexually mature offspring (approximately one year of age) to disperse. This is probably dependent upon such factors as population density and the abundance and dispersion of food resources. It is hypothesised that sexually mature individuals will disperse as soon as they can due to the lack of reproductive opportunities within their natal group. Thus, family rather than extended family groups should exist where circumstances allow.

The majority of activity was concentrated in relatively small areas of the total home range, this area of intensive use, i.e., 90% of locations, occupying on average only 32% of the total home range area, i.e., 100% of locations. It is suggested that by restricting it's activities to a small area an individual may increase the efficiency of it's foraging and territorial defence.

Although there was a moderate amount of overlap between the total home ranges of natural foragers, areas of intensive use were largely exclusive, suggesting that these areas may be defended as territories. The surrounding areas of overlap may act as buffer zones between neighbouring territories, enabling indirect communication between neighbours, through scent marking, thus allowing territorial maintenance without the necessity for aggressive encounters. This hypothesis is supported by temporal space use analysis which indicated that even where extensive range overlap occurred, neighbours rarely encountered one another. These sparsely used overlapping areas also allow for temporary shifts in the position of the areas of intensive use, which may occur in response to changes in local food availability. Crop foragers exhibited greater range overlap than natural foragers. This is thought to occur due to the breakdown of normal territorial behaviour in the vicinity of an artificial resource concentration, in this case, crops of maize and watermelons cultivated on a neighbouring farm. The bachelor male, Henry (M5), also exhibited more extensive range overlap than other natural foragers. This may either be due to his inability to defend a territory, or may occur as a result of trespassing on neighbouring territories in search of a mate or the opportunity for extra-pair matings.

Natural foragers had significantly larger home ranges in winter than in summer whereas the range sizes of crop foragers showed no significant seasonal difference. It is therefore proposed that in a natural environment the home range size of porcupines is largely determined by short term resource availability, larger ranges occurring in winter when food abundance is low and smaller ranges occurring in summer when food is abundant. Thus, porcupines at Nylsvley do not maintain their home ranges at a constant size as proposed by Von Schantz's (1987b) Constant Territory Size Hypothesis, but instead appear to behave as "contractors" (Kruuk & Macdonald 1985), maintaining the smallest possible home range. The plant species eaten by porcupines at Nylsvley are thought to be dispersed in a fairly homogeneous manner such that the minimum territory size required to support a pair will not support additional mature offspring. This may at least partially explain why the porcupines in this area live in family rather than extended family groups. In some other regions, e.g., the Negev desert, resources may be patchily dispersed such that the minimum territory necessary to support a pair can also support several mature offspring, as described by Macdonald's (1983) Resource Defence Hypothesis, thus, in such areas porcupines may live in extended family groups.

Activity levels, measured as distance moved per night and mean nightly speed, also exhibited significant seasonal differences among natural foragers, thus complementing the observed changes in seasonal range size. However, crop foragers travelled significantly greater distances per night in winter compared to summer, in contrast to the aseasonality recorded for range size. Therefore, crop foragers are probably partially dependent on natural forage and this suggestion is supported by the observation that crop foragers only visited the cultivated areas on about half the nights on which they were radiotracked. The general lack of correlation between nightly activity levels and nightly minimum temperature supports the hypothesis that it is seasonal food abundance, rather than a direct effect of seasonal climatic change, that is the major causative factor of the seasonality observed in porcupine behaviour.

The only correlation between ambient moonlight intensity and activity levels was observed in late winter (negative correlation) when cover from vegetation was reduced. It is therefore proposed that porcupines will only exhibit moonlight avoidance behaviour as a local response to reduced cover. There was no evidence for an endogenous activity rhythm linked to the lunar cycle.

A study of the circadian rhythms of both free ranging and captive animals indicated that porcupines are completely nocturnal, showing little evidence of crepuscular activity. The highest activity levels were usually recorded shortly after dusk, declining gradually towards dawn.

SUMMARY

The aim of the present study was to investigate the social organisation, space use and activity patterns of the Cape porcupine (Hystrix africaeaustralis) by means of an intensive radiotracking study. Fieldwork was carried out at Nylsvley Nature Reserve, a 3000 ha area of mixed grassland and deciduous woodland savanna in central Transvaal, South Africa. Ten porcupines were radiotracked between July 1989 and June 1990, individuals being located by triangulation at hourly intervals from dusk to dawn for 5-15 nights each month. Space use patterns were analysed using minimum convex polygons and cluster analysis to determine total home ranges (THR, 100% of locations), normal home ranges (NHR, 95%) and areas of intensive use (AIU, 90%). Activity levels were measured using distance travelled per night and mean nightly speed.

Capture-recapture data, direct observations and space use patterns indicate that the social organisation of porcupines in this area is characterised by family groups comprising a monogamous adult pair and their immature offspring. Pair members usually shared the same burrow, up to six, and utilised similar home range areas with an average overlap of approximately 75%. The social organisation of Hystrix spp. appears to exhibit geographical variation with both family and extended family groups being recorded. It is hypothesised that such variation is dependent upon local population densities and the abundance and distribution of food resources which determine the timing of offspring dispersal.

Individuals utilised their home ranges unevenly, areas of intensive use occupying on average only 32% of the total home range area. Total home ranges of neighbouring pairs often exhibited considerable overlap although areas of intensive use were largely exclusive and are thought to be defended as territories. Temporal space use analysis indicated that neighbours rarely encountered one another and it is therefore proposed that territories are

maintained by scent marking. Resource defence and mate guarding are proposed as the reason for territoriality in porcupines.

Natural foragers had significantly larger home range areas in winter than in summer whereas range sizes of crop foragers showed no significant seasonal difference. Activity levels exhibited similar seasonal trends. It is therefore suggested the that home range size of porcupines in natural environments is largely determined by seasonal food availability.

OPSOMMING

Die doel van dié studie was om die sosiale organisasie, ruimtegebruik en aktiwiteitspatrone van die Kaapse ystervark (Hystrix africaeaustralis) deur middel van 'n intensiewe radio-opsporingsprogram na te volg. Veldwerk is op die Nylsvley natuurreservaat onderneem. Dié reservaat beslaan 'n 3 000 hektaar gebied van gemengde grasveld en bladwisselende boomveld savanna in die sentrale Transvaal, Suid-Afrika. Tien ystervarke is deur radio-opsporing tussen Julie 1989 en Junie 1990 nagevolg. Die posissie van individue is deur triangulasie op uurlikse intervalle vanaf sonsondergang tot sonsopkoms vir 5 - 15 nagte gedurende elke maand waargeneem. Patrone van ruimtegebruik is deur middel van die minimum-konveks-veelhoek metode en trosanalise bepaal. Hierdie is die totale tuisgebiedgrootte (THR, 100% van alle lokaliteite), normale tuisgebiedgrootte (NHR, 95% van alle lokaliteite) en gebiede van intensiewe gebruik (AIU, 90% van alle lokaliteite) gedefinieer. Die afstand beweeg per nag en die gemiddelde spoed waarteen beweeg is word as 'n indikator van aktiwiteit beskou.

Gebaseer op vang-hervang data, direkte waarnemings en ruimtegebruikpatrone in die studiegebied, bleik dit dat die sosiale organisasie van ystervarke hier gekenmerk word deur familiegroepe wat bestaan uit 'n monogame volwasse paar en hul onvolwasse nakomelinge. Pare deel gewoonlik dieselfde gate (tot ses gate per paar) en gebruik soortgelyke tuisgebiede met 'n gemiddelde oorvleueling van 75%.

Die voorkoms van beide familie en uitgebreide familiegroepe dui op die aanwesigheid van geografiese variasie in die sosiale organisasie van Hystrix spesies. Dit word voorgestel dat hierdie variasie die gevolg is van lokale bevolkingsdigthede en die beskikbaarheid en verspreiding van voedselbronne wat die verstrooiings-ouderdom van die nageslag beïnvloed.

Individue gebruik hul tuisgebiede onreëlmatig en gebiede van intensiewe gebruik beslaan slegs ongeveer 32% van die totale tuisgebiede. Die totale tuisgebiede van naaslewende pare toon dikwels 'n groot mate van oorvleueling, alhoewel gebiede van intensiewe gebruik hoofsaaklik eksklusief gebruik en skynbaar as territoriums verdedig word. Tydspesifieke ruimtegebruikpatrone dui daarop dat naaslewende individue selde ontmoet en dit word voorgestel dat territoriums deur reukmerking onderhou word. Die verdediging van bronne en

die beskerming van 'n maat word as rede vir territorialiteit in ystervarke aangevoer.

Ystervarke wat op natuurlike voedsel voed se tuisgebiede gedurende winter is groter as gedurende die somer, terwyl ystervarke wat op landbou gewasse voed se tuisgebiedgroottes geen seisoenale veranderinge toon nie. Aktiwiteitspatrone vertoon soortgelyke seisoenspatrone. Dit word gevolglik aangevoer dat die grootte van ystervarke tuisgebiede in natuurlike gebiede hoofsaaklik deur seisoensveranderinge in voedselbeskikbaarheid bepaal word.

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APPENDIX 1: Individual monthly home range sizes (ha) with mean values (± S.D.) for natural foragers and crop foragers.

		JULY	AUG/SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	JUNE
Getafix (M1)	THR	135	178	77	48	61	46	-	-	-	-	-
	NHR	71	85	65	28	37	34					
	AIU	40	44	28	20	23	23					
Lady (F1)	THR	251	261	152	82	91	210	-	-	-	-	-
	NHR	126	147	73	48	26	85					
	AIU	66	115	47	25	25	44					
Batman (M2)	THR	63	312	298	177	150	140	153	90	195	153	222
	NHR	39	207	133	110	54	69	70	45	133	84	139
	AIU	27	135	82	59	34	22	47	22	104	69	92
Vicki (F2)	THR	-	161	120	169	-	-	-	-	-	-	-
	NHR		102	87	99							
	AIU		78	37	36							
Attilla (M3)	THR	-	-	-	92	106	85	-	83	402	129	251
	NHR				43	23	31		24	143	85	98
	AIU				33	20	29		22	76	65	48
Bodacea (F3)	THR	-	-	-	145	-	-	-	-	-	-	-
	NHR				47							
	AIU				37							
Fish (M4)	THR	-	-	-	154	165	563	268	359	327	399	579
	NHR				84	56	294	187	169	200	188	236
	AIU				41	25	101	77	93	72	159	108
Wanda (F4)	THR	-	-	-	-	-	-	-	302	308	447	-
	NHR								68	136	258	
	AIU								63	100	149	
Henry (M5)	THR	123	307	256	172	109	97	147	118	206	209	164
	NHR	93	153	119	110	59	55	88	87	122	98	94
	AIU	86	110	53	74	51	45	73	38	77	88	40
Bugeye (M6)	THR	-	-	-	-	-	267	189	314	216	504	326
	NHR						92	46	160	106	178	99
	AIU						68	28	64	39	116	85
Natural foragers	THR	170	243	181	152	114	141	163	97	268	164	212
		± 71	± 71	± 93	± 32	± 38	± 83	± 28	± 19	± 116	± 41	± 44
	NHR	97	139	95	82	42	61	68	52	133	89	110
		± 28	± 48	± 29	± 30	± 16	± 26	± 21	± 32	± 10	± 8	± 25
	AIU	64	93	49	47	30	39	49	27	86	74	62
		± 23	± 40	± 21	± 16	± 11	± 18	± 23	± 9	± 16	± 12	± 31
Crop foragers	THR	-	-	-	-	-	563	268	337	284	450	453
							-	-	± 32	± 59	± 53	± 179
	NHR						294	187	165	147	208	168
							-	-	± 6	± 48	± 44	± 97
	AIU						101	77	79	77	141	97
							-	-	± 21	± 21	± 23	± 16

APPENDIX 2: Individual monthly values for mean distance travelled per night (m ± S.D.) with mean values for natural foragers and crop foragers.

	JULY	AUG/SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	JUNE
Getafix (M1)	2882 ± 1086	3291 ± 541	2442 ± 785	1814 ± 485	1712 ± 846	1622 ± 359	-	-	-	-	-
Lady (F1)	3323 ± 1425	4267 ± 1714	3321 ± 893	2390 ± 141	1854 ± 781	2619 ± 813	-	-	-	-	-
Batman (M2)	3276 ± 593	4693 ± 1161	4274 ± 1580	3150 ± 746	3067 ± 1033	2455 ± 1272	2363 ± 655	2394 ± 597	2844 ± 793	3207 ± 1124	4208 ± 1066
Vicki (F2)	-	3459 ± 518	3733 ± 841	2843 ± 927	-	-	-	-	-	-	-
Attilla (M3)	-	-	-	2688 ± 706	1767 ± 678	2754 ± 945	-	2168 ± 664	3629 ± 2113	3027 ± 776	3077 ± 1318
Bodacea (F3)	-	-	-	2500 ± 797	-	-	-	-	-	-	-
Fish (M4)	-	-	-	3090 ± 842	2623 ± 861	3622 ± 1094	4886 ± 1893	4683 ± 2172	5476 ± 1936	5135 ± 1335	5495 ± 1815
Wanda (F4)	-	-	-	-	-	-	-	3686 ± 2094	5357 ± 1027	5416 ± 1647	-
Henry (M5)	3027 ± 582	3955 ± 681	3231 ± 1400	3589 ± 2111	2818 ± 1119	2978 ± 1080	2543 ± 877	2699 ± 736	3144 ± 862	3403 ± 1109	4197 ± 1012
Bugeye (M6)	-	-	-	-	-	3176 ± 1363	2807 ± 927	3332 ± 1177	4709 ± 1325	4240 ± 1694	3775 ± 1073
Natural foragers	3112 ± 1036	3933 ± 1177	3355 ± 1242	2794 ± 997	2325 ± 1018	2632 ± 1150	2539 ± 827	2709 ± 980	3537 ± 1416	3753 ± 1449	3912 ± 1190
Crop foragers	-	-	-	-	-	3172 ± 93	5595 ± 1476	5354 ± 1909	5962 ± 927	6040 ± 783	6736 ± 1763