A functional analysis of scent marking and mating behaviour in the aardwolf, *Proteles cristatus* (Sparrman, 1783)

by

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ABSTRACT

This study attempted to answer how scent marks function in terms of aardwolf *Proteles cristatus* year-round territory maintenance and mating success. A functional analysis of scent marking in the aardwolf was conducted in a two and a half year field study whilst recording 42 000 paste marks. The anatomy and histology of the anal pouch revealed an efficient organ for producing copious amounts of long-lasting fatty pasting secretion, and the apparatus for applying it onto grass stalks. The histology of the penile pad of aardwolf males was similarly geared to production and application of secretion, though its exact function is still not clear. Aardwolves started practising scent marking motor patterns early in life, but physiological maturation of secretion was complete with eight months and independence from their parents only. Cubs practised paste marking by overmarking scent marks of their parents, adjusting their mark-rate to that of the adult followed. After physical and behavioural maturation of paste marking subadults ceased to mark, coinciding with parental aggression, and some remained in their parent's territories for another year. They started to paste again only when attempting to establish their own territory.

Aardwolves scent marked almost exclusively by pasting with their anal pouch. Uncovered faeces away from established middens and urine deposited on middens, predominately by males during the mating season, were however likely to act as additional scent marking agents.

During the non-mating season scent marking patterns suggested that scent marks functioned as a representation of an aardwolf’s claim to a territory area and its readiness to resort to physical escalation. Female and male motivation for territorial marking might differ slightly. There was a great deal of variation in marking activity due to territory size, individual effort, and territory establishment. Aardwolves responded to greater perceived intruder pressure by increasing their marking activity. Midden and den marking and general usage was adapted as well. Borders where intrusions were most likely were marked selectively more than others.

Variation in scent marking activity was even stronger during the mating season. Both sexes increased their rate of marking ouside of their territories in order to advertise to neighbouring mating partners in the weeks around the females’ oestrus. Females only increased their mark-rates when not in attendance by males. Males with high mark-rates scouted in territories of females in pro-oestrus indicating their determination to mate to both their neighbouring males and females. After the mating season when resources, mating partners and food, were scarce scent marking activity was low to increase again when re-establishing territorial borders. At least 62% of observed copulations were extra-pair copulations (EPCs). Males either tried to mate at the critical point for female fertilisation by aggressive intervention or by sneaking copulations avoiding physical escalation. Female encouraged EPCs but still were eager to copulate longer with their partners. They were able to influence the course of the copulation considerably. By defending an exceptionally large territory, as well as having two females, weakened one male’s ability to guard his female partners efficiently from EPCs.

In 43 experiment nights the response of aardwolves was monitored when finding 164 translocated scent marks collected from known aardwolves. An increase of scent marking activity at relevant borders and the demonstration that intimidation was transmitted without physical presence of the marker provided support for the intimidation hypothesis. Aardwolves changed their occupied den in response to it being scent marked by a same-sex intruder. Translocated scent marks of a female in pro-oestrus were able to elicit a visitation of her territory by the neighbouring male suggesting sex attractants in female scent marks. Seasonally the messages transmitted by scent marking changed coinciding with a shift in principally defended resource, food or mating opportunity.

The study contributes to the understanding of the function of scent marking in the solitary aardwolf, by exposing their capability to transmit messages efficiently and their ability of interpretation to secure their food resources and mating opportunities.

"Anyone who has spent days and nights
watching another animal in the wild
will realise that each species
perceives a world of its own -
totally unlike any other"

David Day 1981

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CHAPTER 1

GENERAL INTRODUCTION

The aardwolf (*Proteles cristatus*) is a nocturnal carnivore of the African savannahs, feeding almost exclusively on termites (Richardson 1987a). Its great specialisation and thus dependence on termites as a food source is evident in most aspects of its lifestyle (Anderson 1994). Territoriality was previously reported in the aardwolf and its primary function is believed to be in defending this limited resource from other aardwolves (Richardson 1985). Each aardwolf territory, which ranges in size from 100-600 ha, is occupied by a resident pair with their most recent offspring. The adults vigorously defend their territory against any intruders. It is well demarcated by means of scent marks which are placed strategically, especially along borders and next to middens and dens (Richardson 1990, 1991).

Territory Maintenance

Many mammals scent mark their territories in order to advertise both their presence and ownership of a territory (Gosling 1982; Gorman & Mills 1984). It is however still a subject of debate how scent marks help in maintaining a territory. It is besides disputable whether scent marks actually deter intruders from entering the territory, or from confronting the territory owner. Many carnivores live in large territories which as a result are difficult to monitor steadily. Richardson (1991, 1993) in the recent resurrection of the 'intimidation hypothesis' implied that the function of a territorial scent mark in carnivores, is to advertise an intrinsic physical threat to intruders. Thus if an intruder is encountered by the territory owner physical escalation will always result if the intruding individual does not retreat immediately. In this way scent marks should help to maintain the territory in the temporary local absence of the resident. Despite the large number of studies which have recently been conducted on scent marking behaviour in carnivores (Erlinge *et al.* 1982; Nel & Bothma 1983, Gorman & Mills 1984; Kruuk *et al.* 1984; Clapperton 1989; Smith *et al.* 1989; Richardson 1990, 1991), all were based on field observations alone. As such they do not provide definitive evidence to show how scent marks function in territory maintenance. In addition to extensive field observations this study aimed to take this one stage further by experimental manipulation of the marking behaviour of aardwolves to try and untangle some of the ambiguities posed by previous work.

The Use of Urine and Feces

Scent marking with anal pouch secretion onto grass stalks is the principal means of scent communication in the aardwolf (Richardson 1991), with feces mainly buried on middens and urine voided wherever the aardwolf happens to walk. In contrast feces serve as important scent marking agents in the other members of the Hyaenidae and urine is significant in scent communication in many different carnivore families (Macdonald 1985). Urine may however have a limited scent marking function in the aardwolf, mainly used by males during the mating season (Richardson 1990). This was tested by examining whether urine and feces are placed deliberately do serve as additional scent marking agents during certain periods of the year.

The Function of the Anal Pouch

Not only is little known of the behavioural aspects of scent marking, but anatomical and histological features of the aardwolf related to scent marking have also not been examined in any detail. In particular the histology of the aardwolf's scent marking secretion producing anal pouch and the male's penile pad, has not been studied. To establish whether aardwolves are limited by their ability to produce scent marking secretion, a histological study of the anal pouch, and investigation of its anatomical structure, will help to determine how individual odours are likely produced and applied onto grass stalks. It has been suggested that the penile pad also plays a role during the mating season (Richardson 1985). An examination of its histology and anatomy could therefore improve our understanding of its function.

Ontogeny of Marking

Whether early individual differences in scent marking can be used to predict the status and performance of scent marking by different individuals during adulthood has not been thoroughly studied in carnivores (Bekoff 1989). In order to establish at what stage of their behavioural development male - female differences in scent marking behaviour appear and whether scent marking behaviour develops differently in the sexes one has to observe its ontogeny from early age on. Our knowledge of scent marking behaviour after dispersal and prior to territory establishment in the aardwolf is still incomplete. The behaviour of subadult non-territorial aardwolves was examined in order to determine how they avoided confrontation with territorial residents. It was predicted that they may be using the residents' scent marks to avoid confronting them.

Intersexual Difference in Marking

Male and female aardwolves seem to be marking the specific areas, border and internal areas as well as dens and middens, of their territories differently (Richardson 1987b, 1990, 1991). Their scent marking behaviour will be examined to establish whether this is true and how their marking behaviour is influenced by the size of their territories defended and in response to varying intruder pressure.

The role of marking during the Mating Season

For most of the year scent marking advertises the ownership of food resources of an aardwolf territory and should function to limit intruders from exploiting them (Richardson 1991). In the short winter mating season a switch in decisive resource from food resources to access to mating partners takes place. At this time scent marking should be used to defend an animals partner against intruders in order to maximise ones reproductive success. Observations also suggest that female aardwolves paired to inferior quality male partners seem to advertise their receptivity not only to their partner but also to neighbours (Richardson 1987b, Richardson and Coetzee 1988). Thus it was also hypothesised that individuals may scent mark in a way to gain access to mating partners of neighbouring territories. They marked along borders of their territory and even inside of their neighbours territories presumably to incite visitation by neighbouring males for extra pair copulations (EPCs). Before females come into oestrus high quality males scent mark deliberately outside of their territories with the suggested function of advertising their strength to the females and trying to intimidate their male partners of neighbouring territories in order to obtain EPCs with females (Richardson 1987b). It has been were suggested that these scent marks are left especially frequently on dens and middens, serving as focal points for aardwolf communication (Richardson 1990, 1991). The precise timing of the strategic moves of both males and females would imply that female scent marks ought to contain sex attractants during their oestrus.

Experimental Manipulation of Marking Behaviour

In preliminary experiments aardwolf scent marks were translocated from one territory to another, and most scent marks were found and overmarked quickly (Richardson 1991). By conducting extensive translocation experiments much can be learned about how territorial residents interpret and react to simulated challenges through scent marks by intruders of different sex and familiarity. The reproductive competition among male aardwolves during the mating season suggests that male scent marks are different from those of females (Richardson 1987b). Due to the shift in defended resources, from food to mating partners, seasonal differences in the reaction to scent marks of non-resident aardwolves' found by the residents are expected.

The Importance of Individual Recognition

Another hypothesis, frequently debated in carnivore scent marking is the function of individual recognition (Gorman 1976, 1980; Halpin 1986). Scent marks serving to define a territory boundary and presumably also used in reproductive competition would be expected to have an individually distinctive odour (Gosling 1982; Apps 1988) thus allowing differential reaction to scent marks of non-residents of different familiarity. This hypothesis will be tested by examining the reactions of aardwolves finding translocated scent marks of familiar and unfamiliar identity. Individual differences in mammalian odours are likely to be based on differences in the relative concentrations of components of complex mixtures (Gorman 1980). In the case of the aardwolf the series of esters in the anal gland secretion of the aardwolf would be suited to such a role (Apps *et al.* 1989).

The primary aim of this thesis is to establish what messages are contained in scent marks and their function in maintaining an individual's territory as well as their role in the reproductive behaviour of the sexes. Furthermore the anatomy and histology of the anal scent pouch is investigated as well the ontogeny of scent marking. In order to determine the function of scent marking in the aardwolf the following key questions are addressed:

KEY QUESTIONS

(1) What is the anatomical and histological structure of the anal scent pouch of the aardwolf ?

(2) What is the ontogeny of scent marking in aardwolves ?

(3) Do urine and feces serve as a means of scent communication in the aardwolf ?

(4) Do males and females differ in their scent marking behaviour ? If so, does this relate to a difference in resources being defended ?

(5) Do females incite visitation by neighbouring males during the mating season ?

(6) Does the copulation behaviour of males and females maximise their reproductive success ?

(7) How do scent marks function in the maintainance of territories ?

THE STUDY SPECIES

A brief literature review is given to provide the reader with some background.

Evolution and Taxonomy

It is now generally agreed that the aardwolf is a member of the family Hyaenidae (Wayne *et al.* 1989; Wozenkraft 1989; Werdelin & Solounias 1991), though the relationship of the Hyaenidae to the Viverridae and the Felidae within the superfamily Feloidea is still unclear. Molecular and biochemical data suggest that the Hyaenidae are most closely related to the Viverridae (Wayne *et al.* 1989), although morphological characters propose a closer relationship with the Felidae (Wozenkraft 1989; Werdelin & Solounias 1991). Nevertheless, it is believed that the first hyaenids evolved from non-specialised viverrid-like ancestors into the more specialised bone-crushers of today (Werdelin & Solounias 1991). Recently it was suggested that ancestral aardwolves were phylogenetically preadapted, via their viverrid-like ancestors, to tolerate noxious chemicals and hence the defence secretions of *Trinervitermes* soldiers (Richardson & Levitan 1994). Ewer (1973) considers *Lycyaena* as the most likely ancestor of *Proteles*. Like the present day aardwolf it had sharp-pointed teeth, ill-adapted to breaking bones.

The sole indisputable ancestor of the aardwolf, is *P. transvaalensis* which was described by Hendey (1974) from late Pliocene deposits at Swartkrans in the Transvaal and can be dated at about 1.5 million years B.P. (Brain 1981). This animal was larger and dentally less degenerate than *P. cristatus* (Hendey 1974). Gingerich (1974) pointed out that the extant aardwolf is virtually indistinguishable from *P. cristatus* of one million years ago, which supports the hypothesis that *Proteles* diverged from the ancestral stock sometime in the Pliocene.

Distribution and Habitat

The aardwolf is endemic to Africa and occurs in two discrete populations (Fig. 1.1). The southern population (*P. c. cristatus* Sparrman 1783) ranges over most of southern Africa, extending just into southern Angola, southern Zambia, and south-western Mozambique. A 1 500 km gap separates the southern from the northern population (*P. c. septentrionalis* Rothschild 1902), which extends from central Tanzania to north-eastern Uganda and Somalia, and in a narrow strip along the coast of Ethiopia and Sudan to south-eastern Egypt (Meester *et al.* 1986; Smithers 1983). Aardwolves are absent from most of Zambia, southern Tanzania and West Africa. Prime habitat for the aardwolf is open, grassy plains, although it occupies most habitats with a mean annual rainfall of 100-800 mm. Aardwolves are most common in areas receiving 100-600 mm of rain and are absent from forests and pure deserts (Smithers 1983).

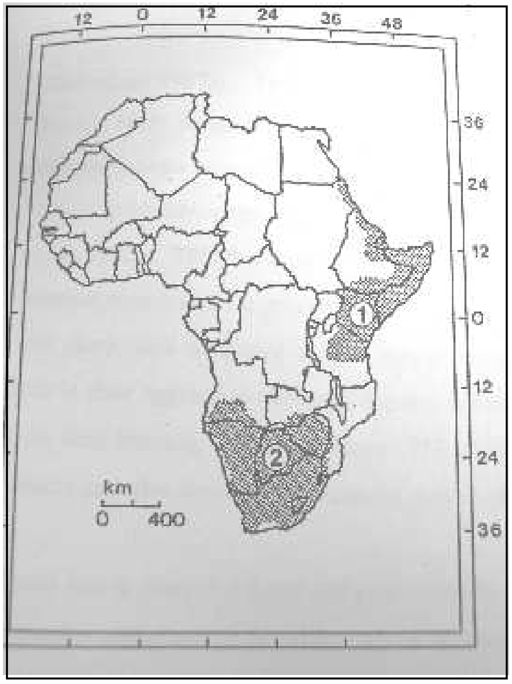

Figure 1.1 Distribution of *Proteles cristatus* in Africa (from Koehler and Richardson 1990). ① *P. c. septentrionalis*; ② *P. c. cristatus.*

General Characters

Like the striped and brown hyaenas, the aardwolf has a muscular neck, large pointed ears and a long erectile mane extending from behind the head down the middle of the back to the tip of the tail (Koehler & Richardson 1990, Fig. 1.2). In southern Africa, adult body mass varies seasonally with the availability of termites with an average of 8-12 kg. There is no sexual dimorphism in size (Smithers 1983; Richardson & Bearder 1984; Van Jaarsveld *et al.* 1995). Like the hyaenas, *Proteles* has a sloping back with forelegs longer than the hindlegs, and a well developed anal pouch for scent marking grass stalks. With its striped body it superficially resembles the striped hyaena, though *Proteles* is less than 50% of its size, with a more regular stripe pattern (Richardson & Bearder 1984; Fig. 1.3). In reference to its generic name the aardwolf has five digits on the front foot and four on the hind, differing from the hyaenas which lack the pollex on the front foot (Roberts 1951; Smithers 1983). The most dramatic differences between the hyaenas and the aardwolf, however, are in the skull and dentition, the whole structure being adapted to the aardwolf's near exclusive diet of termites (Kruuk & Sands 1972; Richardson 1985). Whereas hyaenas have a powerful dentition and strong sagittal crest to crush large bones, the aardwolf has a slender skull and the cheek teeth are reduced to small, widely spaced, redundant pegs (Roberts 1951; Smithers 1983). The broad, near parallel-sided palate extends beyond the molars providing space for the large, spatulate tongue used to lick termites off the soil surface (Richardson 1987a). The tongue is covered with large, hardened papillae of two different shapes

(Flower 1869; Richardson 1985; Anderson *et al.* 1992; Anderson 1994). Large submaxillary glands produce copious amounts of sticky saliva, while the muscular pyloric area, or muscular tooth of the stomach probably compensates for the lack of cheek teeth for the mastication of the termites (Anderson *et al.* 1992). Still the aardwolf has disproportionately strong jaws and skull with well developed masseter muscles and a powerful jaw action (Koehler & Richardson 1990). These features together with sharp, well developed canines were probably retained for fighting (Ewer 1973; Smithers 1983), both in their aggressive territorial disputes and the defence of their young as they often chase jackals from their breeding dens (Richardson 1985, 1987b; Richardson & Coetzee 1988). In old animals the canines are often worn down to rounded stumps (Richardson 1985).

Facial hair is short (1-1.5 cm) and grey, while the muzzle is hairless and grey-black (Smithers 1983), a presumed adaptation to the sticky terpene secretion of the *Trinervitermes* soldiers. Aardwolves of the study area vary in the background colour of their coats from pale buff to dark grey and their stripe colour from light brown to black (Fig. 1.3).

Visual, auditory and olfactory senses are all well developed in the aardwolf, with a noticeably large external appearance to the eyes and ears, while internally the olfactory lobes and auditory bullae are also well developed (Flower 1869; Kruuk & Sands 1972; Smithers 1983; Richardson 1985).

The penis points forwards, containing no baculum, and is sheathed along the ventral surface of the body. The glans penis is covered with small recurved spines (Flower 1869; Wells 1968; Ewer 1973; Richardson 1985). At the base of the penis are a pair of oblong clusters of pale sebaceous glands separated by non-glandular tissue (Flower 1869) with unknown function, that were previously not seen in hyaenas (Wells 1968; but see Chapter 3, Fig. 3.1). The female has two pairs of inguinal teats (Richardson 1985).

Aardwolves scent mark their territories with a yellowish-orange to brownish-black secretion from the anal pouch (Kruuk & Sands 1972; Nel & Bothma 1983; Richardson 1985; Apps *et al.* 1989) that turns black with oxidation upon exposure to the atmosphere (Richardson 1985). The pouch is situated immediately above the anus, with which it shares a common external aperture. The pouch is T-shaped and eversible with sebaceous and apocrine gland tissue (Flower 1869, Pocock 1916).

Ontogeny and Reproduction

In central South Africa, females come into pro-oestrus once a year only, in mid June. Mating usually takes place in the second half of June and the first half of July. Copulation lasts from one to four and a half hours with ejaculation, indicated by pelvic thrusting and tail bobbing, usually after one hour and again at approximately hourly intervals. During the latter part of copulation the female walks back towards her den with the male clinging to her (Fig. 1.4). There is no copulatory tie. Females remain receptive for one to three days and will recycle if not fertilised (Richardson 1985, 1987b).

After a gestation period of approximately 90 days a litter of two to five young is born from mid September through December in South Africa (Shortridge 1934; Stuart 1981; Richardson 1985; Koehler & Richardson 1990). Further north in Botswana and Zimbabwe, the breeding season seems to be less restricted (Smithers 1983).

After about one month the cubs emerge for the first time from their natal den and start to play around the den when the adults are present. From six to nine weeks they play within 30 m of the den (Fig. 1.5). From nine to twelve weeks they may go foraging with an adult and start feeding on termites within a radius of 100 m from the den. From 12 weeks to four months they forage throughout the territory, usually accompanied by a parent. Cubs are weaned by the end of this period and are accompanied for a short period of the night up to seven months (Fig. 1.6), but thereafter forage alone. With the birth of the next year's litter, at one year of age, aggression from their parents increases and cubs start making excursions into neighbouring territories and generally have left their natal territory a month later. Subsequently they seldom return and enter a transient period during which they search for a vacant territory. If a parent dies, a cub of the same sex may remain in its natal territory (Richardson 1985, 1987b).

Males may help rearing the young by guarding the den against black-backed jackals. Paternal care varies, some fathers may spend up to six hours / night guarding the cubs, while the female is away foraging (Richardson 1985, 1987b; Richardson & Coetzee 1988; pers.obs.). Cub mortality can be as high as 68 %, depending on drought conditions or long winters (Richardson 1987a). Captive aardwolves can attain an age of 15 years (Von Ketelhodt 1966).

Ecology

The diet of the aardwolf is well documented. It feeds primarily on nasute harvester termites (*Trinervitermes*). In East Africa on *T. bettonianus* (Kruuk & Sands 1972), *T. rhodesiensis* in

Zimbabwe and Botswana (Smithers 1971), and *T. trinervoides* in South Africa (Cooper & Skinner 1979; Richardson 1987a). The aardwolf feeds on foraging parties of termites by licking them off the soil surface, apparently tolerant of the noxious secretions of the soldier termites (Kruuk & Sands 1972; Richardson 1987a; Richardson & Levitan 1994), and consuming up to 300 000 termites/night (Richardson 1987a). Termite foraging parties or columns vary in size from about 20-40 cm across and may contain up to 3 000 individuals. Aardwolves use both auditory and olfactory cues to locate termites, typically turning to approach columns from downwind (Kruuk & Sands 1972; Richardson 1985). *T. trinervoides* is almost entirely nocturnal but by contrast the larger harvester termite *Hodotermes mossambicus* is mainly active by day and during winter (Nel & Hewitt 1969; Hewitt *et al.* 1972; Richardson 1987a). This is fortunate for the aardwolf because during the winter months in central South Africa, it is often too cold for *Trinervitermes* to emerge at night. At this time aardwolves become more diurnal in order to feed on *Hodotermes* during the afternoon (Richardson 1987a).

Richardson (1987a) estimated that an aardwolf consumes about 105 million termites/year. *Trinervitermes* constitutes the overwhelming majority of these with *Hodotermes* being of limited importance during winter. Only traces of other insects have been observed as being eaten or recorded in faecal deposits. Other studies (Smithers 1971; Kruuk & Sands 1972; Kingdon 1977; Cooper & Skinner 1979) have also shown a prevalence of *Trinervitermes* sp. in the aardwolf's diet, although with a broader spectrum of other surface-foraging termites, wilst rarely recording other insects and arachnids.

During the mid-winter months of June and July in the northern Cape province, aardwolves consume only one-fifth the amount of termites per month as compared to outside the winter months, resulting in a loss of up to 25 % of body mass during this time. Winter is also the time of highest cub mortality, suggesting that the aardwolf is highly dependent on *Trinervitermes* and unable to feed successfully on the alternative food resources available at this time except for irregularly occurring *Hodotermes* (Richardson 1987a, 1987c, 1987d; Anderson 1994).

The aardwolf has a basal metabolic rate of merely 59 % in winter (Anderson 1994) and 70 % in summer of that expected from the allometric Kleiber curve (Anderson 1994). Dependence on a food source that is nutritionally low (Redford & Dorea 1984), filled with chemical poisons (Prestwich 1983), and seasonally unavailable (Richardson 1987a) could be responsible for the lowered basal metabolic rate (Richardson 1987c). Active aardwolves maintain a constant body temperature of 37 °C. Whilst inactive, and particularly during winter, they are able to decrease their body temperature as low as 31.2 °C resulting in energy savings of up to 17.7 %. In winter aardwolves employ heat-saving postures and social huddling to conserve energy and water in the thermally stable den environment as well as spending more time there than in summer (Anderson 1994).

Aardwolves are generally independent of surface water, receiving their water from termites. They drink during long cold spells only, when termites remain inactive, then often walking long distances in search of water (Richardson 1985).

As a consequence of the aardwolf's specialisation on its unique diet, it has invaded a trophic niche which is almost entirely devoid of competitors (Anderson 1994). *Trinervitermes* are largely unavailable during winter and due to a number of physical specialisations aardwolves are unable to exploit alternative food sources. Survival during winter is achieved through a combination of behavioural and physiological adaptations (Anderson 1994).

Aardwolves occupy home ranges that vary from 100 to 600 ha (Kruuk & Sands 1972; Bothma & Nel 1980; Richardson 1985; this study). Richardson (1985, 1987b; 1990; 1991) has shown that home ranges, determined by summing up contiguous hectares in which an adult pair deposited more than one scent mark/ha outside the mating season, are aggressively defended and scent marked as territories. Territory sizes vary with the density of *Trinervitermes* mounds, each territory having approximately 3 000 mounds, with an average of 55 000 termites/mound (Richardson 1985). As the standing crop of these mounds provides approximately one-half the annual consumption of a family of aardwolves, presumably these termites have a high production/biomass ratio to sustain this high predation rate (Richardson 1985, 1986; 1987a).

Behaviour

Aardwolves are mainly nocturnal (Kruuk & Sands 1972; Bothma & Nel 1980; Richardson 1987a) and in the Northern Cape summer, activity begins half to one hour after sunset and ends one to two hours before sunrise. During the winter months activity often begins one to two hours before sunset, lasting until termites become unavailable as the air temperature drops to about 9 °C. Aardwolves cover about 1.7 km every hour while foraging, walking eight to twelve km/night during summer and, depending on ambient temperature, three to eight km in winter (Richardson 1985).

They feed alone except when accompanying their young cubs (Kruuk & Sands 1972; Bothma & Nel 1980; Richardson 1987a; Richardson & Coetzee 1988). During winter, members of the same territory may come together in a loose group, when feeding on *Hodotermes* emerging from a large colony. When they meet another aardwolf from the same territory, both animals raise the mane and hair on the back and approach each other slowly. When recognising each other they lower the mane and pass by each other without further interaction. Occasionally, mainly in a greeting between a mother and her cubs, two animals briefly sniff each others noses before separating (Richardson 1985).

An aardwolf pair defends a perennial territory with their most recent offspring. Apart from aggressive encounters, these territories are maintained by means of scent marking (Richardson 1985, 1987b, 1990, 1991; Fig. 1.7), sometimes called "pasting" (Kruuk 1972; Gorman & Mills 1984). When marking the aardwolf first straddles a blade of grass, then rapidly squats while everting its anal pouch and wiping a smear of secretion (Fig. 1.8), about six mm in length, onto the grass (Kruuk & Sands 1972; Richardson 1985; 1990, 1991). Both sexes scent mark, females about 1.7 times per 100 m walked and males more frequently, on average more than two times per 100 m walked. Pastings are concentrated along territory boundaries, dens and middens and may be entirely related to territory defence and mate acquisition (Richardson 1985). Nel & Bothma (1983) observed aardwolves deposit minute spots of secretion, apparently related to advertising areas traversed while feeding. This latter form of scent marking has not been recorded elsewhere (Kruuk & Sands 1972; Richardson 1985, 1987b).

Like hyaenas, aardwolves defecate mostly at middens (Fig. 1.9), just sometimes defecating at random (Nel & Bothma 1983; Richardson 1985, 1990). Middens are usually one to two metres across and often made of soft, bare sand from the frequent digging of aardwolves. As many as 20 middens may be located throughout the territory, but those near the boundary are used most frequently (Richardson 1985, 1990). To defecate a narrow trench is dug with alternating strokes of the front paws; the animal then turns around and squats over the trench. The first defecation of the evening may be up to eight percent of the body mass of the animal (Smithers 1971; Richardson 1985). The subsequent two or three defecations in summer are much smaller. After defecating the aardwolf fills the hole with sand and usually deposits a few scent marks onto adjacent grass before leaving (Richardson 1985; 1990). The sand content of the faeces may vary from negligible up to 40 % in sandy areas (Bothma & Nel 1980; Cooper & Skinner 1979) or when few termites are available (Richardson 1985).

Aardwolves usually urinate into the same hole used for defecating. But when termites are abundant they may urinate up to six times a night, by simply squatting to urinate on the ground, and then continue foraging (Richardson 1985). A possible role in communication for uncovered urinations left by males during the mating season has been suggested by Richardson (1990).

The aardwolf is generally silent, when not under stress. The lowest form of threat is a soft clucking sound apparently made by opening and closing the mouth. Under more stress, aardwolves utter a deep-throated growl and during fights or when suddenly surprised, give a remarkably loud and explosive roar (Smithers 1971; Richardson 1985). During fights and chases the mane is often fully erected. When slightly disturbed, the aardwolf just fluffs out the hairs of the tail, as frequently seen in playing cubs. Outside of the mating season, resident aardwolves win all intraspecific encounters within their territories, immediately raising their mane and chasing away intruders upon detection (Fig. 1.10). When these are caught, both animals fall to their knees and bite each others necks (Fig. 1.11).

As a mated pair occupies the same territory throughout the year, but since copulations are not necessarily exclusive within the pair, aardwolves may be considered socially monogamous only. EPCs regularly occur between the most aggressive males and female neighbours. Aggressive neighbours may gain access to neighbouring females by rigorously scent marking the territory of a neighbour during the pro-oestrus period of the female, subsequently defeating the resident male in a fight when his female becomes receptive. Cuckolding of less aggressive males holds evolutionary implications. Paternal care necessary for cub survival involves guarding of the den from jackals, an activity that is energetically costly to the male. Males should theoretically guard cubs only if some of them are his offspring. It has therefore been suggested that females should accept extra-pair copulations only after mating with her partner (Richardson 1987b; Richardson & Coetzee 1988). The resulting litter may have mixed paternity, thus providing motivation for the cuckolded male to guard the cubs, although they may also possess "superior" genes from the more aggressive male. From the females’ point of view this should be a stable strategy, unless the cuckolded male has the rare opportunity of access to a female with whom he can breed exclusively. In this case he may leave his promiscuous female to mate with the alternative female (Richardson & Coetzee 1988).

Cubs are raised in dens, usually with single entrances. These may be old aardvark, or porcupine burrows, but more often enlarged springhare burrows or excavations of aardwolves themselves (Richardson 1985, Anderson 1994). Dens are mostly oval shaped at the entrance, about 32 cm high and 42 cm wide, and rapidly narrowing to 20 by 30 cm inside the tunnel. They may be up to 6.5 m long with a chamber (100 x 40 x 25 cm) at the end, usually providing space for one adult and her cubs (Richardson 1985; Anderson 1994; pers. obs.). Dens are regularly used for six to eight weeks before switching to another, and may be re-occupied 6-18 months later (Richardson 1985).

Most of our contemporary knowledge about aardwolves stems from studies within its southern-central distributional range in Africa, with its distinct seasonal and habitat characteristics. Little is known of its habits within the more tropical latitudes of East Africa, with their relatively aseasonal environment. Even within southern Africa the influence the denser savannah habitat in the very south and east of South Africa, or the extreme dry conditions of the Kalahari and Namib desert, will have on the feeding ecology, breeding behaviour and the chemical signalling system of the aardwolf remain undocumented.

Figure 1.2 Intimidated six month old aardwolf with raised mane.

Figure 1.3 Slightly alarmed female adult aardwolf with black, regular stripes.

Figure 1.4 Mating pair of aardwolves. The female carries the male on her back, with him still being inserted, towards her den in order to rid herself of his grip.

Figure 1.5 Four six week old aardwolf cubs playing at the den entrance. The cub on the left already shows interest in a scent marked piece of root.

Figure 1.6 Six months old male aardwolf cub investigates his mothers scent mark. In the background a second cub tries to overmark its mother's scent mark.

Figure 1.7 One aardwolf scent marks a grass stalk with its anal pouch. The second tries to sniff the grass stalk with the secretion on it

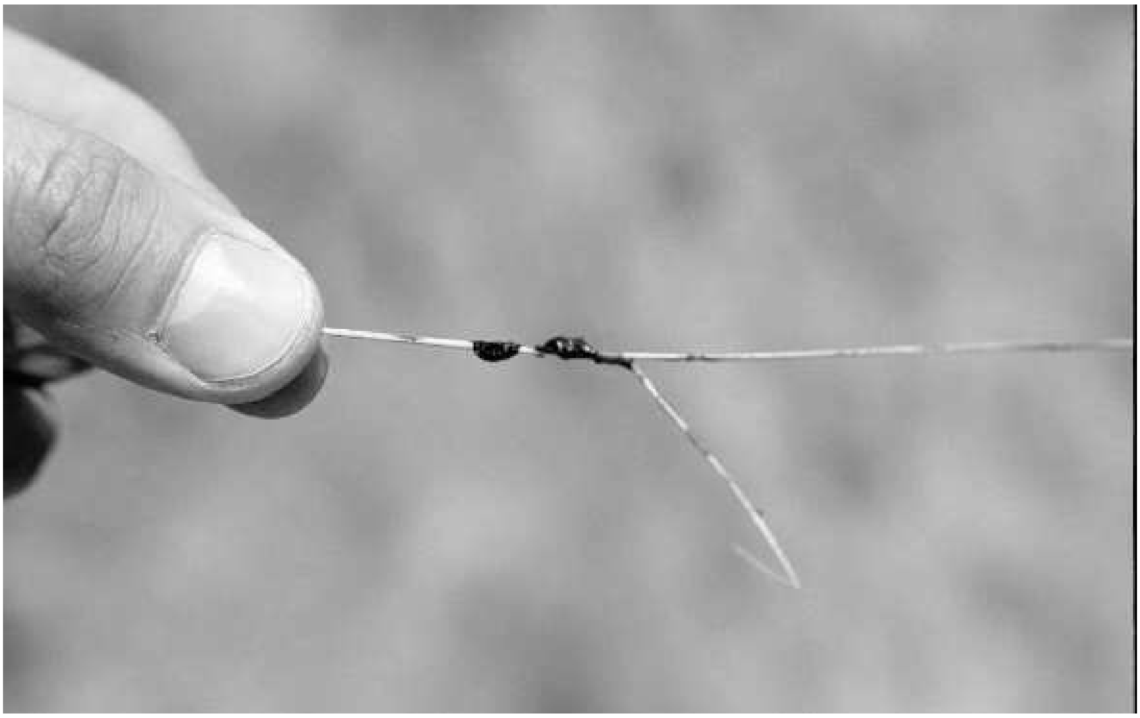

Figure 1.8 Anal pouch scent mark secretion (pasting) on a grass stalk.

Figure 1.9 Three cubs defecate together with their mother (scratching over) on a midden.

Figure 1.10 Aardwolves chasing each other on a winter afternoon.

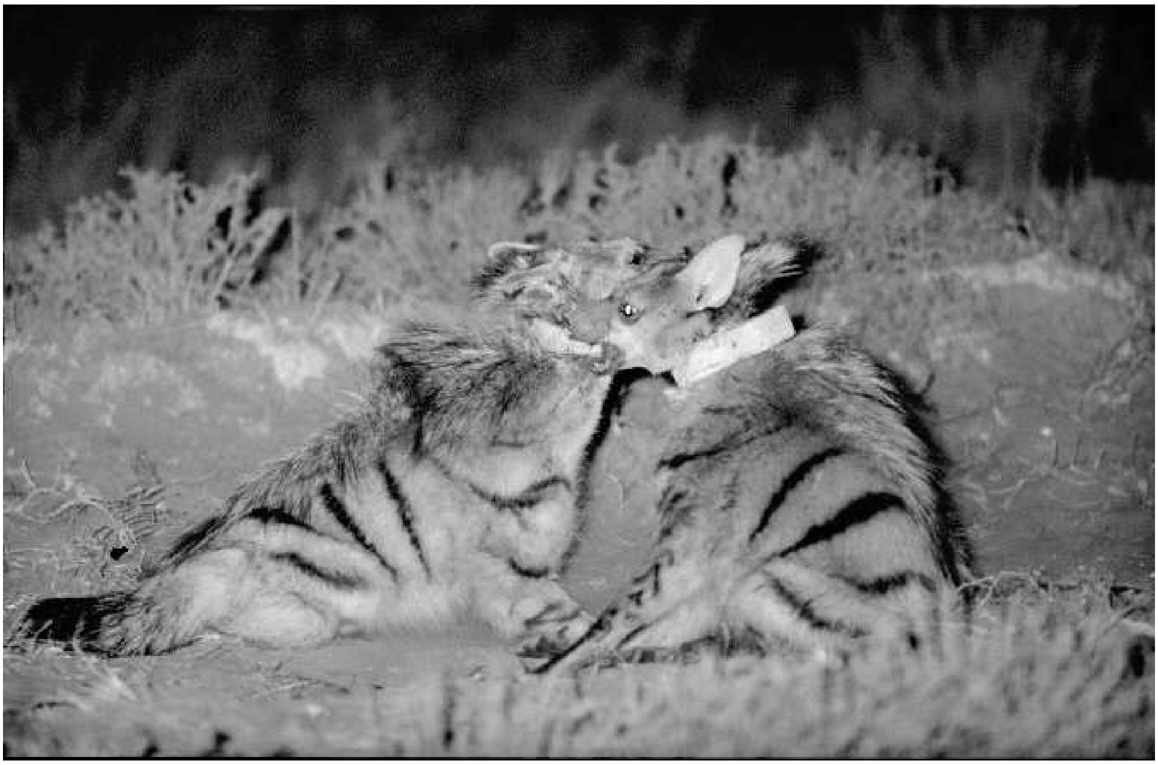

Figure 1.11 Aardwolves fighting on their knees. Two adult males bite each others ears and radio collars in a fight for mating rights.

CHAPTER 2

MATERIALS AND METHODS

STUDY AREA

Location and General Description

The study was conducted on Benfontein Game Farm (28°50'S; 24°50'E), which is situated about six kilometres south-east of Kimberley in the Northern Cape and Free State Province, South Africa (Fig. 2.1). This same study area was used previously by Richardson (1985) and Anderson (1994) in their studies on aardwolf. Benfontein covers 11 400 ha, and the study site is a 4 000 ha portion in the eastern part of the farm. Elements of three major biomes that converge in the Kimberley area (Acocks 1975) are present in the study area. In relation to Kimberley the Kalahari biome lies to the north-west, the grassveld biome to the east, and the Karoo biome to the south. A large pan is situated in the north-west of the study area, with more specialised plant communities around it. The vegetation of Benfontein has been described in detail by Richardson (1985) and Anderson (1994).

Climate

(1) Rainfall The Northern Cape has a "semi-arid continental climate" (Schulze & McGee 1978). There is a distinct dry period during the winter months and a humid period during the summer. In a semi-arid area, rainfall is the most important factor influencing changes in vegetation and therefore in the animal communities (Louw & Seely 1982), including the termites vital to aardwolves. In the Northern Cape rainfall is very variable, both in time and spatial distribution (Tyson 1986).

Rainfall in Kimberley peaks in the late summer months with March usually being the wettest (Fig. 2.2). Precipitation is usually in the form of late afternoon thundershowers. The mean annual rainfall for Kimberley is 431±127 mm (Weather Bureau in Pretoria). The monthly rainfall recorded during the study period was generally lower than the 50 year averages, except for the rains in October 1991 and February 1992, which were much higher.

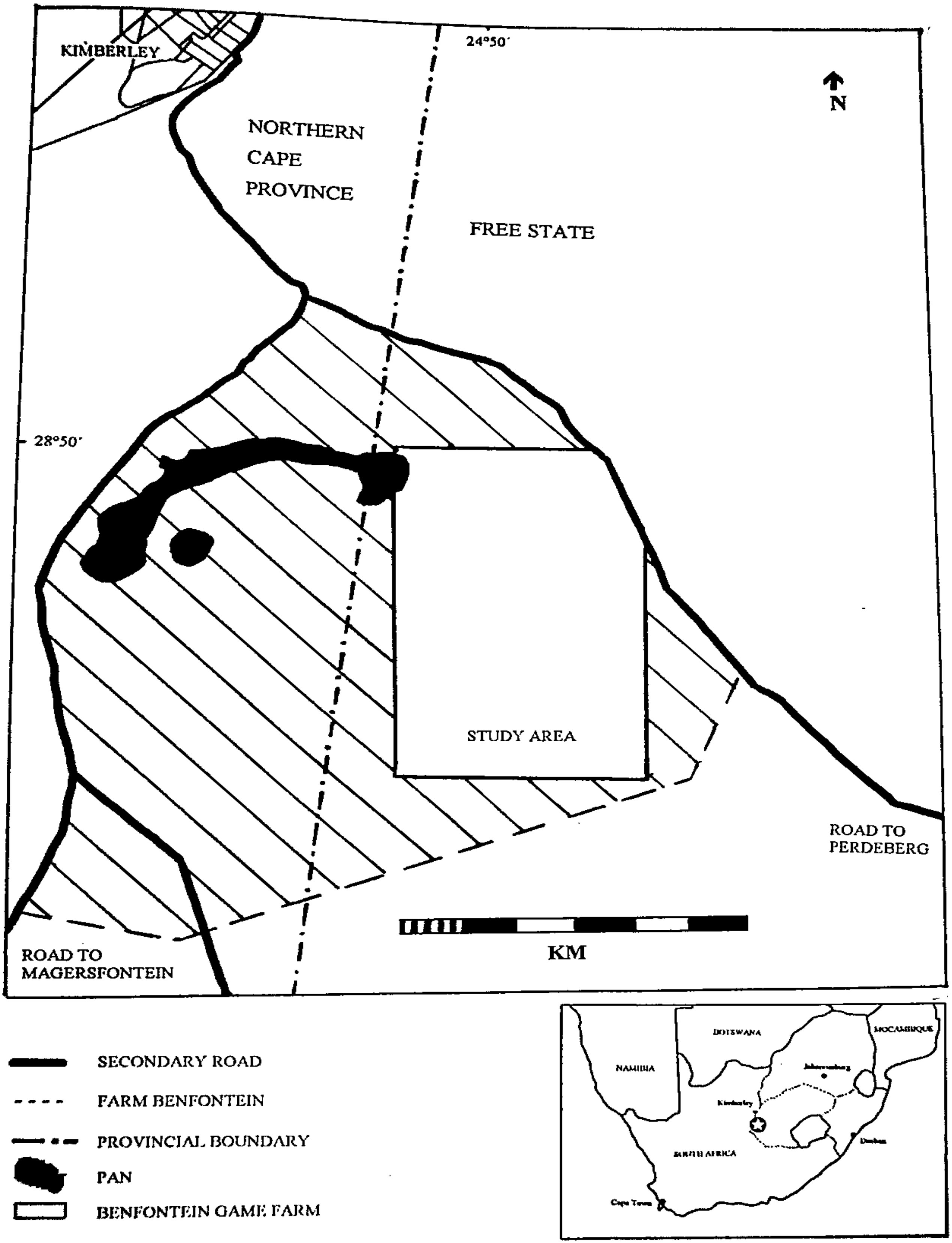

Figure 2.1 The farm Benfontein, showing the main study area and the more important geographical features.

The monthly rainfall for the study period, May 1991 - August 1993 (Kimberley Weather Station, B.J. Vorster airport, Kimberley), compared with the mean monthly rainfall for the last 50 years (Weather Bureau, Pretoria) is presented in Fig. 2.2. Taking the rainfall for the first two years of the study period gave a mean annual rainfall of 347.5 mm (May 1991-April 1992= 347 mm; May 1992 - April 1993 = 348 mm) which is still within one standard deviation of the mean annual rainfall for Kimberley.

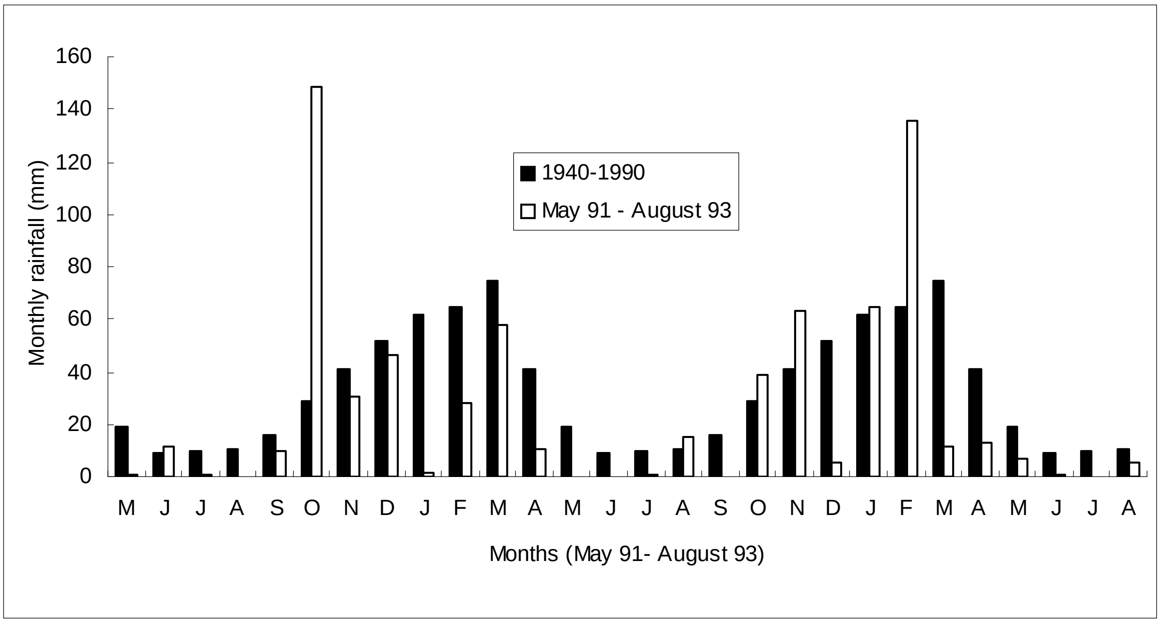

Figure 2.2. The monthly rainfall for Kimberley for the study period (May 1991 - August 1993) relative to the mean monthly rainfall for the past 50 years (1940-1990).

(2) Temperature The mean minimum and maximum monthly temperatures for the study period (Kimberley Weather Station, B.J. Vorster Airport, Kimberley) are shown in Figure 2.3. The winters (May to August) are cold and dry and the summers (November to March) are hot. During winter there is very little cloud cover and the temperature at night often drops below freezing. The hottest day temperature recorded was 39.1°C, the lowest night temperature was - 7.8°C.

Water

After good rains the pan fills with water, creating a fertile, shallow wetland, with a length of up to seven kilometres. During the study period the pan was mostly dry, being partly filled only in October 1991. There is a permanent spring in the north-east of the study area. During this study the aardwolves used the spring for drinking and the pan wetland on a number of occasions. Following good rains, pools of stagnant water persist in the veld for a few days, and a small pan in the centre of the study area held water for a week or two after a thundershower.

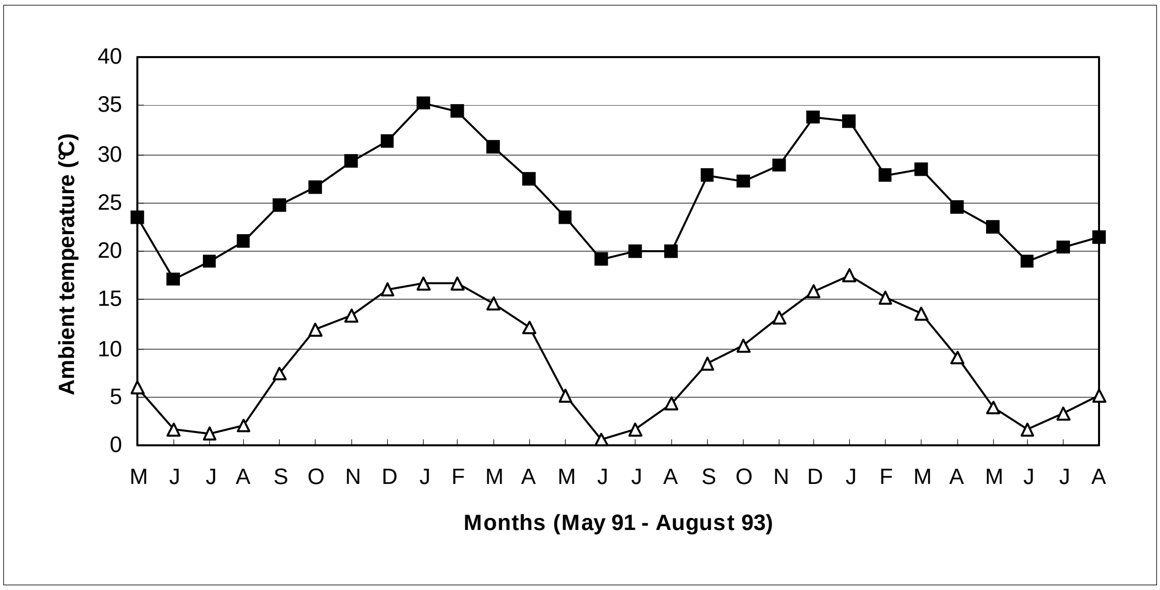

Figure 2.3 The mean maximum and minimum temperatures for every month of the study period (May 1991 - August 1993).

Topography

Benfontein Farm can be divided into five geographical regions. In the north-west is a large, closed depression or pan with a substrate primarily consisting of calcium carbonate (calcrete). A calcrete layer also underlies all the soils surrounding the pan. Around the pan, rising gradually in altitude, are the pan slopes (Fig. 2.4). Further away from the pan the ground levels out and a belt of red Kalahari sand occurs to the south-east, which also has an underlying calcareous tufa. Sand depth increases to the south and east and trees, mainly *Acacia erioloba*, grow here (Fig. 2.5). A few dolerite koppies are situated along the southern-eastern, southern, and south-western boundaries of the farm, just beyond the southern-eastern limits of the study area. Two prominent drainage lines run down to the eastern sector of the pan. They are rather shallow depressions, their soils being periodically waterlogged.

Indigenous Fauna

From 1891 to 1970 Benfontein was utilised as both a sheep and game farm (Richardson 1985). Since then Benfontein has been run primarily as a game farm, with a few thousand hectares in the southern part of the farm still used for cattle ranching. There are approximately 5 000 springbok (common and scientific names of all animal species cited in the text are listed in Appendix 1) on the farm making it the most numerous indigenous ungulate. Other antelopes include blesbok, black wildebeest, steenbok, common duiker, and greater kudu.

Figure 2.4 Pan slope vegetation with walking aardwolf in the foreground in winter 1992.

Figure 2.5 Kalahari sandveld in the south of the study area with long grass, termite mounds and *Acacia erioloba* trees.

No large carnivores survive on the farm, but a number of smaller species still occur. The two largest are the black-backed jackal and the caracal. They represent the aardwolf's sole potential predators on Benfontein. Other carnivores include the bat-eared fox, Cape fox, black-footed cat, striped polecat, and the small-spotted genet. Other potential predators of aardwolves in the study area and surrounding farmland include man (Anderson 1988) and two birds of prey, the giant eagle owl, and martial eagle.

The two mammals most likely to compete, to a very limited extent, with the aardwolf for its food source are the aardvark (Melton 1976; Willis *et al.* 1992), and the bat-eared fox (Nel 1978; Bothma *et al.* 1984). The springhare, porcupine, and aardvark are important to aardwolves, since their burrows are frequently used by them (Willis & Anderson 1990).

GENERAL METHODOLOGY

The general methodology which has been used throughout the study is detailed in this chapter. These techniques are therefore pertinent to various chapters of the thesis, whilst more specific methods are described in detail at the start of the relevant chapters. The field work for the study was conducted over a period of 28 months, from May 1991 until August 1993. During this time I visited the study area on 530 occasions, amounting to over 3500 hours of field work.

Mapping of the Study Area

Richardson (1985) used 420 metal stakes to mark aardwolf middens, dens and prominent landmarks in the study area. Anderson (1994) supplemented this with a further 120 stakes over his study. These *ca* 1 m long stakes were marked with self adhesive tape (red, yellow, white, green, and blue) which was visible from distances in excess of 300 m at night in the light of a spotlamp. The stakes were driven into termite mounds which prevented them from being knocked over by black wildebeest and other animals. In addition all gates and some poles along the length of the fence-lines were marked. In the southern study area 50 trees were colour coded with reflective tape stuck on metal pieces, about 2 m above ground. During the study the reflective tape on nearly all the previous markers was replaced and an additional 94 stakes were placed in the study area giving a total of 684 marked points (Fig. 2.6). Richardson’s (1985) map of the area was used as the marker reference, onto which I plotted Anderson’s markers as well as my own new marker points.

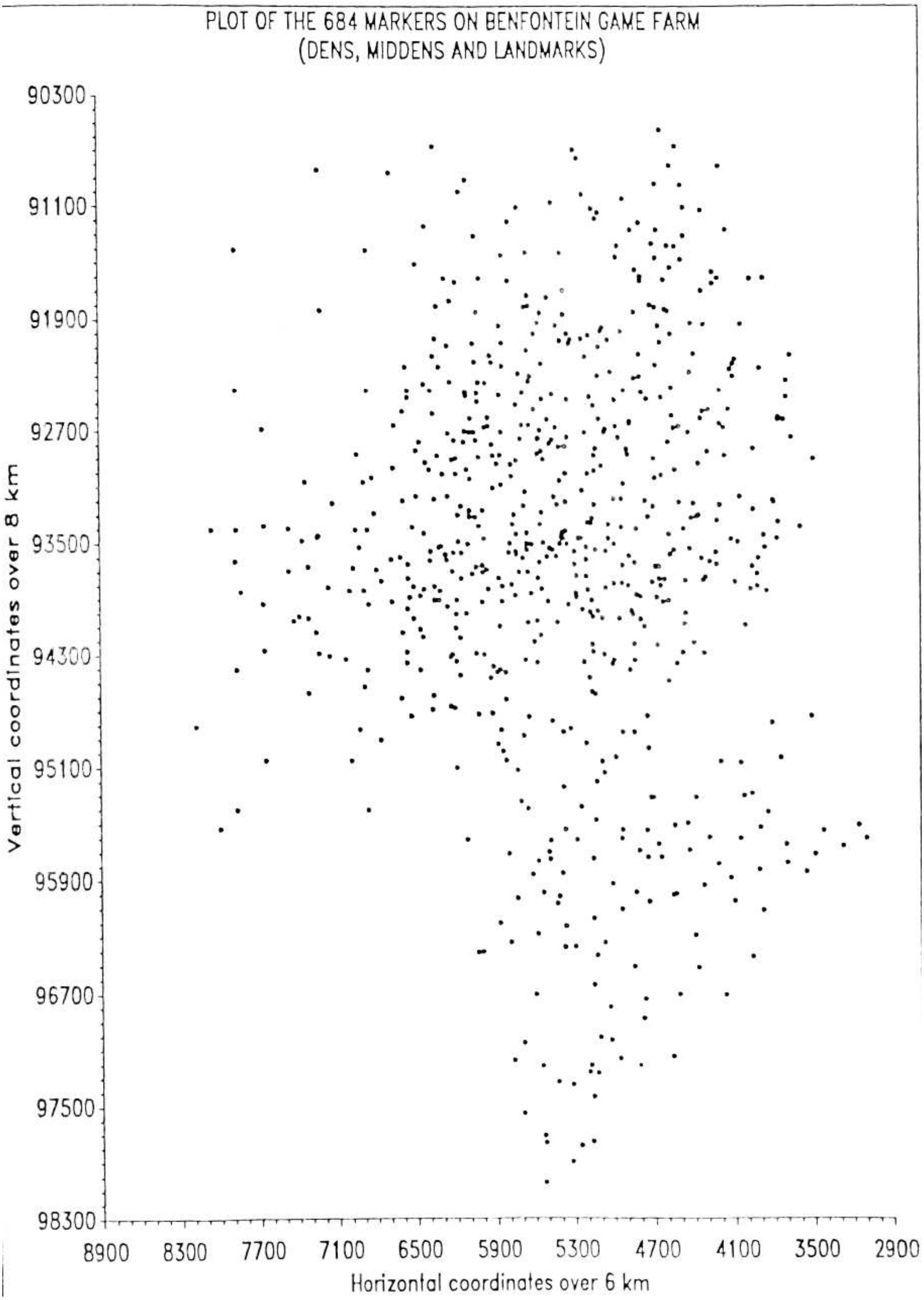

Figure 2.6 Plot of the 684 markers within the study area on Benfontein game farm.

In 1982 De Beers Survey Department surveyed 50 of Richardson's (1985) 420 colour coded stakes, spaced well out across the northern part of the study area. Their localities were plotted onto an enlargement of a 1:50 000 government survey map and were used as reference points for plotting the positions of the remaining stakes (Richardson 1985). This was done by means of a hand-held compass and triangulation. The coordinates of all the following stakes, trees, fence posts and gates were calculated by Richardson (1985) and later by me in the following manner. Using the coordinates of the 50 original stakes as reference points a grid matrix with 100 m divisions was drawn up to cover the map of the whole study area (60x80cm). A transparency of this grid was made and fitted over the map of the study area. The coordinates of all the markers were then estimated to the nearest 10 m (Richardson 1985).

Meteorological Information

Maximum and minimum temperatures, rainfall, wind speed, and relative humidity were provided by the Kimberley Weather Office at the B.J. Vorster airport, which is about five km west of Benfontein.

Immobilisation and Radio-tracking of Aardwolves

Some aardwolves had been radio-collared by previous researchers (Anderson 1994). However it was occasionally necessary to locate and immobilise aardwolves without radio-collars. Animals were located by parking the vehicle at a good vantage point and scanning the area through a pair of binoculars, in the late afternoon in winter and early evening in summer. At night aardwolves were searched for by driving along roads, and through the veld, while scanning the area with a handheld spotlamp.

Aardwolves were immobilised on 32 occasions. They were darted from the vehicle when standing still while foraging or when lying down. The dart was fired using a Telinject dartgun (Telinject SA, Randburg, RSA) from distances of 10, 12, or 15 m (Anderson 1994), after the range was checked against the focus of a camera's telephoto lens. The dartgun was calibrated using the minimum amount of pressure needed to dart at these three distances (Richardson 1985). All 1.5 ml darts were marked with reflective tape to facilitate recovery at night (Richardson 1983; McKenzie 1989).

The drugs used in the dart were a combination of 12-20 mg/kg ketamine hydrochloride (Ketalar, Parke-Davis Laboratories (Pty) Ltd., Isando, RSA) and 0.15-0.30 mg/kg acetylpromazine (ACP, Centaur Labs (Pty) Ltd., Johannesburg, RSA) (Anderson & Richardson 1992; Richardson & Anderson 1993). Immobilisation of aardwolves was usually effective in inducing anaesthesia within five minutes.

Individuals remained anaesthetised for between 20-45 minutes during which time they were earmarked, weighed, measured, blood samples were taken and they were fitted with radio-collars. The body mass was recorded using a 10 kg and 2.5 kg spring balance (Pesola, Switzerland). The length of all four canines was measured as the maximum distance from the tip of the tooth to the gum on the lateral side of the tooth, using a pair of callipers. Also the condition of the canines (broken, chipped, or worn) was recorded. In addition the size of the males' testes and females' nipples were measured with callipers and the secretory condition of both anal pouch and penile pad assessed. The colours of secretions were also recorded. Radio-collars were fitted to adult aardwolves only. When the aardwolves started recovering from the drugs they were put out into the veld and watched for at least two hours until they were walking steadily again.

Radio-collars consisted of a SB2-AVM transmitter (AVM Instrument Company Ltd, Livermore, California, USA) in the 148-151 MHz band powered by a 3.6 v D-size lithium battery. These were embedded in dental acrylic, whilst the collar itself was of four centimetres wide industrial conveyor-belting, which was riveted in place. Several radio-collars transmitted signals for more than two years at a range of more than two kilometres. Most of the antennae, sticking out through the top of the nylon sheeting, broke off after several weeks reducing the signal range to between 500 m and 1000 m.

The telemetry equipment used to locate aardwolves was a Yaesu FT 29O R II receiver (Yaesu Musen Co., Tokyo, Japan) and two three-element Yagi type antennas. The antennae were mounted, facing forwards, at an angle of 90° to each other, to a metal frame fastened on the back of the vehicle. A switch box inside the vehicle enabled the driver to switch from one antennae to the other, such that an equal signal strength from each side meaning that the aardwolf was directly in front of, or behind, the vehicle.

Marking and Recognition of Aardwolves

Aardwolves were recognised on the basis of (1) their body stripe patterns, colour of coat, face, (2) their radio-transmitter frequencies, (3) reflective tape colour on their radio-collars, (4) natural ear cuts and nicks, and (4) man-made ear markings.

To facilitate later recognition, nearly all aardwolves darted for the first time were earmarked. One or two small V(s) were cut from the aardwolf's ear(s) using a sterile scalpel blade. The wounds were treated (Kemi Spray, C.E. Industries (Pty) Ltd., Kempton Park, RSA) and the animals were injected subcutaneously with a wide spectrum antibiotic (Combimycin, C.E. Industries (Pty) Ltd., Kempton Park, RSA).

Age Classification of Aardwolves

Richardson (1985) distinguished five aardwolf age classes, on the basis of growth and subsequent damage of the canines. Since aardwolves have extremely reduced molars and pre-molars it is not possible to determine their age on the basis of tooth eruption and wear, as is done for other carnivores (*e.g.* Kruuk 1972; Mills 1981; Lindeque & Skinner 1984). Following the study of Anderson (1994) three broad age classes were differentiated; namely cubs (<1 year old), sub-adults (1-2 years old) and adults (>2 years old).

Observation of Aardwolves

After an initial habituation phase of between three and 10 days the newly radio-collared aardwolves were not disturbed by the vehicles presence and the lights. They were followed in a 4x4 pickup truck from distances of 10-30 m. This vehicle proved ideal having an excellent ground clearance and I sat fairly high, increasing the visibility in long grass. Study animals were followed with the vehicle engaged in low range four-wheel drive. In this manner engine’s revs remained fairly low without riding the clutch or creating too much noise. This also reduced the chance of stalling the vehicle. Being in four-wheel drive, it was possible to drive out of an aardvark hole without unnecessarily disturbing and/or losing the study animal. The 55-watt spotlamp used for night observation had a swivel mount and was attached to a metal frame directly above the driver's window. Attached to the lamp was an extended handle which could be held while resting the arm on the window sill.

Observations were recorded on a Phillips pocket dictaphone, enabling me to keep the animal in visual contact. A 10x50 pair of binoculars were used for more detailed observations. All of the aardwolves were accustomed to the presence of the vehicle and to the sound of my voice. However, they were easily disturbed when they detected a person standing outside the vehicle. During winter, aardwolves were followed from the time they became active (15h00-17h00) until they retired to their dens (18h00-01h00). In summer they were followed from the time they became active, just after sunset, until 03h00 in the morning. On a number of occasions, particularly when conducting translocation experiments with scent marks, aardwolves were followed for their entire active period to determine which middens and dens they visited and to which den they retired.

The method used to plot the movements of aardwolves was based entirely on the use of the coloured markers. The first observation was made when I first located the focal animal and subsequently, whenever it passed near a marker, changed direction, or when there was a noticeable change in its behaviour. On average an observation was made every ten minutes. For each observation the aardwolf's bearing and distance to the nearest marker was recorded. Bearings were given by using the 16 points of the compass - N, NNE, NE, ENE, E ect. The estimations of these bearings were made by using the sun, moon, Southern Cross, and three well lit man-made features. They were a radio tower, a mine dump, and a mine headgear, 10-20 km from the study area and lay almost exactly to the east, north and west. When I was near the extremities of the study area these bearings had to be slightly adjusted. Distances over 30 m were estimated to the nearest 10 m. These data were used to calculate the coordinates of the aardwolf's position as it moved around (Richardson 1985, 1987a). For checking computer calculated distances between consecutive observations the odometer reading of the vehicle was noted to the nearest 50 m at each observation.

Recording of Behaviour

Different categories of behaviour were recorded using instantaneous and continuous sampling techniques (see Martin & Bateson 1986). Those behaviours of a more general nature (*e.g.* feeding on termites, walking) were recorded by instantaneous sampling at about 10 minute intervals over the course of the night following the focal aardwolf. Rare but important actions such as sniffing and showing flehmen towards grass stalks, defecation and urinations, and also interactions with other animals were continuously sampled. Thus every time a particular behaviour was observed or performed towards another individual this was noted.

Behaviour was divided into the following categories for the purpose of the study:

Marking and Eliminative Behaviour

Scent marking while travelling and feeding: All scent marks (pastings) were recorded with a counter, and whenever the position of the focal animal was recorded, every ten minutes on average, the total number of marks was noted the aardwolf left since the last observation (Richardson 1991).

Scent marking on middens and dens: When an aardwolf visited a midden or a den and marked at it, then these marks were recorded as having been done there and kept separate from those since the last observation. Middens were defined as sites where there were at least two separate defecations and which showed signs of sand having been scratched over the feces. Dens were holes large enough to sleep in which aardwolves either used during the study or had the potential for usage or were visited regularly.

Defecating and urinating: whenever an aardwolf defecated or urinated the position of the defecation at or away from a midden was noted, together with scratching movements or without.

Investigatory Behaviour

Sniffing: when an aardwolf walked up to a grass stalk with an existing scent mark and deliberately sniffed it for more than three seconds this was noted in an observation.

Flehmen: The act in which the upper lip is drawn up in order to increase gaseous flow over the vomeronasal organ in order to assess the scent of a scent mark, urine, or feces (Estes 1972).

Interactive Behaviour

Four interaction types were combined from 20 different classified behaviours shown during interactions of aardwolves:

Greeting: Two or more animals approach one another within one metre without raising their dorsal hair, then simply walked past one another. Sometimes they briefly sniffed each others' noses, head, or anal region.

Hair-raising: Raising (pilo-erection) of the dorsal hair of neck and back while approaching each other. When recognising a resident of the same territory at close quarters aardwolves lowered their hair, and usually walked off. Sometimes one made a brief lunge at the other, then trotted off. Hai2-raising does not include any occasions when a chase was involved.

Chasing: Chasing another aardwolf away for a distance of at least 10 m. Snapping or bites of the chaser to the chased hindquarters were included here.

Fighting: Brief fights occurred when aardwolves involved in a chase caught up to each other and the chased would face the chaser. On other occasions an aardwolf would face the attacker without prior chasing. They would fall to the ground biting each others necks, ears, sides and legs, often drawing blood while kneeling on the ground (Fig. 1.5).

General Behaviour

Walking or running: These two behaviours were recorded only when the observed aardwolf did not feed since the last observation. An aardwolf walks at about three kilometres per hour when not feeding while a speed in excess of 10 km / hour was recorded as 'running'.

Definition of Terms

'Territory' will be used in the sense of a spatial reference for dominance (Marler & Hamilton 1966), but is intended to imply some degree of exclusive occupancy as envisaged in the views of territory advanced by Burt (1943). The term 'owner' will be used for the individual or group that actively defends the territory. 'Intruders' are animals within the territory that can potentially replace the owner.

Definition of Territory Boundaries

The territory of each aardwolf was defined using the method of Richardson (1990, 1991), except that he defined territories for aardwolf pairs defending one territory and not for individuals as I hereafter did. A matrix of 1-ha cells was placed over the study area, then all the 1-ha cells that had at least one pasting were plotted on a single map for each aardwolf for each summer season separately. After an aardwolf had been followed for approximately 20 km the outer boundary of its core area was rather clearly defined simply by the coincidence of the plotted path it followed. In these cases it was possible to recognise movements that could be considered as excursions by the animal's striking off at an angle of > 45° to the core area border.

Aardwolf territories were therefore defined as all those ha cells enclosed within the core area, but excluding cells traversed during excursions only. Where the outer path crossed only the inner corner of a ha cell (covering < 1/8 of the cell area), that cell was excluded from the territory. In most cases this method clearly defined territory borders, but where the border line was not defined because of insufficient observations, it was determined by joining up the cells along the shortest line between the defined cells on either side. Boundaries were defined as being fixed for a year, and were redefined after the end of each mating season.

Because adjacent same-sex territories often had a number of cells common to both, and to allow for slight changes in boundaries, the border zone was defined as being 200 m wide. Where borders ran diagonally across cells, the border zone was defined as being at least the diagonal width of a cell

(141m). Internal cells were defined as never being in contact with the border cells of an adjacent territory. Where this occurred because of overlapping territories, the internal cell concerned was reclassified as a border cell (Richardson 1990).

Scent Marking Rates

Rates of scent marking were defined as the number of scent marks deposited by an individual per 100m travelled. Relative density of scent marks was calculated by summing up all the marks deposited by each adult in each of the two zones of the territory, then dividing these values first by the zone area (in ha) and then by the total observation time of that individual in this zone. These values are, therefore, corrected for differences in territory area and observation time, thus allowing comparisons between sexes and territories. Differences in the densities of marks between internal and border cells within territories were analysed by comparing the observed total number of marks in each zone with the expected values, which were determined by the area of the zone.

Scent Mark Characteristics

Physical characteristics of a number of scent marks were measured with a 50 cm ruler for the height of the grass stalk and height of paste secretion above ground, measuring along the length of the stalk to the nearest mm. Paste length of collected scent marks was measured with callipers to the nearest 0.1 mm.

To determine the dry weight of a paste mark secretion 20 grass stalks were collected, each with one secretion more than 5 mm in length. The grass stalks were dried for six hours in an oven at 90 °C. Afterwards the grass stalks were cut into smaller segments with secretion on and weighed on a scale to the nearest 0.1 mg. Then the secretion was removed with a scalpel blade and the grass stalk segments weighed again. The difference gave the average dry weight of 20 secretions.

At irregular intervals I left the vehicle to examine the colour of freshly deposited secretion on grass stalks. This was done several times throughout the course of the night following aardwolves of different age and sex.

Marking Site

Scent marks were recorded as either being deposited along a road (r), within one metre of a termite mound (t), or within two metres of dens (d) or middens(m). When scent marks were not associated with any of the previous landmarks they were recorded as being deposited in the veld (v).

Data Management

All observations recorded on dictaphone were transcribed the next day onto paper. These were later entered onto computer in the form of database files. Specialised SAS programs (SAS Institute Inc., Cary, NC, USA) were used to plot the paths of the aardwolves. All the data collected during direct observation, were analysed assuming a uniform speed of movement from one observation to the next. These data were allocated to each hectare in proportion to the mean distance travelled per hectare, when an aardwolf traversed several hectare blocks since the last observation. In this way data were collected on the scent marking rates, distance travelled within, time spent within, feeding rates, and visit frequency for each hectare in each night. The two latter parameters were however not considered for analysis during this study.

As behavioural data normally violate many of the assumptions of parametric statistical tests (Martin & Bateson 1986), all analyses were done using non-parametric methods as detailed in Siegel (1956), Siegel & Castellan (1988), and. Sokal & Rohlf (1981). The most commonly used statistical techniques were the chi-squared test, Kruskal Wallis one-way ANOVA, Mann Whitney U-test, Spearman rank correlation, and Wilcoxon signed ranks test. Unless otherwise stated all tests were two-tailed. In the case of the Mann Whitney U, and Wilcoxon signed ranks-test Z scores are displayed corrected for ties.

CHAPTER 3

ANATOMY AND HISTOLOGY OF THE ANAL POUCH AND PENILE PAD OF THE AARDWOLF

INTRODUCTION

Aardwolves maintain territories and may advertise their reproductive condition by means of scent marking (pasting) with their anal pouch (Kruuk & Sands 1972; Richardson 1987b, 1991). A small amount of secretion made up of a complex mixture of fatty acids and their esters (Apps *et al.* 1989) is smeared onto grass stalks (Kruuk & Sands 1972). The grass stalk may also be covered with secretion from an additional cluster of sebaceous glands (Flower 1869; Richardson 1985) between the penis and testes. Due to its proximity to the male penis it is hereafter referred to as the penile pad (Fig. 3.1). The anal pouch is characteristic of all the Hyaenidae. While in the striped and spotted hyaenas the penile pad has not been reported (Rieger 1981; pers.comm., H. Kruuk[*]), it is present in both males and females in the brown hyaena (pers.comm., M.D.Anderson[†], M.G.L.Mills[‡]; pers. obs.).

Flower (1869) has given an accurate description of the anatomy of the aardwolf anal pouch which is hereafter repeated in order to expand on it in the results (measurements in inches were replaced by measures in millimetres): The wide transverse follicle, or pouch, lies immediately above the anus sharing with it a common external aperture (Fig 3.1). The pouch is lined by a soft thin membrane of greenish colour, studded over with minute orifices, each in the centre of a small papilla. The pouch is 38 mm in width and 26 mm deep and its walls are glandular and six millimetres thick. Some of the longitudinal bands of muscular fibres from the rectum pass over the pouch and are inserted into the skin above it. Circular fibres pass around it, enclosing the pouch and anus in a common sphincter. On each side, about 15 mm from its lateral margins of the pouch, is an aperture large enough to admit an ordinary-sized probe to the oval shaped lateral glandular sacs (length = 45 mm, width = 25 mm). These thin-walled sacs are encased in an indistinct layer of muscular fibres and lax cellular tissue and connected each with the anal pouch by a six millimetre pedicle.

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Figure 3.1 Sexual organs, anal pouch and penile pad of an adult male aardwolf. (a) partially sheathed penis; (b) active penile pad; (c) testes; (d) anus; (e) anal pouch. Photograph by P.R.K. Richardson.

In the same account Flower (1869) described the penile pad as well: The skin covering the under surface of the posterior part of the penis, immediately in front of the scrotum (Fig. 3.1) is raised for a space of 30 mm in length and 25 mm wide, by a pair of oblong clusters of yellowish sebaceous glands, placed close to the middle line, but with a narrow non-glandular interval between them (Flower 1869).

During the anal pouch pasting an aardwolf bends a grass stalk forward by walking over it, sometimes lifting one fore-leg and turning slightly as it does so. It continues to move forward until the base of the grass comes to lie between its hind legs and the stalk runs forward under its belly. Then the aardwolf, with its tail vertical in the air and the back legs slightly bent, depending on the length of the grass stalk, extrudes its anal pouch (Fig. 1.7; Fig. 3.2a), quickly feels for the grass stalk, and upon sensing the stalk moves forward, pulling the posterior surface of the muscular wall of the everted anal pouch along the grass stalk, at the same time retracting it.

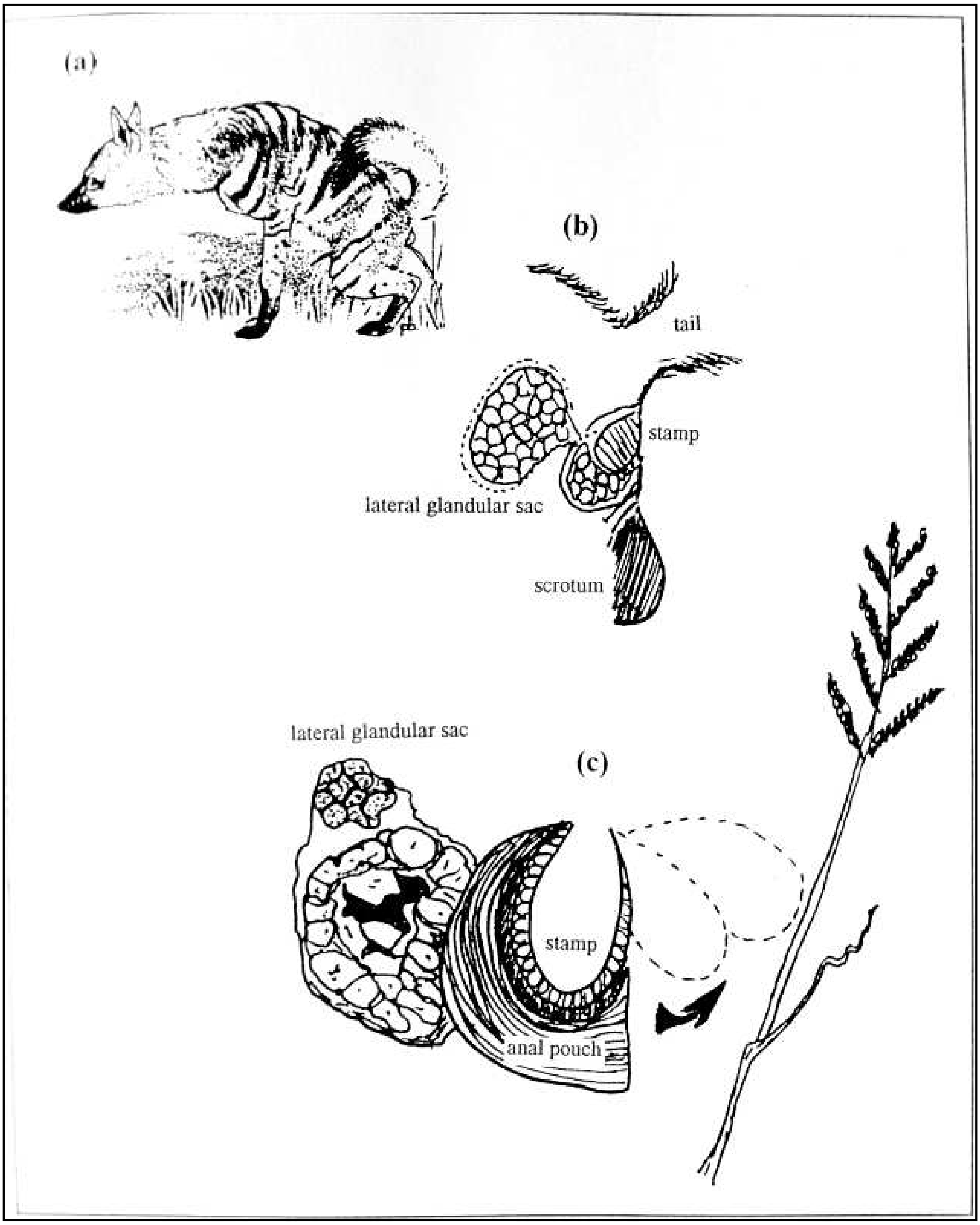

Figure 3.2 Anatomy of the anal pouch of the aardwolf. (a) aardwolf lifting tail while scent marking; (b) cross section of aardwolf hindquarters showing position of lateral glandular sacs and anal pouch with stamp-like surface of posterior fold; (c) enlarged cross-section showing movement of cornified fold out of the anal pouch to apply secretion onto grass stalk and cross-section through lateral sac with lobules and central cavity. (a) after Macdonald 1985, (b) & (c) by Tania Anderson.

A small amount of fatty secretion is smeared on the stalk (Kruuk & Sands 1972; Richardson 1985). This process normally takes from one to three seconds to complete. If the mark is an overmark aardwolves exert special care and the pasting procedure may take up to five seconds.

Though numerous studies have concentrated on the scent- marking strategies of the various members of the Hyaenidae (Kruuk 1972, 1976; Kruuk & Sands 1972; Mills *et al.* 1980; Mills 1990; Richardson 1991) less attention has been given to the anatomy and in particular the histology of their scent producing glands (Flower 1869; Schaffer 1940; Matthews 1939; Ewer 1973; Mills *et al.* 1980, Macdonald 1985). As part of a comprehensive long-term study of scent marking in the aardwolf the anatomy, histology and consequently the phylogeny of the scent producing structures was examined.

MATERIALS AND METHODS

The colours of freshly deposited scent marks and the colours of secretions of immobilised aardwolves were recorded throughout the study (general methodology).

A freshly road-killed female aardwolf was picked up on the 17th March 1993 and a male aardwolf on the 21st June 1993 in an area east of the study site between Kimberley and Perdeberg. The female was a juvenile of about seven months and the male was an adult of approximately three years, judging from tooth-wear (Richardson 1985). In both animals the anal pouch was excised, and additionally the penile pad in the male, and tissue samples were fixed for a week in 10% phosphate buffered formaldehyde solution. Pieces from various parts of the pouch and penile pad of the glands were dehydrated with ethanol, embedded in paraplast and sections 2 µm thick were cut on a microtome. Paraffin sections and cryocuts were stained according to Table 3.2 and examined with an Aristoplan, Leica light microscope. Representative areas of the glands were stained with haematoxylin and eosin and photographed with Kodak Ektachrome 64 film at magnifications of 4x, 40x and 100x.

RESULTS

Colours of Secretion

Colours on grass stalks: The secretion colour of marks examined when freshly deposited onto grass stalks (n ≈ 1 000) differed between individuals and sexes. The changes in colours depending on age and sex of the producing aardwolf are summarised in Table 3.1. Generally the amount of secretion deposited increased from a thin film in young cubs to small pieces of secretion in 4 - 9 months old cubs. The largest secretion deposits were produced by adults. When freshly deposited secretion was examined on grass stalks through the course of the night some adult females' secretion changed from dark brown to greenish - yellow. Variation in secretion colour due to season was also observed. Adult male secretion seemed to become more black with a bluish sheen during the mating season. Scent marks by adult females were often separated in an upper bright orange secretion piece above a second brownish piece during this time. After a few hours of exposure to the air and sun all scent mark secretions turn black from oxidisation (Richardson 1985; Apps *et al.* 1989; pers. obs.).

Table 3.1 Colours of fresh anal pouch secretion on grass stalks deposited by aardwolves of different ages and sex.

AGE	COLOUR MALE	 FEMALE
7 weeks	yellowish translucent	yellowish translucent
4 -5 months	orange - light brown	orange - light brown
9 months	light brown - dark brown	orange, greenish, light brown
Adult	dark brown - bluish black	orange, greenish, light brown to dark brown

Sometimes a thin, barely visible smear of brown secretion was seen on the grass stalks marked by a male, about 60 mm above the prominent anal pouch secretion. This may have stemmed from the active penile pad, when the stalk was run along the central grove during scent marking.

Colours in anal pouch: The dead young female had small quantities of an orange coloured secretion whilst the adult male had a large amount of black secretion present in his anal pouch. The penile pad of the male was producing a reddish-brown secretion. When examining anal pouches of aardwolves immobilised for radio-collaring, adult males had mainly dark brown to bluish black secretion. Adult females' pouches contained secretion in colour from bright orange, greenish to light brown. When a hand raised female aardwolf started to scent mark smooth objects for the first time at seven weeks with her anal pouch the secretion in her anal pouch was yellowish-translucent.

Anatomy of Scent Pouch and Penile Pad

Anal Pouch: The following descriptions are made from observation of two dissected aardwolves and supplement description in the introduction after Flower (1869): The anal pouch of the aardwolf is of epidermal origin and through muscle action it can be everted and retracted again. The dorsal part of the pouch is turned outwards, its hairless cornified surface acting like a stamp (Fig. 3.2c). The accumulated mixture of sebaceous and apocrine secretions is deposited on the grass stalk. The "stamp" surface is round and measures about 30 mm across when extruded for wiping. When the stamp surface is retracted again it gets daubed anew with secretion. In this resting position most of the secretions in the pouch get mixed and are stored ready for the next application (Fig. 3.2b).

Penile pad: The penile pad is about 10 mm high with circular muscular fibres passing around the furred base, enclosing the pad in a sphincter. In the centre of the non-glandular longitudinal central grove of the pad is a thick, bristle-like hair. The surface with the central hair is covered, when active, by dark-brown to reddish secretion of higher viscosity than the anal pouch secretion. Flower (1869) must have measured the width of the pad as 25 mm when it was active for scent deposition, for when inactive it was just 15 mm wide and the surface was dry and clean. It was not possible to observe the deposition of secretion from the pad unless one would have lain under the aardwolf in the process of pasting. Thus how exactly secretion is applied on grass or possibly a female’s back during copulation is open to speculation. Penile pads were seen to be differentially active in the same immobilised males at different times of the year (n = 7; Table 3.2). During the same month of year pads of different males were differentially active.

Table 3.2 Secretory activity of the penile pad in immobilised aardwolf males during the non-mating season. ■ = active, □ = inactive.

Name	November	January	February
Orion	□	□	
Eclipse	□		■
Joseph		■	
Eros			□
Luca			□

Histology of the Anal Pouch and Lateral Glandular Sacs

When making a section through the thick wall of the pouch one can see numerous yellowish-white sebaceous glands close to the epidermal wall surface and below them blue-black apocrine glands (Fig. 3.3). The histology of the sebaceous glands is best described when sectioning the lateral glandular sacs, containing exclusively sebaceous and no apocrine glands. The sacs have a large cavity within and covered around the cavity a large number of flattened glandular bodies, or lobules, of a brilliant orange colour separated from each other by a thin layer of connective tissue (Fig. 3.2c; Fig. 3.4). When making a transverse section each of these cauliflower-like lobules consists of a large number of acini clustered round a central cavity acting as a reservoir, which communicates by a minute aperture with the cavity of the large sac. This cavity is entirely filled with a fatty sebaceous secretion, bright orange in colour and with the consistency of cream-cheese. From the large central cavity of the paired lateral sacs the secretion is led via the pedicles and through the orifices into the anal pouch where it mixes with apocrine secretion. In the wall of the anal pouch the minute orifices from the lobule cavities open directly onto the epidermis of the anal pouch surface. The mode of secretion of the acini is by holocrine decomposition of their cells (Fig. 3.5).

Apocrine glands are solely present in the walls of the anal pouch. Underlying the lobules of the sebaceous glands are numerous well-vascularised strongly branched-out tubular apocrine glands (Fig. 3.3). Deeply stained secretory granules produce decapitation secretion into the lumen of the acini (Fig. 3.6). The secretion is transported from the branched clusters of the tubular gland into a straight intra-epidermal duct, in between lobules of the sebaceous glands, to the surface of the anal pouch epidermis. Both types of glands, sebaceous and apocrine, originate from the primary epithelial germ.

Histology of the Penile Pad

When making a cross-section through the two halves of the penile pad exactly the same arrangement of sebaceous and apocrine glands relative to its epidermal surface can be seen as described for the anal pouch wall (Fig. 3.7). Two different positions of the penile pad deforming the glandular mass composed of sebaceous and apocrine glands, can be hypothesised (Fig. 3.8a = rest, Fig. 3.8b = active). When the penile pad is actively secreting the lips are pulled back, ready to deposit secretion. In the process of pulling back the lips secretion will be discharged from the glands to the surface of the pad.

Histochemical Reaction of Tissues

Tissue from the male aardwolf anal pouch and penile pad was exposed to various histochemical reactions and the results are displayed in Table 3.3.

Table 3.3 The histochemical reaction of tissues from the aardwolf anal pouch and penile pad. - no reaction; + to +++ increasingly strong reaction.

Substance	Reaction (Pearse 1968)	Section	Sebaceous gland	Apocrine gland
Free lipids	Oil Red	Frozen	+++	-
Polysaccharides	Periodic Acid/Schiff	Paraffin	-	++
Acid muco-polisaccharides	Alcian Blue	Paraffin	-	-
Lipo-fuchsin	Schmorl	Paraffin	-	+
Mucus	Mucikarmin	Paraffin	-	-
Iron	Perle's method	Paraffin	-	+++ (pigment)

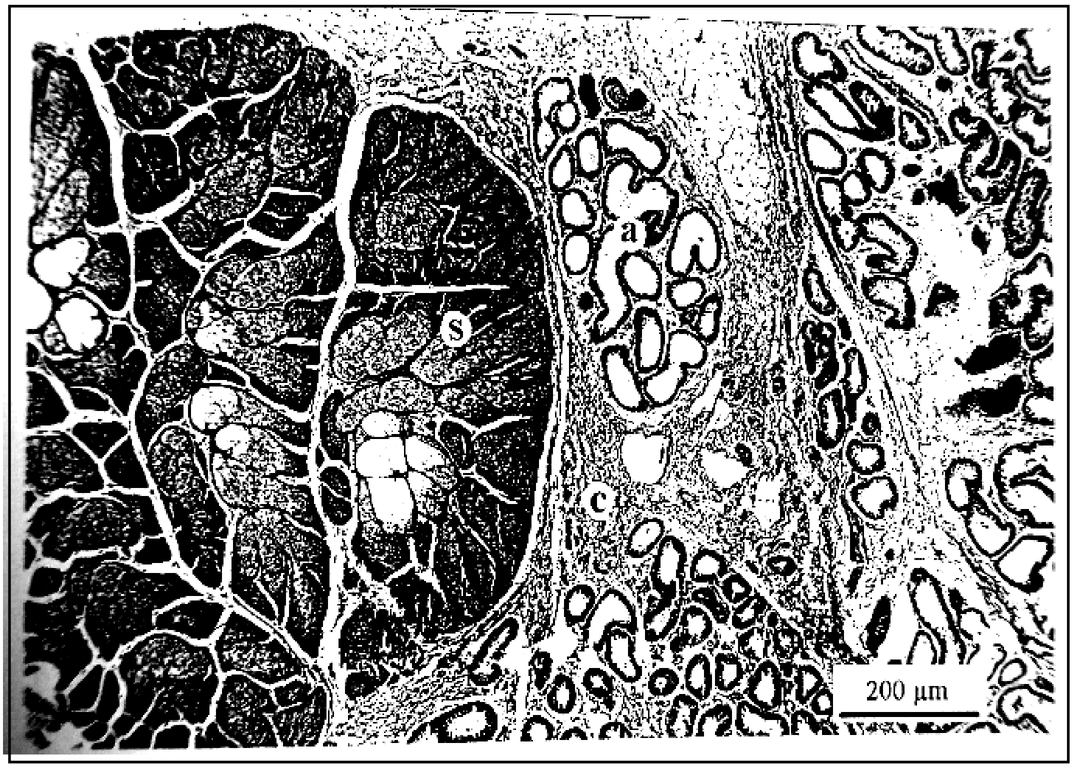

Figure 3.3 Histological cross-section of the wall of the anal pouch showing s = sebaceous holocrine glands, a = apocrine glands, c = connective tissue.

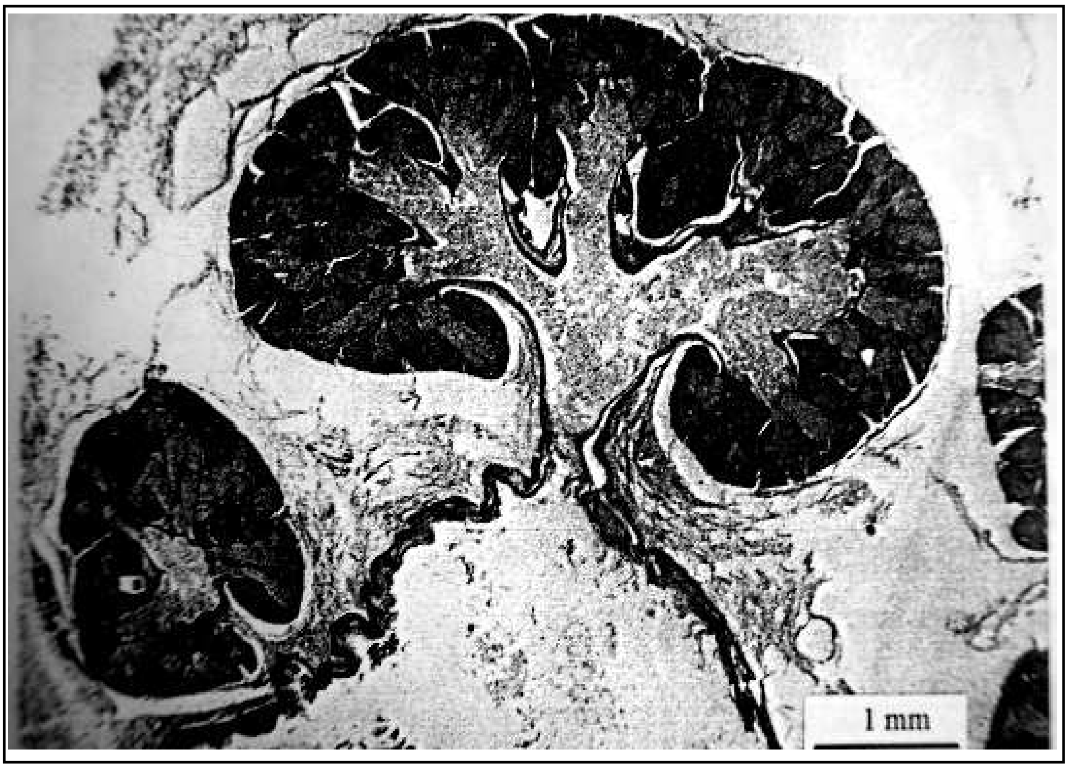

Figure 3.4 Transverse section of lateral sac lobule showing acini secreting sebaceous secretion into cavity.

Figure 3.5 Transverse-section detail of anal pouch showing holocrine secretion through decomposition of acinus gland cells.

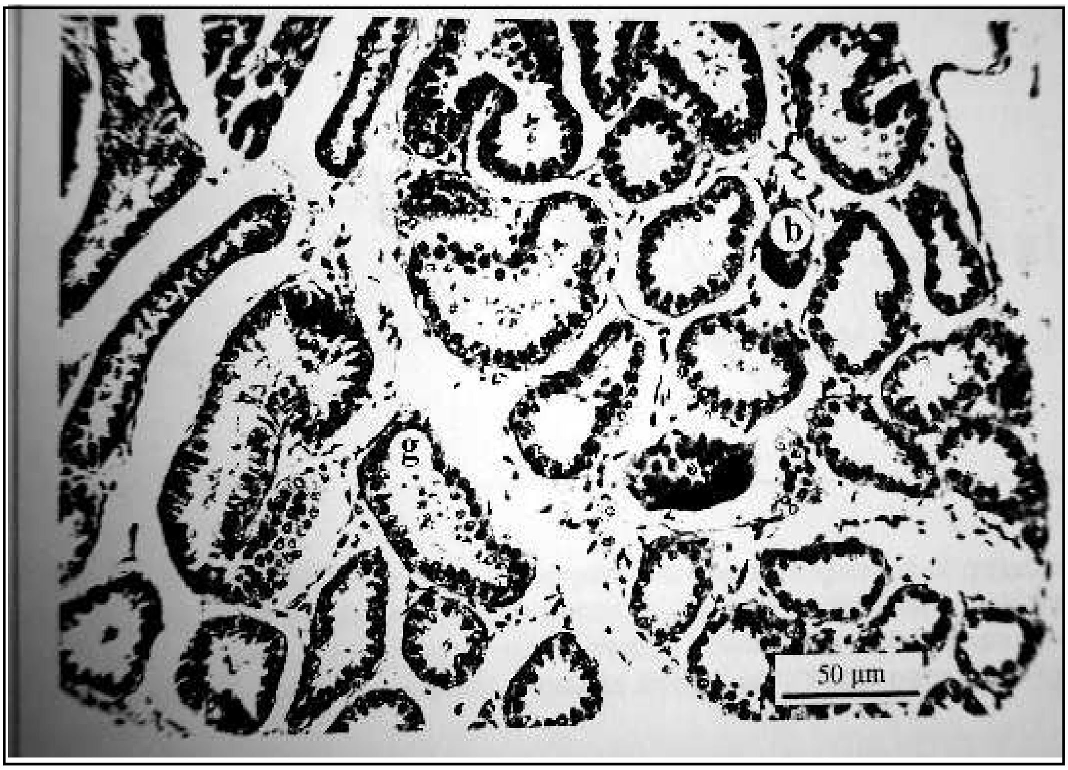

Figure 3.6 Cross-section detail of apocrine glands from anal pouch. Deeply stained secretory granules =g, produce decapitation secretion into the lumen. b = blood vessels

Figure 3.7 Cross-section through penile pad showing sebaceous gland (s) lobules embedded in connective tissue and below glandular tubes from branches of tubular apocrine glands (a). Also visible are parts of the stiff central hair-bristle (h) opening on the epidermis (e)

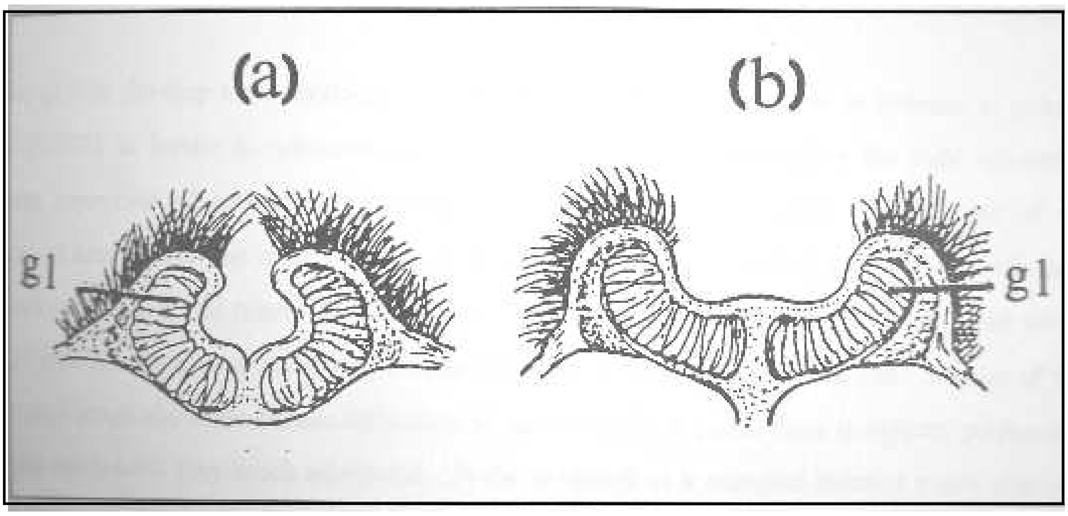

Figure 3.8 Cross-section through the penile pad showing arrangement of glandular mass of lobules of sebaceous glands and tubular apocrine glands. Hypothesised positions of pad during rest and in active position (a) in rest = inactive position. (b) active position with lips pulled back, ready to deposit secretion. Modified from Ewer (1973) page 93, Fig 3.8 for *Arctictis* gland.

DISCUSSION

Aardwolves are able to deposit scent from two separate scent producing structures, the anal pouch and the penile pad. The large amount of sebaceous secretion that is stored in the lateral sacs warrants that secretion availability will not become a limiting factor, since a relatively large sized secretion deposited by the anal pouch onto a grass stalk weighs about 0.002 g (Chapter 5) only. While assuming a maximum deposition of 500-600 pastes per night (Richardson 1985; Chapter 8) this would require about one gram of secretion. Judging by the size of the lateral glandular sacs I estimate that an adult male aardwolf would have about 10 g of sebaceous secretion in storage.

Through the muscle action of everting and retracting the anal pouch sebaceous and apocrine secretions are discharged from the lateral sacs and the pouch walls. These presumably mix inside the epidermal pouch during walking to form the secretion that is wiped onto grass stalks. The different colours of secretion on grass stalks are presumably due to the different ratios and stages of mixing. The bluish-black secretion of an adult male is a result of the high percentage of the accumulations of lipo-fuchsin, a common metabolite of apocrine tissue (Mills *et al.* 1980) in the secretion. Females seem to produce less apocrine scent gland secretion than males, so the lighter-coloured fatty sebaceous secretion is more prominent, giving yellow-orange to greenish, light to dark brown colours. The deposition by females during the mating season of two spatially separated secretions of different colours might serve an additional visual function during this time of the year. It is probably due to the incomplete mixing of the sebaceous fatty gland secretion, orange in colour when fresh, and the black apocrine secretion.

Apocrine glands develop their secretory portion and thus become functional in humans at puberty only (Pinkus (1972) in Lever & Schaumburg-Lever 1975). This could explain the light coloured solely sebaceous secretion of juvenile aardwolves, lacking apparently the dark lipo-fuchsins of apocrine secretion. Later in life the mixed secretion becomes increasingly thicker and darker with increasing productivity of both gland types. Up to the age of four to five months male and female cub secretion is of similar colour. At nine months of age male subadults have darker secretion than females of the same age. At that stage the male-female difference in apocrine gland production is already pronounced and remains as such until they reach adulthood. In the aardwolf as a seasonal breeder testes size was seen to increase during the mating season (M.D. Anderson [§], P.R.K. Richardson [**] pers.comm.; pers. obs.). The darker blue-black marking secretion of adult males during this same time could be a result of increased apocrine gland activity. The production of scent marking chemicals is likely to be related to the hormonal status of an individual (Ebling 1977). In addition the size of testes has been shown to correlate positively with the volume of the snout scent glands (morrillo) together with higher rates of scent marking and reproductive success of dominant males in capybaras (Herrera 1986, 1992).

The reactions of the stained microtome cuts for the sebaceous glands of the aardwolf (Table 3.3) and the brown hyaena (Mills *et al.* 1980) anal pouch are similar. Differences in the reaction are mainly due to differences in strength of reaction. In the apocrine gland tissue of the aardwolf no free lipids were traceable while in the brown hyaena there was a slight reaction. For acid muco-polisacchides there was no reaction in the aardwolf apocrine gland while in the brown hyaena there was good evidence. An additional test for mucus was also negative in the aardwolf. The reaction on lipo-fuchsin was much less in the aardwolf than in the brown hyaena, staining mainly the secretory granules in the former. As one would expect in two different species the composition of apocrine secretion of aardwolves and brown hyaenas are slightly different (Mills *et al.* 1980; Apps *et al.* 1989).

The anatomy and use of the anal pouch of the aardwolf, for scent marking, compares well with that of the spotted hyaena (Flower 1869; Matthews 1939; Kruuk & Sands 1972; Macdonald 1985; M. Gorman in Mills 1990). In the striped hyaena the pouch wall glands, which I assume to be sebaceous, are aggregated to form on either side a pair of auxiliary gland masses opening independently into the pouch by a number of scattered apertures (Pocock 1916). In the brown hyaena the auxiliary glands are even further differentiated (Murie 1871, Mills *et al.* 1980). The pouch in itself is differentiated into an upper and when everted outer bilobed section on which the whitish secretion of the large sebaceous glands

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gathers, and on each side of which lies an area where the black secretions of apocrine glands accumulate (Murie 1871, Mills *et al.* 1980).

In contrast to the function and anatomy of the anal pouches the sebaceous gland clusters of the penile pad have received little attention (Flower 1869, Richardson 1985; Koehler & Richardson 1990). Its presence in the male aardwolf only and in both female and male brown hyaena (M.G.L.Mills pers.comm.[††], pers. obs.) but absence in the other two hyaena species (H.Kruuk pers. comm.[‡‡] Wells 1968) raises further questions. Presently we have no clear explanation for the function of the penile pad in aardwolves. Since it is only present in males it might accomplish a function during the mating season, possibly for marking the genitals of the female during copulation. This secretion could serve to inform other competing males that this female has already copulated, and the sniffer could possibly even identify the male that copulated before by the scent (Chapter 9). However it was seen to be active as well in some males outside the mating season, but not in others and thus could not be linked to a particular season. However, as no males were immobilised during the mating season, these data do not preclude the possibility that it is presumably related to mating. Alternatively its function could be in adding a further mark to grass stalks supplementary to that of the anal pouch. Likewise in the brown hyaena it was seen to grow larger (fatter) in some animals than others, or even in the same animal at different times (M.G.L Mills, pers.comm.).

The penile pad’s histology in the aardwolf reveals that the sebaceous and apocrine glands are essentially arranged as in the wall of the anal pouch. The function of the bristle-like hair in the central groove is unknown although it can be assumed that it serves a sensory function, possibly while feeling for the grass stalk to be marked. Although actual deposition of secretion could not be witnessed due to its hidden location under the belly amidst fur, the thin dark brown smears on grass stalks above the actual fatty secretion from the anal pouch, could have stemmed from the pad. The expulsion of the secretion could function as in the relatively simple perineal glands of the Paradoxurinae (Pocock 1915a,b). As the lips of the pad, acting as a form of storage pocket for the secretion, are pulled back by muscles the pressure from the pad’s deformation exposes the secretion of both gland types to the pad surface, where it is wiped off.

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The penile pad might be a primitive scent producing structure retained from viverrid-like ancestors of the aardwolf (Werdelin & Solounias 1991; Richardson & Levitan 1994). Otherwise it could be a recently developed structure that is also present in both sexes in the brown hyaena.

CHAPTER 4

ONTOGENY OF SCENT MARKING

INTRODUCTION

The importance of fully understanding behavioural development cannot be emphasised too strongly (Bekoff 1989). Without detailed knowledge of how the behaviour of individuals unfolds throughout their lives, we can only guess at the supposed adaptive significance of various ontogenetic patterns and how they may be related to the immediate situation in which a young animal finds itself and its later reproductive activities (Tinbergen 1963; Bekoff 1989). Unfortunately, there are still only scanty data on the development of behaviour for most members of the Carnivora (Bekoff 1989). A few studies of the Hyaenidae contain developmental data of various degrees of sophistication, mostly for the spotted hyaena (Golding 1969; Kruuk 1972; Frank 1986a, b; Glickman *et al.* 1987; Henschel & Skinner 1987; Mills 1984, 1985, 1989; Mills & Gorman 1987; Woodmansee *et al.* 1991) and the brown hyaena (Owens & Owens 1978, 1979, 1984; Mills 1983, 1984, 1989). Specific information on ontogeny of scent marking in the wild is limited to recording the first observation of the motor pattern of squatting and wiping the anal pouch region over a grass stalk, and the onset of secretion of the paste in the spotted (Kruuk 1972) and the brown hyaena (Owens & Owens 1979; Mills 1990). No sex differences in pasting frequencies of prepubertal spotted hyaenas have been found by Mills & Gorman (1987) in the wild and Woodmansee *et al.* (1991) in a captive colony.

In this chapter I will try to document the development of the scent marking motor patterns, the onset of secretion by the anal pouch, and the spatial and temporal distribution of paste marking in young aardwolves. The development of scent marking will be described from the time when it first appears until the dispersal of subadults. Further questions asked were: (I) Is there individual variation in scent marking frequencies and when is it shown for the first time? (II) Are differences in marking frequencies of males and females (Chapter 5) already present in juvenile aardwolves? (III) Up to what age do cubs remain in their parents' territory and what is their marking behaviour until they leave it?

METHODS

Observations on cubs and subadults were made sporadically, often whilst waiting at dens for the focal adult to leave. When adult males started guarding the cubs it was recorded when cubs were first seen above ground and what behaviour patterns they displayed. Most of the information on young cubs was collected from four litters during two summer seasons. A total of 30 cubs and sub-adult aardwolves were observed during the study period from May 1991 - August 1993. Due to early mortality just 24 were named and 13 cubs were immobilised, earmarked, and sexed when about four to five months old. These were followed as focal animals sporadically and for various time periods until they dispersed. Their scent marking behaviours were recorded and later analysed together with their plotted movements. Mark-rates were calculated from the total distance the focal cub was followed divided by the number of marks deposited and expressed as Marks / 100 m walked. It was always recorded if the cubs were alone or in the company of adults or other cubs. Because of small sample sizes for individual cubs the mark-rates of the same individual on different nights were used for statistical testing.

Observations were also made on a female aardwolf who was about one week old when her mother was killed. She was handraised and kept at home by Mark and Tania Anderson until 9.5 months old.

RESULTS

One - Two Month old Cubs

Cubs of five litters were first observed above ground, but still close to the entrance of the breeding den at about one month old. At this age they started to play around the den entrance and tried to sniff the guarding male around his anal pouch, face, neck and body. By six to seven weeks the first sniffing and overmarking movements on roots and grass stalks within five metres of the den, were observed. These behaviours were stimulated when the attending male marked close to the den, closely observed by the cubs which approached, sniffed and tried to overmark his scent mark. The motor pattern of squatting over the object to be marked, as well as their wiping movement was still awkward, and cubs often stumbled in the process. At about seven weeks the handraised female aardwolf started to scent mark smooth objects on the ground such as the rim of a glass. Her anal pouch started to produce a thin yellowish translucent secretion which smelled slightly cheesy but not nearly as powerful as the secretion of adult aardwolves.

Three - Four Months

During this period the cubs interest in scent marks increased further. From two months of age on they first tried to feed on *Trinervitermes* when within 50 m of the den and in attendance of a parent. On one occasion three cubs who were two and a half months old each tried to overmark the male's scent mark up to three times in a row. With increasing age their excursions together with one parent extended over longer periods and distances of up to 300 m from the den. They also started to visit middens which lay further away from the breeding den. By the end of this period cubs started to foray by themselves or returned alone to the den after accompanying an adult on a feeding trip.

Hand-raised cub: The female cub showed great interest in the scent marks of wild aardwolves when taken for walks in the veld by a human caretaker. She carefully sniffed scent marks for up to two minutes and tried to overmark them repeatedly. Little secretion was deposited and she had difficulties in feeling for and hitting the grass stalk while bending it between her hindlegs. Interestingly for an aardwolf she alternately sniffed the pastings with each nostril.

Five - Nine Months

Cubs started to mark on their own increasingly from five months age on. By this age cubs foraged throughout the territory, but not yet beyond its boundaries, periodically returning to the den. This is interesting as it suggests that cubs have learnt their territorial borders. They were normally weaned with the completion of their fourth month (Richardson 1985).

Cubs follow parents: When an adult left the den between one and four cubs followed it for various distances and time periods and tried to overmark their scent marks (Table 4.1). The cubs' mark-rates were significantly correlated with the mark-rates of the adults they were following (Spearman Correlation coefficient; $r_s = 0.583$; $p < 0.05$; n= 16 nights; Table 4.1).

Later the mark-rates of both sexes of cubs were plotted against the total distance they followed male and female adults during one evening (Fig. 4.1). There was no data for female cubs following male adults and female cubs did not scent mark when walking alone. From the data displayed three behavioural patterns, independent of the distance followed, were visible (encircled by ellipses):

(a) Cubs of both sexes marked at similar low rates when following female adults (range: 0.12-0.34 mks/100m; Mann-Whitney U-test; Z = -0.37, n = 9, p>0.05; Table 4.1).

(b) The mark-rate was always higher when male cubs followed male adults than when following female adults (MWU-test: Z = -2.65, n = 11, p<0.01), though the range in mark-rate was much greater. For distances of over 1.2 km high mark-rates were reached with up to 30 overmarks thus resembling the mark-rate of the adult male they were following.

(c) Once male cubs were more than nine months old they marked at a rates resembling those of adult males (MWU-test: Z = -0.97, n = 16 nights, p>0.05; Table 4.2; Fig. 4.2a). The mark-rate of male cubs marking on their own is plotted and encircled by an ellipse in Fig. 4.1. In contrast nine month old female cubs very rarely marked when on their own.

Often the adult paused to look back for the cub when it fell back more than 30 metres. They waited until the cub caught them up at a run, having spent time trying to find and overmark all the adult's marks. A cub took several times as long as an adult to overmark a scent mark, often in excess of 10 seconds. Up to the age of eight months the secretion left by a cub was a barely visible smear, often detectable only through smell by the observer. At this age the adult male sometimes showed aggression towards his sons trying to follow him, grabbing them by the ears and neck while shaking them. Male cubs acted submissively but in spite of these punishments they still continued to follow their father and overmarked at up to nine months of age. After this time they ceased to scent mark completely. At nine months most grass stalks marked by male cubs showed some orange secretion. Sometimes they had to give up trying to overmark the grass stalk with the adult secretion in order to remain in contact with the adult.

Table 4.1 Incidences when cubs followed adults and overmarked their scent marks. Identity of cubs corresponds to Fig. 4.1.

Cub sex & ID	Age (months)	Adult sex	Time (min)	Distance (Km)	Adult # of marks	Adult mks/100m	Cub # of marks	Cub mks/100m
F1	4.5	F	112	2.52	12	0.48	4	0.19
F2	5	F	26	0.80	3	0.37	2	0.25
F3	5.5	F	134	1.75	6	0.34	3	0.17
F4	5.5	F	60	1.02	11	1.10	2	0.20
M1	5	M	13	0.24	2	0.82	2	0.82
M2	5.5	F	112	2.50	23	1.02	5	0.12
M2	5.5	M	21	0.41	19	4.75	3	0.73
M3	5.5	F	134	1.74	6	0.34	6	0.34
M3	5.5	F	148	2.25	33	1.32	3	0.22
M4	5.5	F	85	1.20	10	0.83	3	0.25
M3	8	M	35	1.20	41	3.42	30	2.50
M3	8	M	13	0.60	22	3.67	11	1.83
M3	8.5	M	20	0.85	22	2.59	20	2.35
M1	9	M	15	0.42	5	1.19	5	1.19
M1	9	M	17	0.65	19	2.92	3	0.46
F5	9	F	27	1.00	18	1.80	3	0.30
Totals or average	6.41		1002	19.62	269	1.80	117	0.85

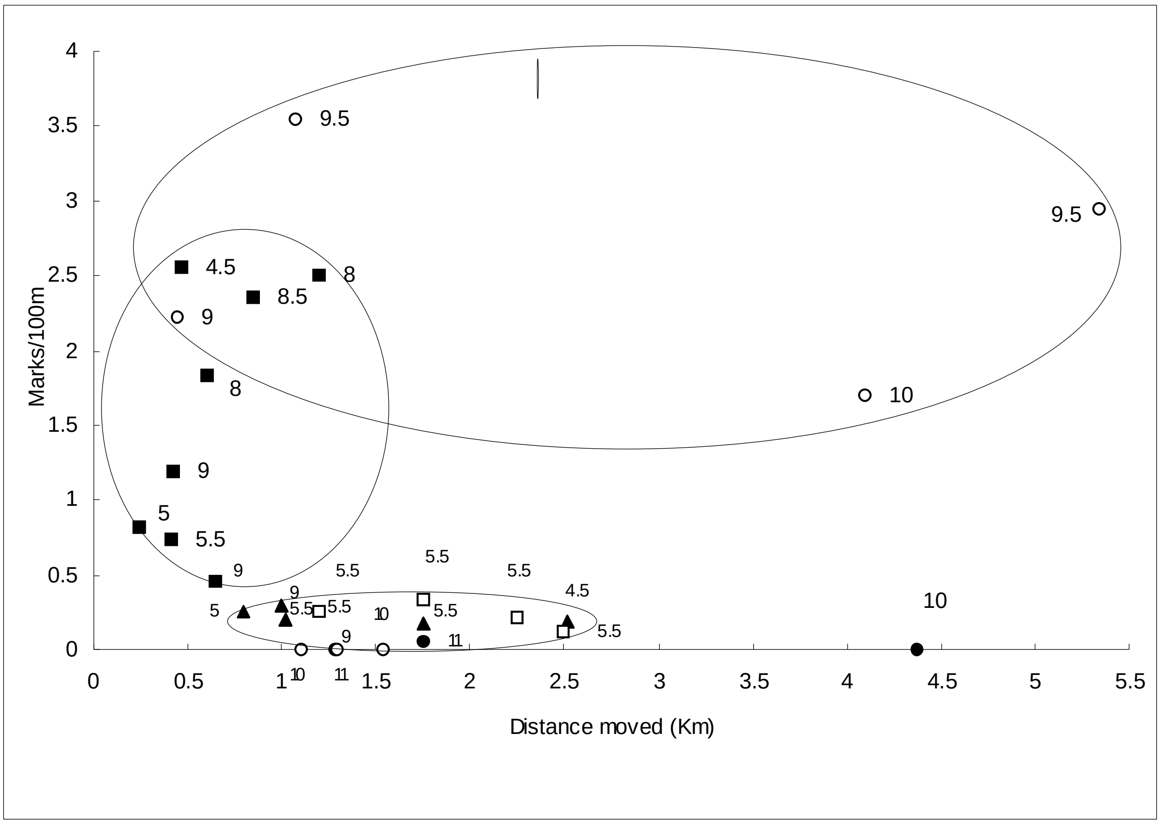

Figure 4.1 Mark-rates (mks / 100 m moved) of male and female cubs when following their male or female parents and trying to overmark their scent marks or when travelling and marking alone (Table 4.1 & 4.2). Their age (4.5 - 11 months) is displayed next to the symbols. ■ = male cub follows male adult; □ = male cub follows female adult; ▲= female follows female adult; ○ = male cub marking alone, ● = female cub marking alone.

Table 4.2 Marking rates of solitary cubs older than 9 months.

Cub - sex & ID	Age (months)	Time (min)	Distance (Km)	# of marks	mks/100m
M1	10	43	1.10	0	0
M1	10.5	129	1.54	0	0
M1	11	45	1.29	0	0
M2	9	26	0.45	10	2.22
M3	10	241	4.12	71	1.70
M5	9.5	105	5.34	157	2.94
M5	9.5	52	1.07	38	3.55
M5	11	372	5.69	0	0
F1	9	32	1.29	0	0
F2	10	181	4.37	0	0
F2	10.5	89	1.75	1	0.06
Total or Average Males	10.2	1013	20.60	276	1.30
Total or Average Females	9.83	302	7.41	1	0.02

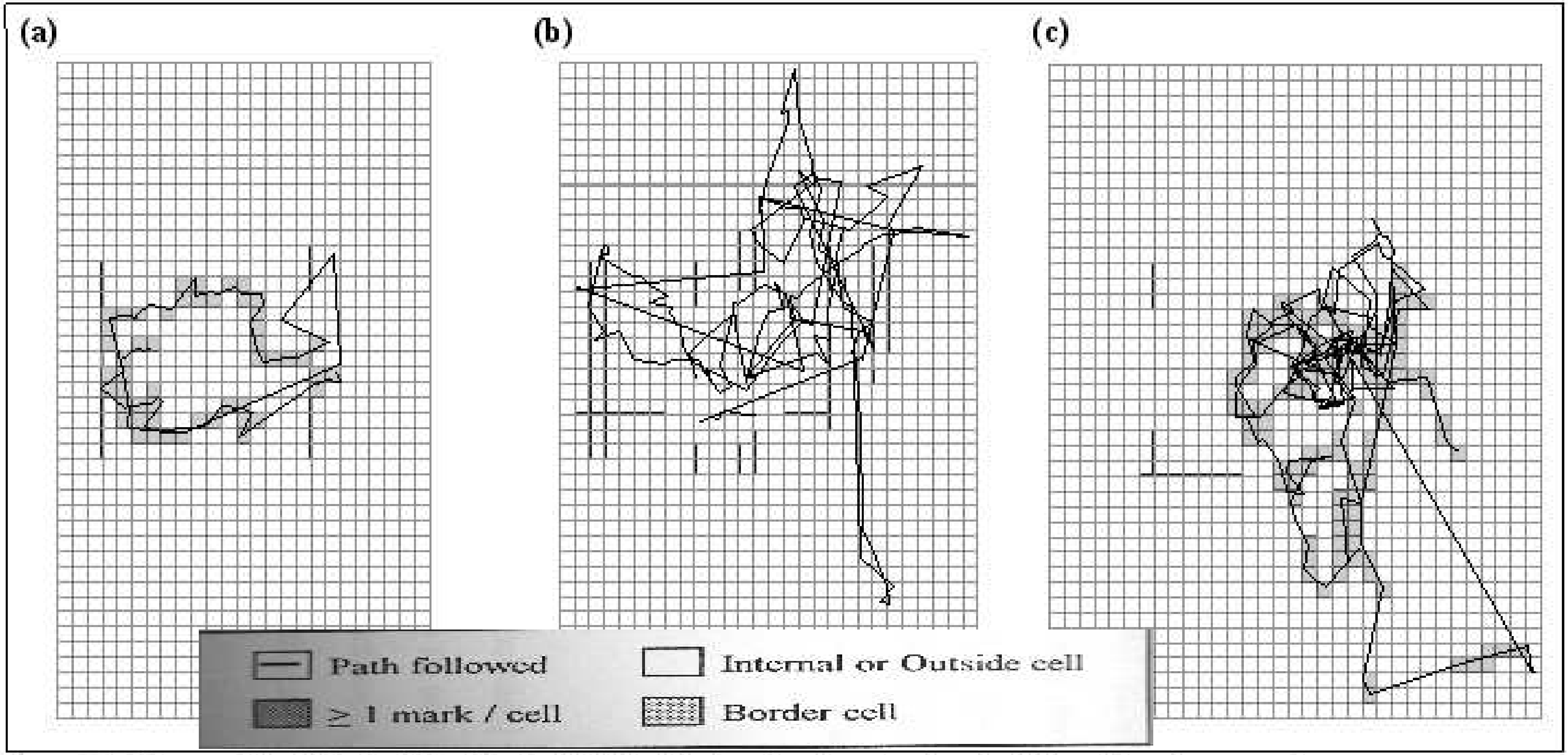

Figure 4.2 Movements (solid line) of M5 relative to his father's territory borders. Scent marked 1-ha cells and movements.
a) when 9.5 months old in August 1991. Followed for 2:45 hrs, 7.0 km and left 195 scent marks.
b) when 11 - 17 months old. Movements without scent marking in non-mating season September 1991 - March 1992. Followed for 20:05 hrs, 16.3 km , and did not leave any scent marks.
c) when 18 - 21 months old. From the start of winter 1992 (mating season) when he started to mark again until he left the area when female aardwolves came into oestrus. Followed for 25:10 hrs, 35.7 km, and left 500 scent marks until he disappeared with 21 months of age.

Male -female differences: When the sex of the cubs was known from four to five months of age differences in marking effort were discernible between male and female cubs, females always marking less (Table 4.1; MWU-test: $Z = -2.15$, $n = 16$, $p<0.05$) and very rarely on their own.

Individual differences: Three male cubs, of two litters raised jointly by the old female Electra and her adult daughter Echo, showed differences in their marking effort. Two male cubs (M2 &M3 of Table 4.1, 4.2) seemed to scent mark more diligently, taking great care and longer time to hit the grass stalks marked by the adult. They followed their father more frequently and marked more often on their own than the third male cub (M4). However data were too limited for statistical treatment.

Hand-raised female: At six months the female cub exhibited flehmen repeatedly after prolonged sniffing of wild aardwolves' scent marks and tried to overmark them afterwards, when taken for walks. Her pasting motions were less secure than that of wild cubs of the same age. When followed by the caretaker through the veld at nine months she repeatedly sniffed scent marks of strange wild aardwolves but did not overmark them systematically. In common with wild female cubs her rate of marking seemed to decrease at this age.

10 - 17 Months

By the end of winter when about ten months old, male cubs (subadults) ceased to mark completely. This was probably precipitated by increasing aggression from the adult male as well as the female preparing for new cubs. At this age subadult males were now independent, sleeping separately in their own dens (Table 4.2, see M1 & M5). One female cub (F1) had ceased to mark on her own with nine months already and another (F2) did not leave any scent marks when ten months and older (Table 4.2).

Two male sub-adults (M1 & M5), one radio-collared, were followed when older than 10 months. Most of the other individuals either dispersed or disappeared earlier whilst some could not be followed due to the termination of the study. When 11 months old both subadult males still fed and ranged inside their fathers' territory and were chased and bitten by both their parents when found. When located on 20 nights and followed for a total of 16.3 km for 20 hours the subadult M5 did not scent mark at all until the start of the next winter when 17 months old (Fig. 4.2b). During these months he stayed mainly in the eastern part of his parents' territory, little frequented by them, and also made excursions to the north and south into adjoining territories. By the end of this period he appeared to be fully grown and in good condition.

18 Months - Dispersal

When 18 months old at the onset of winter M5 started to mark again. He marked the eastern part of his parents' territory and the area to the south-east of it. First at low mark-rates (0.22 mks/100m) and then gradually increased his mark-rate over the next 2.5 months to 3.11 mks/100m, at the time when females started to come into oestrus (Fig. 4.2c). At this time he and his father often followed the scent mark trail of the other and overmarked each others scent marks. M5 finally disappeared when he was 21 months old and before actual matings took place. His marking patterns from nine to 21 months of age are summarised in Fig. 4.3.

Figure 4.3 Mark-rates of cub M5 from 9 - 21 months of age.

DISCUSSION

Aardwolf cubs were able to go through the motions of pasting when six to seven weeks old, though their scent glands were still inactive. This is similar to both spotted and brown hyaenas which start pasting when six weeks old (Mills 1990). While the 'black' secretion is already secreted at four months in brown hyaena cubs the 'white' secretion in the brown as well in spotted hyaenas is secreted only when over one year old (Kruuk 1972, Mills 1990). Although increasing amounts of thin secretion were already visible and detectable by smell in aardwolves from seven weeks on, the thick yellowish, sebaceous secretion, seen in adult aardwolves, equivalent to that of the other hyaenas' 'white' paste, was produced only when they were eight to nine months old. What we see here is a gradual thickening of the sebaceous secretion with ripening production of the sebaceous glands. From the previous chapter (Chapter 3) we understand that in males an additional darkening of the scent marking secretion took place which probably coincided with increasing production of dark apocrine secretions. The production of a long-lasting secretion coinciding with the father's first aggression against the cubs could indicate the onset of sexual maturity.

The cubs' initially low mark-rates, and the fact that they seldom marked on their own is probably due to physiological and behavioural immaturity (Marchinton *et al.* 1990). It is striking that the cubs adjust their mark-rate to that of the adult they follow; a low mark-rate for females and a higher for males. That juveniles follow their parents, especially male cubs their fathers, for the purpose of overmarking their pasted grass stalks and thus learning how to effectively scent mark has not been recorded in the Hyaenidae before. Another reason for the cubs to follow their parents could be in order to find food easier. In addition it was observed both in captivity (Woodmansee *et al.* 1991) and the wild (Mills & Gorman 1987) that subadult spotted hyaenas' pasting was facilitated by the immediately preceding pasting activities of other hyaenas. The fact that the cubs' marking pattern followed that of the adults may just mean that marking by the parent acted as a stimulus for the cubs to do the same. However that cubs tried to overmark each of their parents' marks diligently, and that they continued to follow them even when the adult moved away rapidly and was not finding food, implies that they do so mainly for learning how to scent mark.

The case of the hand-raised female offers an interesting insight into the importance of practising the scent marking motor pattern and learning from their parents through imitation. Her scent marking movements were more awkward than that of wild cubs of an equivalent age having less opportunity to practice and no parent to imitate. In common with wild female cubs she did not overmark grass stalks repeatedly and mark any more when nine months old whilst walking on her own, followed by the caretaker through the veld.

This practising of the behaviour patterns involved in marking can be compared with some members of the Viverridae. The carnivore family considered to be most closely related to the Hyaenidae (Wayne *et al.* 1989; Werdelin & Solounias 1991). Genets scent marked with the perineal glands, though at low frequencies, at four months of age (Roeder 1984). At 30 days of age the African dwarf mongoose was seen to mark with the cheek glands for the first time, when 40 days it performs the 'leg-lift' type of anal marking and finally the 'hand-stand' anal marking at 60 days (Rasa 1973). The Mustelidae provide more data for comparison. Anal drag was already performed by sexually immature stoats at two and a half months, when they first moved outside the nest (Erlinge *et al.* 1982). Pine marten cubs even started to mark their surroundings at eight weeks, though in attendance of their mother when leaving their nest (Ludwig 1994). When the subcaudal pouches of European badgers less than six months old were examined they contained little or no secretion (Kruuk *et al.* 1984).

Soon after cubs started displaying adult mark-rates and were able to deposit secretion similar to those of adults they stopped marking completely. The cessation of marking at this age, when they were demonstrating both physiological and behavioural maturity for scent marking, could be a result of them being perceived as rivals by the territory holders. Cessation of behaviour may have been evoked in order to evade punishment and expulsion from the territory by their parents. If they continued to scent mark they would be seen as directly challenging their parents for territory take-over (Richardson 1991, 1993, Chapters 5 & 9). At this age they basically become permanent trespassers in their parents' territory. This was clearly demonstrated in the case of M5 who trespassed for almost seven months without marking once. At last he grew large and strong enough to start challenging his father in the eastern portion of his territory. It is however not clear why he increased his mark-rate and overmarked his father's scent marks at the time when the adult females were coming into oestrus. This may have been a challenge to try and take-over part of his parents' territory or to advertise to his mother or neighbouring female for mating purposes (Chapter 6).

The cessation of marking by M5 would support the intimidation hypothesis (Hediger 1949; Richardson 1991, 1993; Chapter 5 &9). Intruders into foreign territories stop to scent mark in order to avoid detection, as aardwolves rarely marked when outside of their territories (Richardson 1991; Chapter 5 & 9).

Female cubs seem to cease marking earlier than males. If we assume that females reach sexual maturity earlier than male aardwolves this would force them to discontinue marking earlier to avoid confrontation with their parents. However I did not observed a female cub staying in their parents territory for as long as the two subadult males and therefore did not see physical aggression as frequently towards female cubs. As yet it is not known when the aardwolf sexes reach sexual maturity.

As spotted hyaenas approach puberty an increase in rates of pasting behaviour has been found (Woodmansee *et al.* 1991). This is a common pattern in mammals (Yahr 1983) and has generally been linked to an increase in gonadal activity. Little data on the ontogeny of scent marking in the other members of the Hyaenidae is available, so one has to rely on comparisons with the Viverridae. In the ontogeny of scent marking in the African dwarf mongoose no absolute cessation of scent marking occurs but a gradual supersession of initially frequent 'cheek marking' by anal marking takes place (Rasa 1973). Cheek gland secretion in this species is believed to act as a threat substance while anal gland secretion may serve to identify the marking individual. Since subadult mongooses do not leave their social group immediately upon sexual maturity they modify their marking behaviour and cease to cheek mark, which might otherwise be misunderstood as a challenge of status by the dominant adult pair. Subadults do however leave their anal mark identity in frequencies similar to the rest of the group (Rasa 1973).

Individual differences possibly observed in the three male cubs (M2, M3, M4) of two litters raised jointly by the two adult females could be attributable to their different mothers. One cub was certainly larger than the other two, weighing 10-20% more, but despite this size difference not discernibly dominant over the other two. He may have been one female's offspring while the two were offspring of the second female. The two smaller cubs seemed to scent mark more frequently and with greater eagerness and followed their father more often than the larger male cub. They also marked more often on their own and up to a later age. These early differences in individual marking effort could precede later individual differences in adult marking effort (Bekoff 1989; Richardson 1991; Chapter 5). Such early differences in the marking frequencies of individuals suggests there may be a genetic component involved in determining future behaviour e.g. future mating vigour as adults. Marking frequency is also often associated with dominance (Ralls 1971) and individual differences in the marking frequencies of captive subadult spotted hyaena were positively correlated with dominance rank (Woodmansee *et al.* 1991).

Differences in marking effort between male and female cubs was evident from when the sexes could first be determined at four months. Females rarely followed the father on scent marking trips, marked rarely on their own, never reached high mark-rates, and ceased to mark earlier than males as they reached sub-adulthood. These early differences are reflected in the gender related variation in marking rates amongst resident adult aardwolves (Richardson 1987b, 1990, 1991; 1993; Chapters 5 & 6). In contrast observations on spotted hyaenas during the prepubertal period failed to report sex differences both in the wild (Mills & Gorman 1987) and in a captive population (Woodmansee *et al.* 1991). In their extensive review of sex differences in social play Meaney *et al.* (1985) concluded that for species in which there are large sex differences in adult social roles, one would expect to see sex differences in developmental strategies. However in behaviourally and physically monomorphic carnivores, as in the case of the aardwolf, one would predict minimal sex differences in early development (Meaney *et al.* 1985). Parallel to this in mammals, paternal care and monogamy are usually associated with a reduction in sexual dimorphism (Kleiman 1977; Ralls 1977). Despite being of similar size at all times of development male and female cubs displayed clear differences in their development of scent marking behaviour, contrary to the above hypotheses.

CHAPTER 5

SCENT MARKING PATTERNS AND USE OF SPACE DURING THE NON-MATING SEASON

INTRODUCTION

The aardwolf has been used by Richardson (1991, 1993) as a model to explore the assumptions of territorial scent marking in solitary carnivores. Due to abounding definitions and hypotheses in the field of territoriality (Kauffman 1983) and scent marking in territory advertisement (Gorman 1990; Gosling 1990; Richardson 1991) some of the concepts fundamental to this chapter will have to be introduced.

Scent marks are deposited in patterns that seem to maximise their advertising power, and thus detectability by intruders:

(I) Scent marks are often concentrated along the border, to minimise the time between an intruder entering a territory and it encountering a scent mark. This creates a 'bowl' effect with a high mark density along the border and a lower one in the interior (wolves, Peters & Mech 1975; coyote, Bowen & McTaggart Cowan 1980; spotted hyaena in Ngorongoro Crater, Kruuk 1972). The 'hinterland marking' is in partial contradiction to this. In very large territories (300 - 1 000 km ^{2}) of brown and spotted hyaenas in the Kalahari residents could not visit border areas frequently enough to deposit a higher density of scent marks there (Gorman & Mills 1984). Despite brown hyaenas still marking at higher rates in the border areas (Mills 1990) the density of marks still increased with more intensive use towards the centre of the territory.

(II) Marks are deposited along paths used by conspecifics (gerenuk, Gosling 1981; suni, Somers *et al.* 1990), and at conspicuous landmarks, like defecation sites (spotted hyaena, Kruuk 1972; African civet, Randall 1979; ferret, Clapperton 1989; spotted and brown hyaena, Mills 1990).

(III) Sections of the territory border rarely trespassed by intruders (e.g. large bodies of water) are less intensively marked than active borders between adjoining territories (Kruuk 1978; Stamps *et al.* 1987). Aardwolves (Richardson 1990, 1991) and spotted hyaenas in the Krüger National Park (Henschel & Skinner 1991) deposited their scent marks in accordance with the above patterns (Richardson 1993).

A more disputed question is how territorial intruders interpret these scent marks and thus how they may function in territory maintenance:

The assumption of the intimidation hypothesis is that scent marks help to intimidate and thus deter intruders from entering the territory (Hediger 1949; Geist 1965; Johnson 1973). When detecting signs of the territory owners some carnivore species did in fact retreat or showed anxiety (Kruuk 1972, Rothman & Mech 1979; Erlinge *et al.* 1982; Harrington & Mech 1983). However intruders are not always deterred from entering scent marked territories when the owner was locally absent (Gosling 1982, 1990). Gosling (1982) proposed the scent matching hypothesis based on animal conflict theory (Maynard Smith & Parker 1976) by using polygynous ungulates with small territories as a model. Scent marks establish an asymmetry of contest between the resident and intruder. The territory owner saturates his territory with the smell of his scent marks. When he finds an intruder inside his territory he present himself to be smelt so that the intruder can match his scent with that of his scent marks. Since the resident has more resources to loose he will be more prepared to escalate the encounter into a fight for ownership of the territory than the intruder. While risking high injury costs in a fight, it is advantageous for both contestants to identify the owner correctly. When scent matching occurs, the asymmetry is recognised and the intruder often retreats without cost to either contestant (Gosling 1982, 1990, Gorman 1990). However as there are cases contradicting the intimidation hypothesis a number of large carnivore species do not perform such ritualised scent matching either (spotted hyaena, Kruuk 1972; wolf, Rothman & Mech 1979; aardwolf, Richardson 1991).

Both hypotheses support the assumption that the density of scent marks in an area serves as a cheat-proof measure of time of occupation by the author (Gosling 1982). The density of marks will also advertise the intensity of use and thus the chance of encountering the resident (Clapperton 1989; Smith *et al.* 1989; Richardson 1991).

Richardson (1993) used the following arguments in support of the intimidation hypothesis on how scent marking functions in large territories, where permanent monitoring is impossible: Scent marks must function in the temporary absence of the residents. Their density indirectly communicates to intruders the potential of being found by the owners, while the marks themselves threaten intruders with attack if they are found. Territory owners must carry out this threat if intruders are encountered, otherwise there will be no deterrent to intruders and territory maintenance will be redundant. The response of intruders to scent marks will depend on their motivation and the value of the exploitable resource. Although scent marks can not exclude intruders entirely, they may limit the degree, in both time and space, to which the territory is intruded and so indirectly protect its resources.

The basic scent marking pattern of aardwolves during the non-mating season was described by Richardson (1990, 1991) on Benfontein farm for the years 1981-1984. A territorial pair defends a clearly delineated territory of 100-600 ha with a discrete amount of termite food (Richardson 1987a) through overt aggression and pasting. Both partners of each territory mark more often along the borders, creating a ‘bowl-effect’ of paste mark density. Male and female share the same territory and therefore defend the same borders, with border limitation being effective above a certain threshold in scent mark density only. Male border mark-rates decrease as a function of territory size and thus males with small territories showed higher border mark-rates than large-territory owners. Scent marks are deposited at highest densities in small territories. Females seem to concentrate more on marking in the interior of the territory, thus the scent marking behaviour of the sexes differs (Richardson 1991).

This chapter is exclusively concerned with the non-mating season territorial scent marking patterns. I do not explore other functions scent marking has been associated with, like marking for confidence (rabbits: Mykytowycz *et al.* 1976), optimal foraging (red fox: Henry 1977); stimulation of mates (Brown 1979), or pair bond formation (wolves: Rothman & Mech 1979). The last two functions will be discussed in the mating season chapter (Chapter 6).

Richardson noticed differences in the pasting behaviour of males and females, but analysed the data for both sexes together and few territories only. Now with more data one can look at differences between the sexes again, which may elucidate if there is difference within one species in the sexes’ territorial drive. Richardson (1990, 1991) suggested that territories are defended to secure exclusive access to termite food, to feed themselves and their most recent young. Is this the same motivation for both male and female, or can differences in the marking behaviour highlight the differences in motivation between the two sexes? The present study took place after a strong upheaval in the aardwolf population following the 1986 dieoff through locust poisoning (Richardson & Coetzee 1988). At the start of the study most territories were again fully occupied by a male and a female pair. It was tested if the basic patterns documented in 1981-1984 re-established after the dieoff. Further does the scent marking data and observation of intrusions and physical conflicts of aardwolves support the intimidation hypothesis?

METHODS

Physical properties, and the marking site of scent marks were measured and recorded as detailed in Chapter 2 (General Methods). Likewise the same general procedures were used for recording the movements and scent marking behaviour of territorial resident aardwolves.

The scent marking pattern for adult aardwolves is described for the two non-mating seasons (summer = September - April), referred to as season 91 and 92. Thirteen adult aardwolves, seven males, and six females, were followed. Of those five males and five females were included in the analysis and followed for 1 409 km, observed for 1 208 hours and a total of 23 224 scent marks were recorded. For the other three animals sample sizes were too small for statistical analysis.

RESULTS

Scent Mark Traits

Scent mark length and weight: During this study aardwolves always straddled the grass stalks before pasting them and the thin smears deposited varied in length between 2.2 and 18.5 mm (mean = 7.3 ± 3.2 mm, n = 99). Female paste lengths (mean = 8.5 ± 3.8 mm, n = 38) were significantly longer than males' (mean = 6.6 ± 2.6 mm, n = 61) (Mann Whitney U-test, hereafter MWU-test: Z = -2.59, n = 99, p<0.01). The mean dry weight of a paste greater than five mm in length was 1.75 mg (n = 20).

Scent mark height: The height of the secretion on 121 grass stalks varied with the height of the grass (Fig. 5.1). It appears that on very short grass aardwolves mark as near the top as possible. On longer grass they mark within 10 cm of the top, with a mean maximum height of about 26.6 ± 4.8 cm on very long grass (> 32 cm). The highest paste mark found was at 35 cm while the lowest was at 4.5 cm.

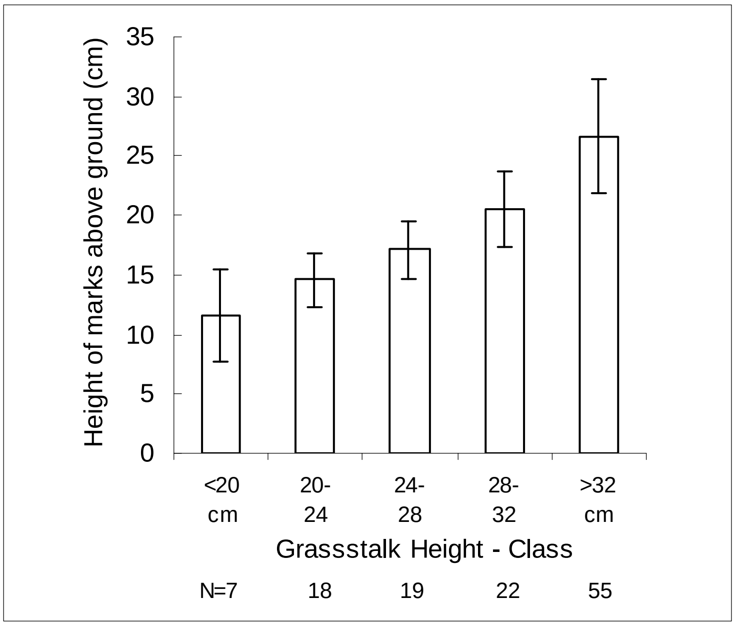

Figure 5.1 Mean height above ground of paste mark secretion on 121 grass stalks of different lengths ± one standard deviation (SD).

Aardwolves deposited one type of scent mark only, the “Type 1” described by Nel and Bothma (1983), while “Type 2” consisting of minute spots was not observed.

Marking Site

Often scent marks were deposited near some form of land mark, with marks deposited by all aardwolves at dens, middens, on roads, and close to termite mounds amounting to 40 % (Table 5.1).

Table 5.1 Percentages of all scent marks recorded at and away from land marks for all adult aardwolves and for males and females separately in the two seasons 91 & 92.

Land mark Type	Adult Marks %	Male Marks %	Female Marks (%)	Male vs. Female p of χ^2-tests
Veld (away from land mark)	60.1	59.3	61.2	n.s.
Termite Mounds	24.5	24.4	24.6	n.s.
Dens	5.1	5.0	5.4	n.s.
Middens	5.0	5.4	4.4	< 0.01
Roads	5.3	5.9	4.4	< 0.001
Totals (n)	23 460	13 702	9 758	

There was no significant difference between the sexes in terms of the frequency at which they scent marked at dens, termite mounds and away from obvious land marks in the veld. Significant differences were though found in the marking at middens and along roads (Table 5.1). Males marked more at both. When the four different landmarks were pooled there was no significant difference in the frequencies at which males and females of each pair marked at landmarks (chi-square test $\chi^2 = 0.03$, df = 1; Fig. 5.2). However there were significant differences in the frequencies of marking between four territories ($\chi^2 = 953.23$; df = 3; $p < 0.001$). Use of landmarks for scent marking differed between territories probably depending on availability of landmarks from 27 % to 50 %.

Overmarking

When moving along a territory boundary aardwolves frequently sniffed scent marks and then overmarked them. On average 27 % (n = 2607 marks; 20 nights sampled) of pastes aardwolves made were overmarks on existing scent marks. The sexes did not differ significantly in their average percentage of overmarks from each other (MWU-test, Z = -1.66, $p > 0.05$, n = 20). Males overmarked on average 29.8 % of their marks a night (n = 1442; 10 nights sampled, range 15.9 - 43 %) as indicated by prior sniffing of a grass stalk, while females overmarked 23.7 % (n = 1165; 10 nights sampled, range 12.8 - 68.1 %). The percentages for each night were probably dependant on the size of the territory and on the density of existing scent marks in the area visited that particular night. The time these existing scent marks were sniffed varied considerably. It was not known whether those scent marks were old marks of the focal animal or those of its partner, cubs or non-resident intruders. The behaviour of aardwolves towards scent marks of different origin was investigated by placing marks collected from different aardwolves throughout the focal animals territory (Chapter 9).

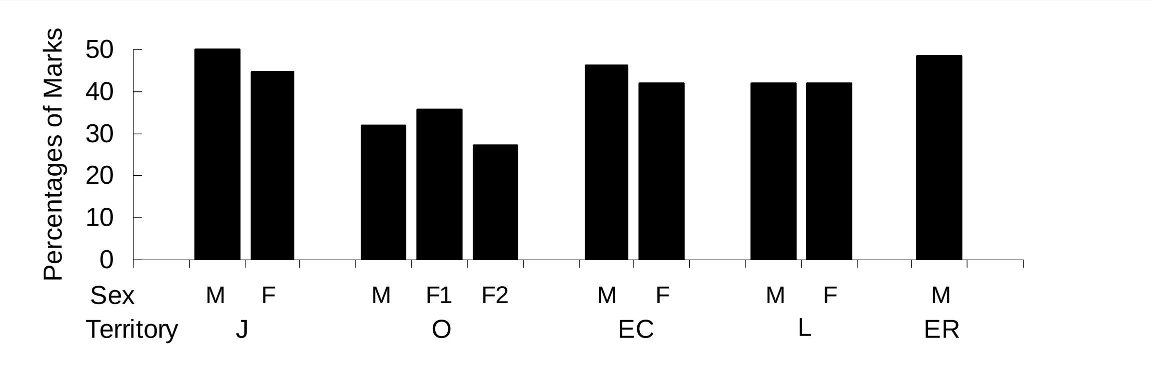

Figure 5.2 Percentages of marks at landmarks for Males (M) and Females (F) of different territories (J; O with 2 Females; EC; L; ER with data for the male resident only).

Outline of Territory Borders during Seasons 91 and 92

The outline of the territories during seasons 91 and 92 for each sex separately is shown in Fig. 5.3.

Overlap in the Partners Territory Borders

The territories defined by each individual male’s and female’s marking pattern were similar in size, and a pair defended almost the same borders adjacent to other neighbouring territories (Fig. 5.3). This was the case in three of the four territories observed (J, EC, L). The fourth and largest territory (O) was shared by the two females Electra and Echo, each defended a slightly different border to the north, west and east, but the same border to the south where two other territories existed. Their male Orion’s borders encompassed both his females borders and extended even further overlapping with them again at the southern border (Fig. 5.4).

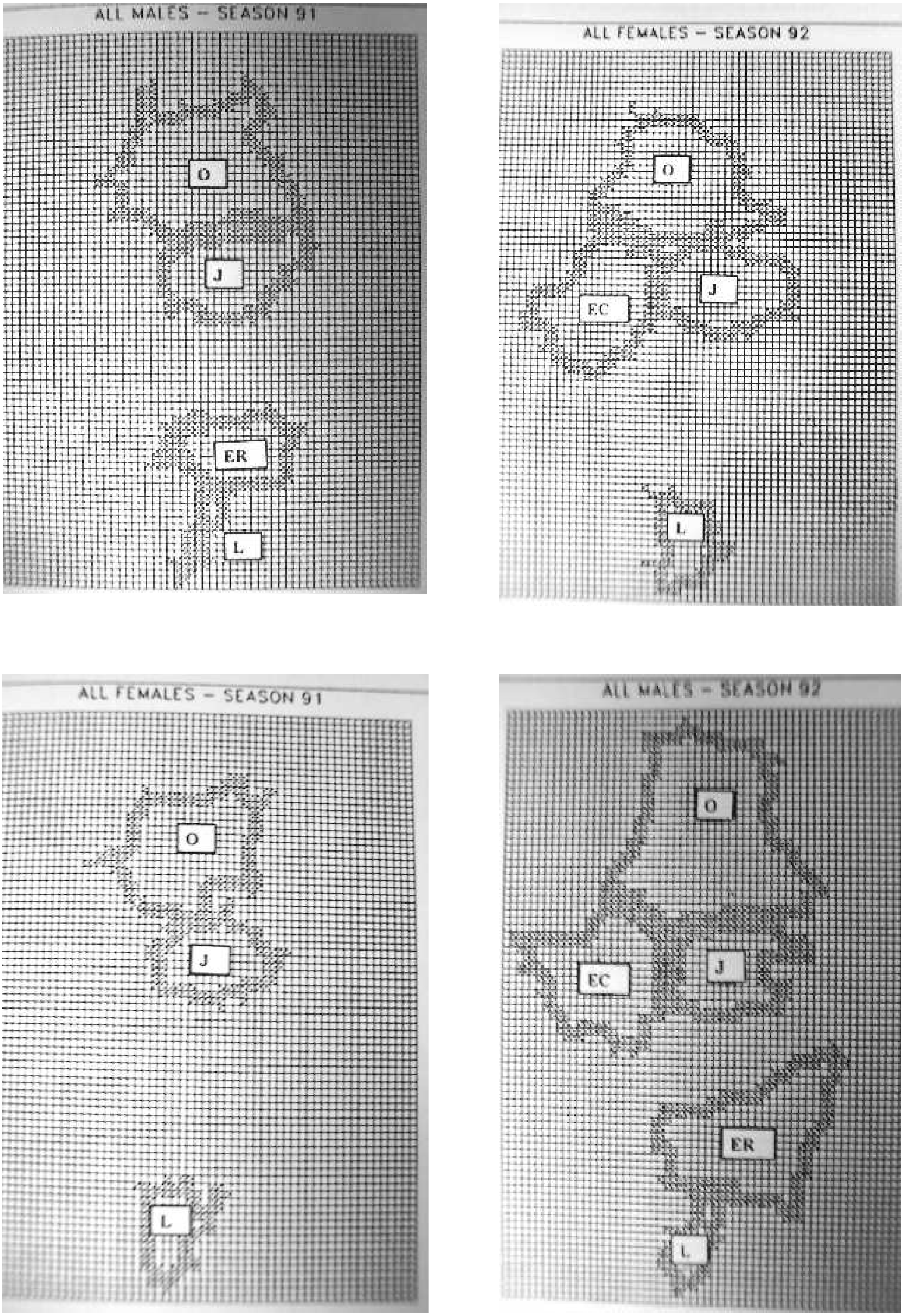

Figure 5.3 The outline of the territory borders during season 91 and 92 for males and females separately. Letters inside territory borders identify territories as listed in Table 5.2.

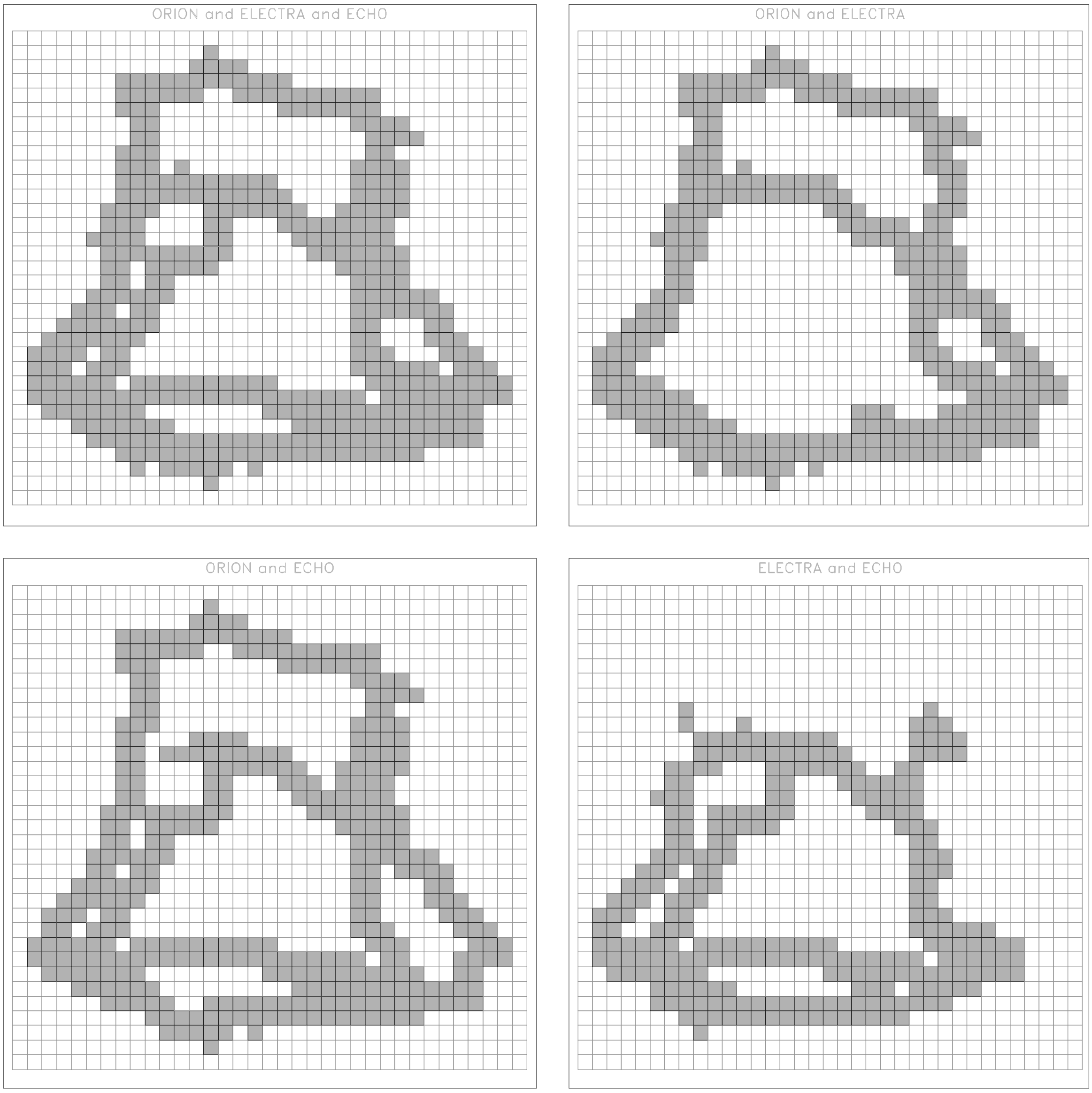

Figure 5.4 The outline and overlap of the territorial borders of Orion, Electra, and Echo the adult aardwolves of territory O in season 92.

Incidence of Marking and Time Outside of Territories

A summary of the 23 224 pastings recorded during the two non-mating seasons is presented in Table 5.2. It is apparent that both males and females marked very little outside their territories - usually they left less than 2 % of all their recorded marks there. Thus they marked at a much lower rate when travelling outside of their territories. The three instances where aardwolves deposited more than 3% of their marks outside their territories, were all cases where the individuals concerned were changing their old or establishing new territorial boundaries and were either still marking part of their old territory borders or were making excursions into neighbouring territories.

This study shows that the incidence of aardwolves marking outside their established territories is very low (male = 0.6 %, female = 1.6 %). I also had the impression, while following the male neighbours Orion and Joseph, that they knew exactly where the territorial border was. The border between these territories was clearly defined. This became especially evident when Joseph (territory J) stopped scent marking as soon as he crossed the border line to Orion's territory on his many feeding intrusions (Fig. 5.5).

It is evident from Joseph's excursions outside of his territory (Table 5.2), as well as for all the other aardwolves that the percentage of pastes deposited outside territories was less than the percentage distance travelled and time spent outside the territory.

Mark-rates

Border versus Internal: Aardwolves marked at higher rates (marks per 100 m walked) in the border cells than in the internal cells of their territories (MWU-test: $Z = -2.09$, $n = 36$, $p < 0.05$; Table 5.2). This difference was statistically significant using the data for the two non-mating seasons for each adult individually. However when testing the sexes separately neither males ($Z = -1.28$, $n = 18$, $p > 0.05$) nor females ($Z = -1.72$, $n = 18$, $p > 0.05$) marked with higher rates in the borders. This shows that the rates at which males and females marked their territories varied considerably (Table 5.2).

Males versus Females: Females had slightly lower rates in both areas than males (Fig. 5.6) though differences between the sexes were not significant, neither in their border mark-rates (MWU-test: $Z = -1.06$, $n=18$, $p>0.05$), nor in their internal mark-rates (MWU-test:, $Z = -0.44$, $n = 18$, $p > 0.05$). Although there were differences in the mark-rates at which males and females marked internal and border cells, there was no consistent pattern discernible. Whilst in some territories males marked at higher rates than females, this was reversed in other territories. Furthermore in some territories the border cells were marked at higher rates whereas in other territories the internal cells were marked more than the border cells.

Mark-rates versus Territory Size: In order to test whether these anomalies in scent mark-rate could be explained by different territory size, border and internal mark-rates were plotted for males (Fig. 5.7) and females separately (Fig. 5.8). The mark-rates of border cells were listed against their territory size for each season. Neither males (Spearman Correlation coefficient; $r_s = 0.267$; $p > 0.05$; $n = 9$) nor females ($r_s = 0.05$; $p > 0.05$; $n = 9$) showed a significant inverse correlation between their border mark-rate and territory size.

Table 5.2 Number of marks deposited, mark rates, distances travelled within, and time that adult aardwolves spent in the internal, border area, and outside their territories, during non-mating seasons 91 and 92. * Rate = Marks / 100 m travelled

			Marks											
			Outside		Border		Internal				Distance in km		Time in hours	
Territory	Name	Area (ha)	No	Rate *	No	Rate *	No	Rate *	Total	% Out	Total	% Out	Total	% Out
							Season 91							
J	Joseph	273	10	0.05	1138	1.55	1634	1.71	2782	0.36	189.6	10.93	178.3	15.05
J	Calypso	187	9	0.14	527	1.71	360	1.14	896	1.00	68.8	9.16	71.2	6.86
O	Orion	486	15	0.45	1027	2.06	1329	1.96	2371	0.63	120.9	2.73	85.4	3.56
O	Electra	343	12	0.28	360	0.94	428	0.92	800	1.50	89	4.84	100.7	5.33
O	Echo	224	66	0.64	334	1.09	274	1.55	674	9.79	58.6	17.75	61.2	16.75
L	Luca	69	9	2.25	508	3.04	28	2.35	545	1.65	18.3	2.02	18.2	2.36
L	Jezebel	214	32	0.43	656	2.02	129	1.58	817	3.92	55.1	26.23	45.5	21.32
ER	Eros	205	11	0.34	233	1.85	36	0.86	280	3.93	20.1	16.22	17.8	16.87
							Season 92							
J	Joseph	246	4	0.05	873	1.94	548	2.47	1425	0.28	75.7	11.10	54.3	12.15
J	Calypso	262	7	0.10	1102	2.81	927	2.00	2036	0.34	92.3	7.26	85.5	5.61
O	Orion	631	8	0.36	1189	2.07	2491	2.26	3688	0.22	169.9	1.29	112.3	0.45
O	Electra	387	7	0.10	1058	2.79	1893	1.98	2958	0.24	140.3	4.85	147.7	2.51
O	Echo	290	6	0.69	262	2.05	130	0.72	398	1.51	31.6	2.85	36.9	3.79
L	Luca	98	0	0	697	2.70	86	1.16	783	0	36.0	7.78	26.5	4.91
L	Jezebel	136	7	0.12	292	1.60	97	1.57	396	1.77	30.4	19.74	21.7	10.14
EC	Eclipse	344	15	0.34	470	1.36	289	0.77	774	1.94	76.6	5.74	44.5	3.15
EC	Nike	339	8	0.04	432	1.24	252	0.79	692	1.16	87.9	24.35	68.6	31.49
ER	Eros	398	11	2.12	683	2.31	227	1.32	921	1.19	47.9	1.04	31.7	2.21
All Males	Total		83	0.18	6818	1.98	6668	1.83	13569	0.61	755	6.09	569	7.71
All Females	Total		154	0.22	5023	1.83	4490	1.49	9667	1.59	654	10.71	639	10.03

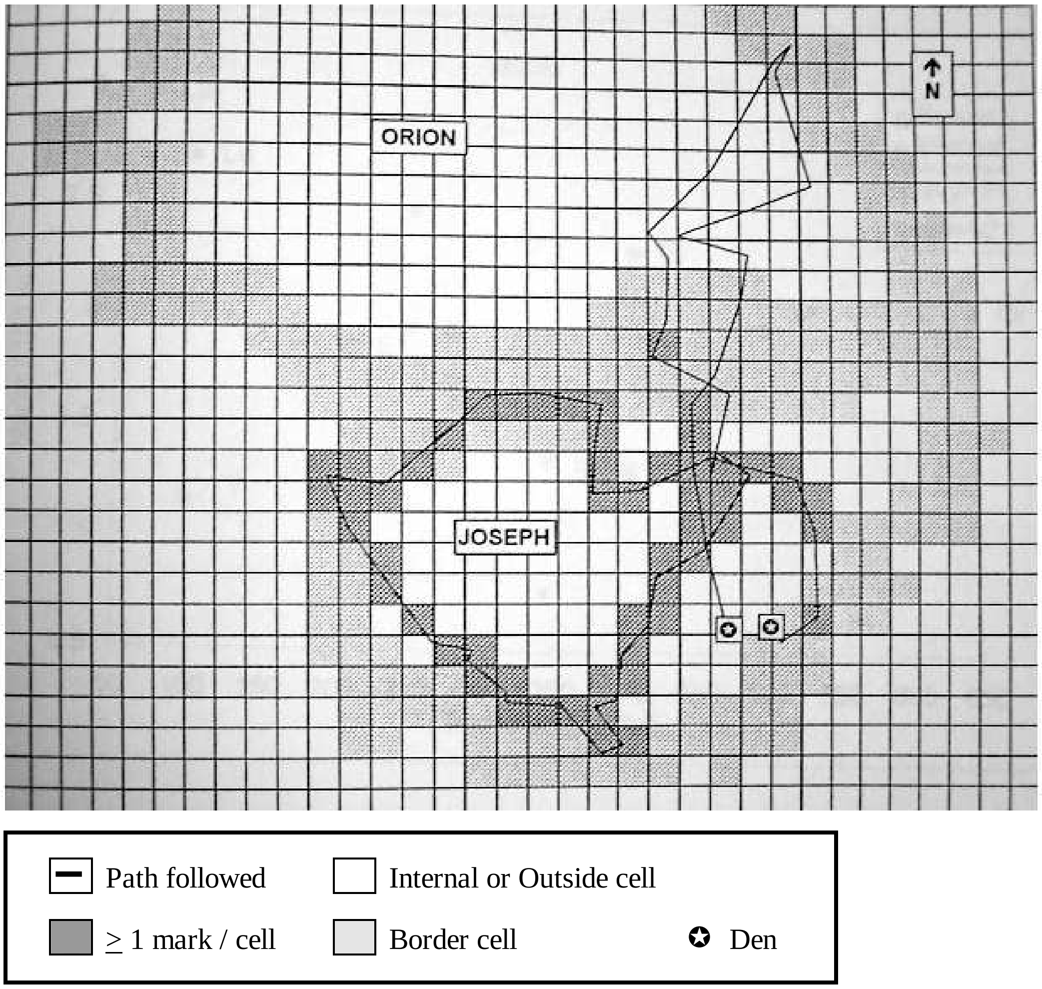

Figure 5.5 Grid- map of Joseph intruding into Orion's territory.

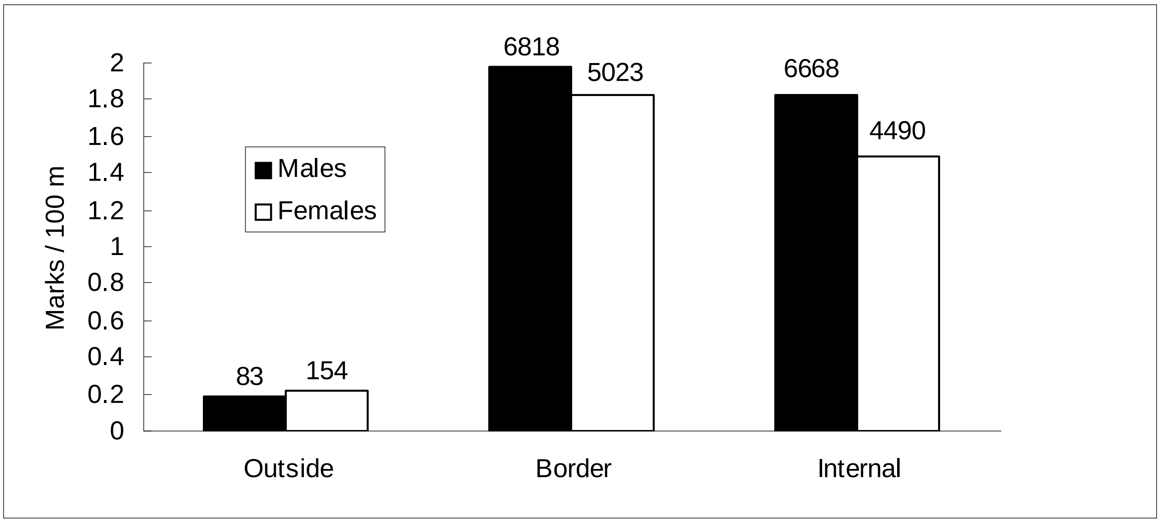

Figure 5.6 Rates at which male and female aardwolves marked the different zones of their territories during the seasons of 91 & 92 combined. Total numbers of marks are indicated.

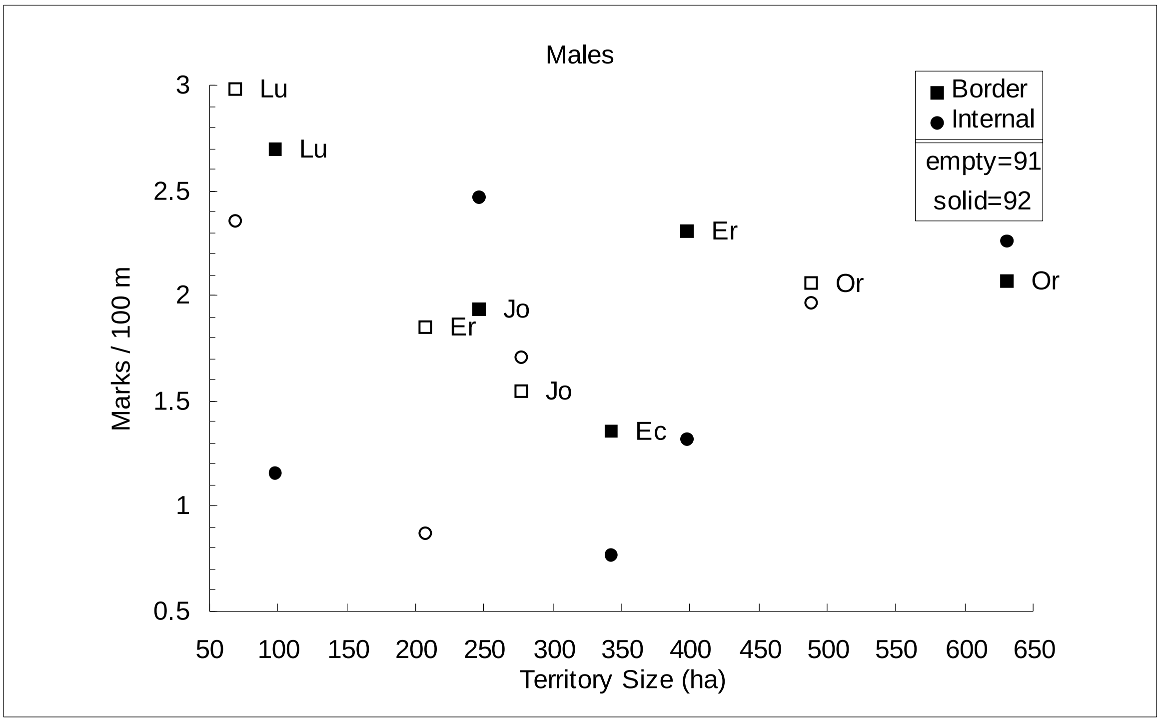

Figure 5.7 Male border and internal mark-rate for seasons 91 and 92 plotted against territory size.

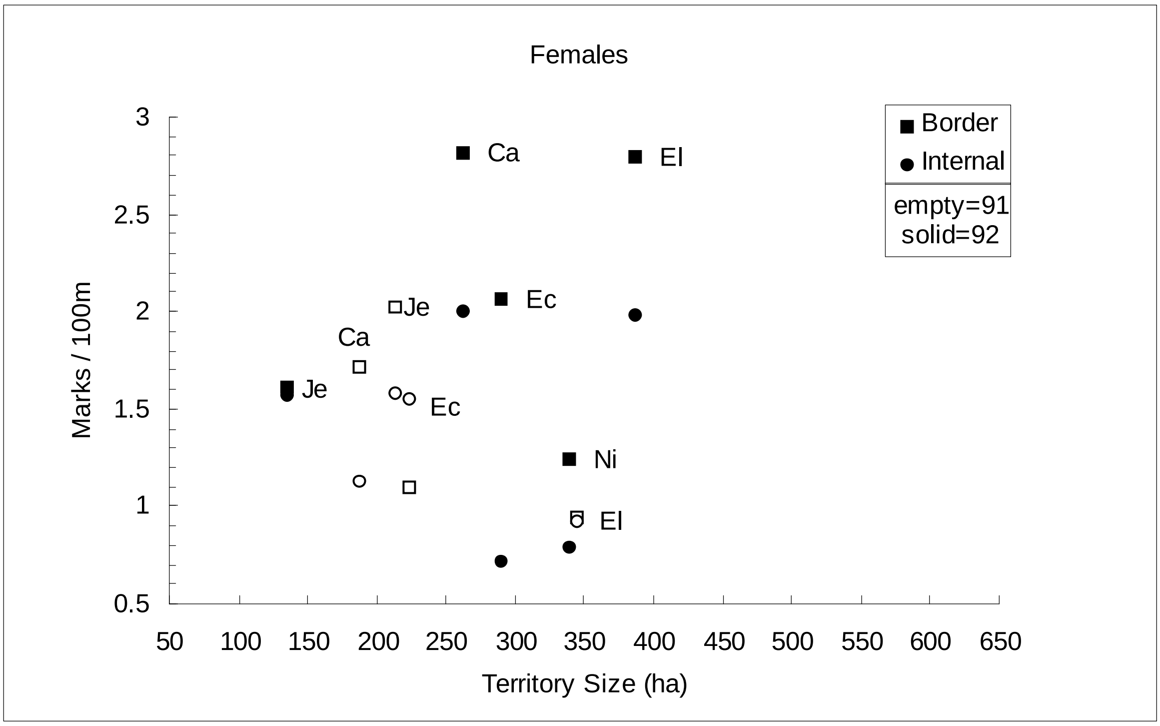

Figure 5.8 Female border and internal mark-rate for seasons 91 and 92 plotted against territory size.

Densities of Marks

Differences in the densities of marks between border and internal cells for each season and individual separately were analysed by comparing the observed total number of marks in each zone (Table 5.2) with the expected values, according to the surface area (in ha) of the zone (Table 5.3). These densities were not corrected for observation time. In one third of the territories (n = 6) there were no significant differences in densities. Of the other two thirds (n = 12), which showed significant differences between border and internal ha-cell densities, eight were due to more marks per border cell than internal cell while the other four had higher densities in the internal ha-cells. The overall pattern was thus not clear-cut again. Due to this the predictions of the ‘bowl’ type of territorial marking with more scent marks in the border (rim) than in the inside (hollow) held true for 44% of the territories only. The four territories with significantly higher densities of scent marks in the internal areas would have fitted more the ‘hinterland’ marking shape. But still six territories could not be fitted to any of the two marking strategies due to no significant differences in densities between the two areas.

Table 5.3 Density of marks in the five territories, comparing each individual for internal and border area during seasons 91 and 92. χ^2-tests comparing the observed total number of marks in internal (I) and border (B) area with the expected values, according to the surface (in ha) of the two areas.

			Surface (ha)		**Density (Mks/ ha)**		**Mks (I &B)**		
Territory		**Name**	**Internal**	**Border**	**Internal**	**Border**	**Total**	χ^2	**p**
J	91	Joseph	125	148	13.07	7.69	2772	193.31	<0.001
J	91	Calypso	81	106	4.44	4.97	887	2.68	n.s.
J	92	Joseph	99	147	5.54	5.94	1421	1.66	n.s.
J	92	Calypso	137	125	6.77	8.82	2029	35.47	<0.001
O	91	Orion	266	220	5.00	4.67	2356	2.69	n.s.
O	91	Electra	186	157	2.30	2.29	788	0.01	n.s.
O	91	Echo	66	158	4.15	2.11	608	71.28	<0.001
O	92	Orion	401	230	5.21	5.17	3680	27.24	<0.001
O	92	Electra	213	174	8.89	6.08	2951	98.52	<0.001
O	92	Echo	135	155	0.96	1.69	392	28.26	<0.001
L	91	Luca	4	65	7.00	7.82	536	0.33	n.s.
L	91	Jezebel	36	178	3.58	3.69	785	0.08	n.s.
L	92	Luca	19	79	4.53	8.82	783	35.38	<0.001
L	92	Jezebel	43	93	2.26	3.14	389	8.04	<0.005
EC	92	Eclipse	177	167	1.63	2.81	759	54.34	<0.001
EC	92	Nike	176	163	1.43	2.65	684	62.25	<0.001
ER	91	Eros	94	111	0.38	2.1	269	114.12	<0.001
ER	92	Eros	218	180	1.04	3.79	910	151.16	<0.001

For comparing individual aardwolves' scent mark densities a value for marks in each internal and border 1-ha cell, corrected for observation time, was calculated for each aardwolf and season. The relative densities of marks (marks / ha-cell / hr) are presented in Table 5.4.

Table 5.4 Relative densities of marks (marks/ ha-cell/ hr) in internal and border areas of the five territories for seasons 91 and 92.

		Relative Density (Mks / ha / hr)					
Terri-		**Season 91**		Territory	**Season 92**		Territory
tory	Name	Internal	Border	size (ha)	Internal	Border	size (ha)
J	Joseph	0.124	0.123	273	0.300	0.203	246
J	Calypso	0.115	0.179	187	0.125	0.333	262
O	Orion	0.104	0.191	486	0.081	0.146	631
O	Electra	0.051	0.046	343	0.079	0.189	387
O	Echo	0.213	0.068	224	0.039	0.156	290
L	Luca	6.363	0.467	69	0.882	0.251	98
L	Jezebel	0.428	0.134	214	0.400	0.226	136
EC	Eclipse	-	-	-	0.069	0.210	344
EC	Nike	-	-	-	0.063	0.109	339
ER	Eros	0.075	0.217	205	0.071	0.239	398

Relative Density of Marks

Relative mark densities for internal and border cells were plotted against territory size for males (Fig. 5.9) and females (Fig. 5.10) separately to test if these individuals left varying densities of marks in border cells dependent on their territory size. Male densities of marks in border cells were inversely correlated with territory sizes (Spearman $r_s = -0.667$, $p < 0.05$, $n = 9$). Thus males in smaller territories were leaving an increasingly higher density of marks in the border cells than males with larger territories. This pattern was not significant for females ($r_s = -0.40$; $p > 0.05$, $n = 9$). These observed patterns for border densities were reversed for the sexes when internal area relative densities were considered. The male pattern was not significant ($r_s = -0.617$; $p > 0.05$; $n=9$), while that for females was ($r_s = -0.717$; $p < 0.05$; $n = 9$) relative to the territory size. Thus females with smaller territories marked at increasingly higher densities in their interior than females with larger territories. These results show that males and females emphasise marking the two zones differently.

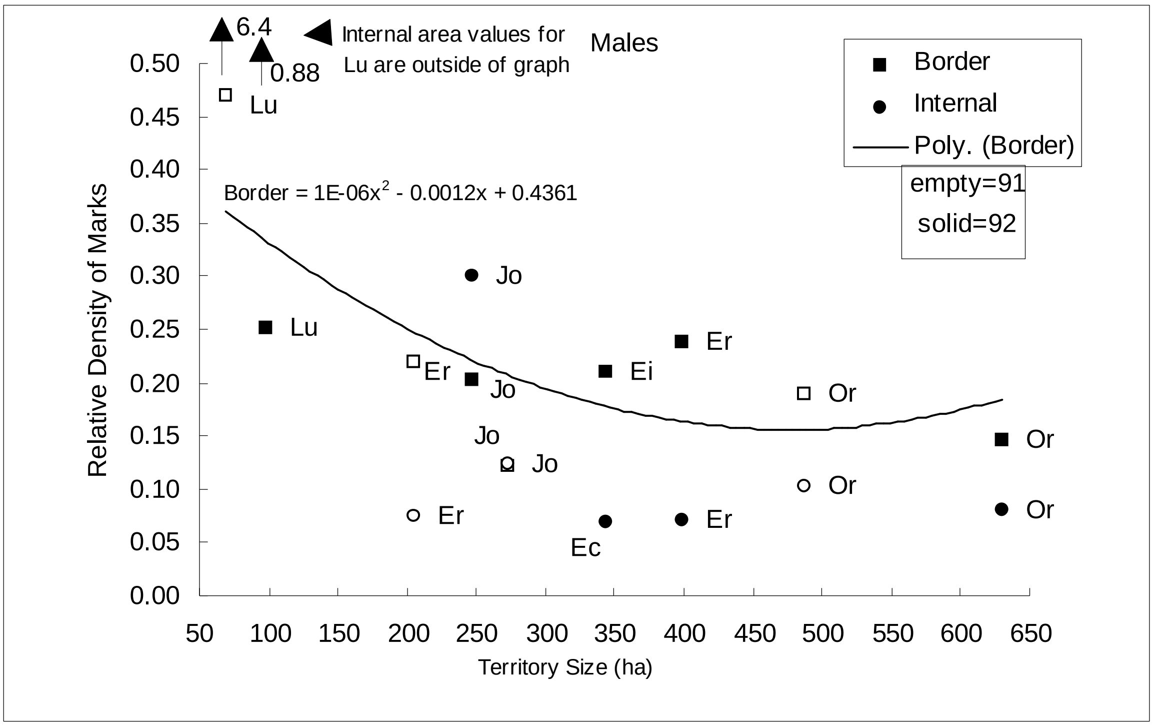

Figure 5.9 Relative densities of scent marks for internal and border cells plotted against territory size for males during non-mating seasons 91 and 92. Equation for quadratic function polygon for border relative densities of marks is included in the graph.

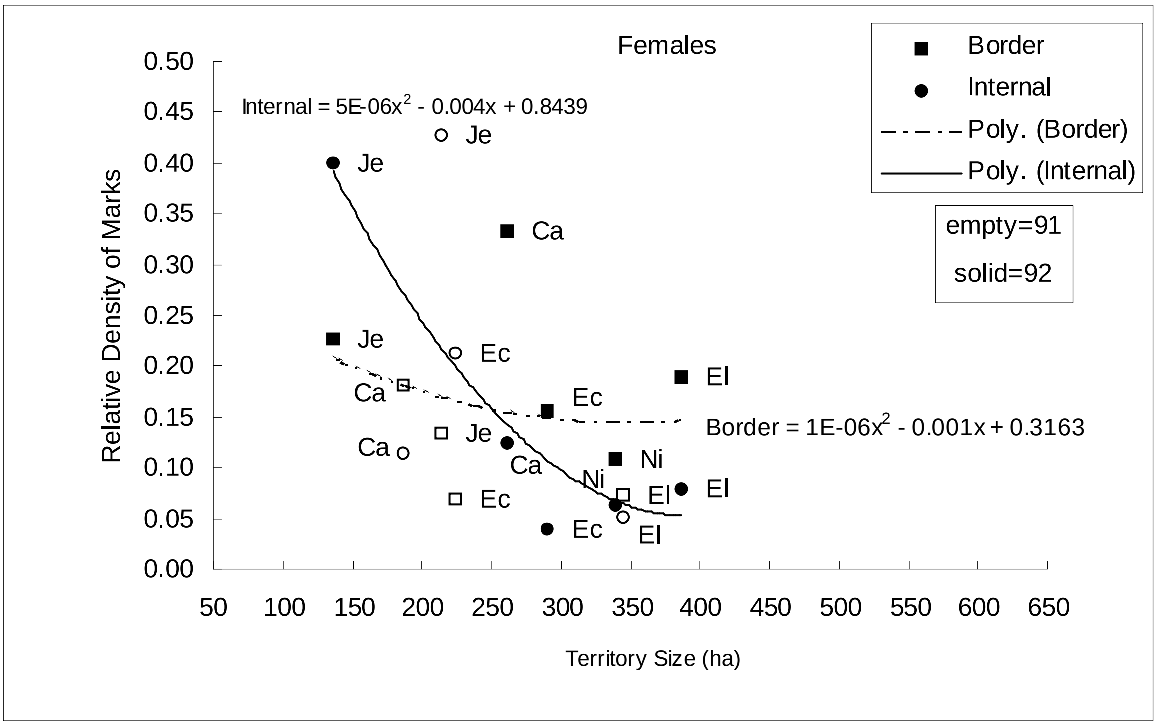

Figure 5.10 Relative densities of scent marks for internal and border cells plotted against territory size for females during non-mating seasons 91 and 92. Equations for quadratic function polygons for border and internal relative densities of marks are included in the graph.

When trying to fit the ‘bowl’ or ‘hinterland’ marking systems for relative densities of marks there was also much variation between the aardwolves defending different territory sizes. Contrary to the predictions a ‘hinterland’-type marking with highest relative densities of marks in the interior was found in the smallest territories (< 200 ha), both for males and females. There was a switch to the ‘bowl’-type at about 200 ha and continued, though with decreasing differences between border and internal relative densities through to the biggest territories with more than 600 ha for males and more than 300 ha for females.

Marking Effort

Territory Size: Despite the above pattern that males with small territories were able to deposit increasing densities of scent marks per border cell, the actual number of marks and thus marking effort in the border per time unit (hour) does not show the same pattern. The number of marks deposited per hour observation in the border or internal area by each individual was plotted against territory size for the two seasons. Male marking effort was not correlated with territory size, neither for border (Spearman $r_s = 0.467$, $p > 0.05$, $n = 9$; Fig. 5.11) nor for internal areas ($r_s = 0.2$, $p > 0.05$, $n = 9$). Likewise no significant correlation was found for females (border: $r_s = 0.033$, $p > 0.05$, $n = 9$; internal : $r_s = -0.217$, $p > 0.05$, $n = 9$; Fig. 5.12). The range in territory size between the largest and smallest male territory was more than nine fold. In contrast female range in territory size was merely three fold.

Figure 5.11 Marking effort as marks per hour left in border or internal area against territory size for males during both non-mating seasons.

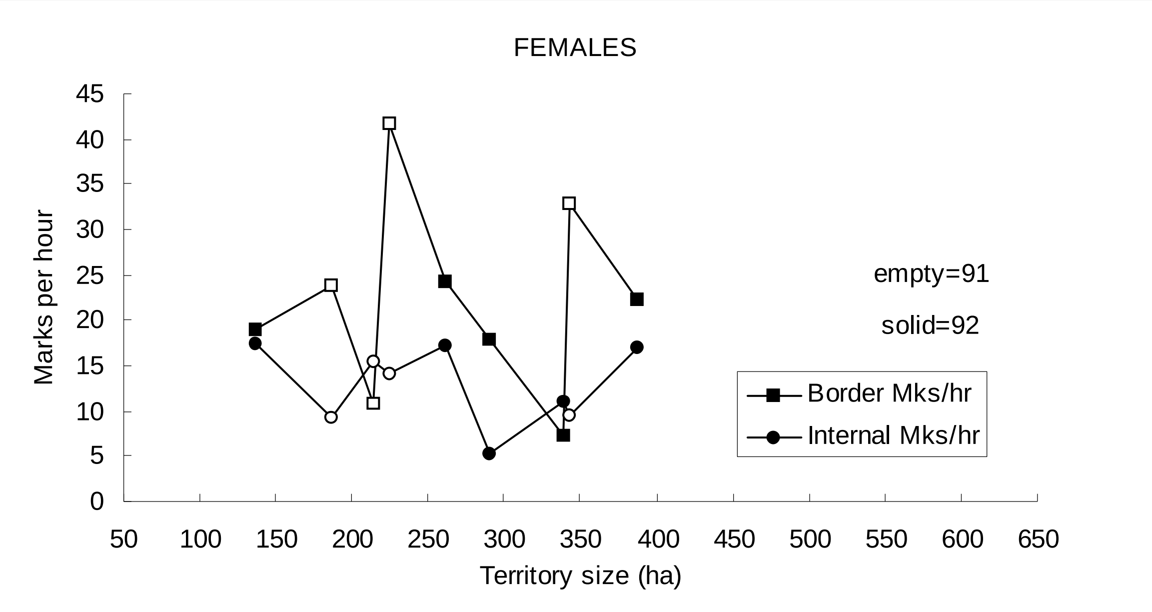

Figure 5.12 Marking effort as marks per hour left in border or internal area against territory size for females during both non-mating seasons.

Several significant differences were however found comparing marking effort (marks left per hour) for:

Border versus Internal: Males and females pooled marked more often per hour in their border areas than in their internal area (MWU-test: Z = -3.259, n = 36, p < 0.05).

Males versus Females: Males left significantly more marks per hour in their border areas than females (Z = -2.209, n = 18, p < 0.05). Their internal marking effort was also stronger though was not significantly different (Z = -1.899, n = 18, p > 0.05).

Seasonal difference: In their border areas males and females combined deposited more scent marks per hour in season 92 than during 91 (Z = -1.956, n = 18, p = 0.05). The difference between the seasons for the internal area was not significant (Z = -0.622, n = 18, p < 0.05).

Territory Establishment

In the non-mating season 91 I witnessed a shift of territory by the female Jezebel (Je). After plotting her paths during the 91 mating season and from observations of previous aardwolf researchers (M.D. Anderson [*] and P.R.K. Richardson [†], pers. comm.) it was apparent that she was moving to a new territory, but continued to visit and mark parts of her old territory (Fig. 5.13).

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[†] P.R.K. Richardson, University of Pretoria, Dept. of Zoology and Entomology, 0002 Pretoria

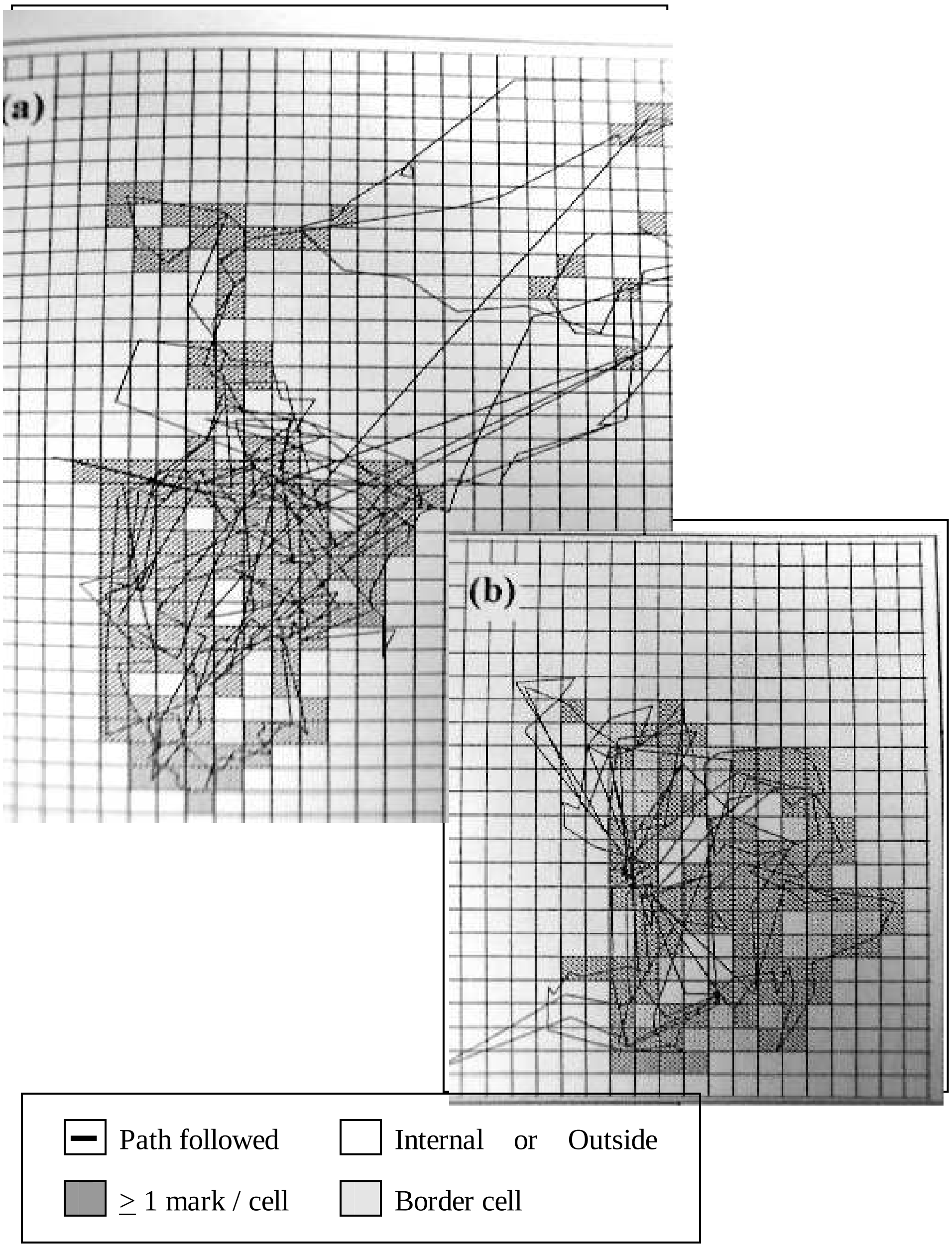


Figure 5.13 Pattern of marking by Jezebel in season 91 (A) and 92 (B).

After Jezebel's mate was killed at the start of non-mating season 91 she paired up with a new partner, the young adult male Luca (Lu). Luca defended the smallest territory recorded during this study and showed the highest mark-rates (Marks/100m; Fig. 5.7) and relative mark densities (Mks/ha/hr; Fig. 5.9) in both border and internal areas of all males during 91. In season 92 he increased his territory size by 29 hectares and marked at lower rates and densities than in 91. Jezebel reduced her territory by 78 ha and also reduced her mark-rate in both internal and border areas of her territory (Fig. 5.8) but her internal relative mark densities (Fig. 5.10) only from the 91 to the 92 season. Thus initial higher mark-rates while founding a new territory, in border and internal areas and subsequent reduction of the mark-rate after successful establishment was apparent in both sexes.

Border Marking

Not all parts of the border were equally well marked. The territory that Orion defended in season 91 served as an example. It was surrounded on all sides by other aardwolf territories, except to the north-west where it meets the pan basin and where there are virtually no termite mounds (Richardson 1985). Orion both marked this area at a lower mark-rate (MWU test Z = -2.309, d.f. = 1, $p<0.05$) and left a significantly lower density of marks there (chi-square test $\chi^2 = 19.05$, d.f. = 1, $p<0.001$; Fig. 5.14) than in the cells which were bounded by other territories.

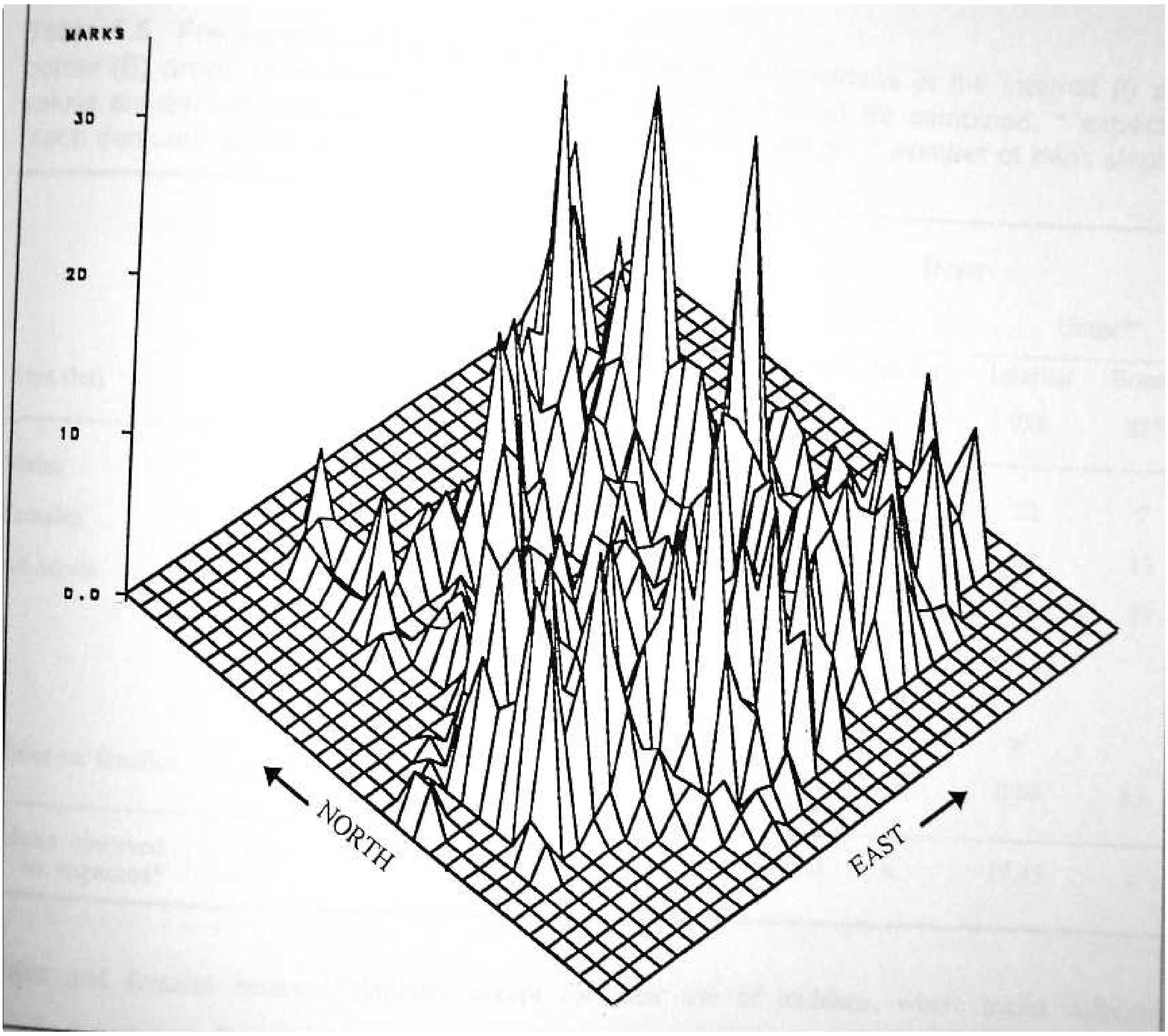


Figure 5.14 3D-map of Orion's season 91 territory showing lower densities of marks along north-western border, uninhabited by aardwolves. The map is plotted as if seen from the south west at an altitude of 45° above the horizontal.

Middens and Dens

On most occasions aardwolves deposited one or more scent marks when they used middens for defecating. Middens were also visited specifically for the purpose of pasting. Temporarily unused dens and dens where other aardwolves slept were used and pasted by the focal animals followed. Aardwolves however never marked at the dens that they were presently using themselves for sleeping.

Males versus Females: Differences in the use and visitation for pasting purposes of middens and dens by males and females for both seasons combined are analysed and together with the data is displayed in Table 5.5.

Table 5.5 Frequencies of pasting and use of dens and middens in the internal (I) and border (B) areas of all territories during both seasons 91 and 92 combined. * expected values are derived from the total surface areas of the two areas. ** number of dens slept in (each den counted once per season and animal only).

	Middens				**Dens**			
	Pasting		Usage		Pasting		Usage**	
	Internal	Border	Internal	Border	Internal	Border	Internal	Border
Area (ha)	938	817	938	817	938	817	938	817
Males	62	81	50	73	67	35	22	7
Females	56	61	92	53	69	29	42	13
All adults	118	142	142	126	136	64	64	20
				Chi-squared test				
	χ^2	p	χ^2	p	χ^2		χ^2	
Males vs. females	0.53	n.s.	13.89	s.	0.51	n.s.	0.00	n.s.
Adults: observed vs. expected*	6.79	s.	0.02	n.s.	17.02	s.	17.45	s.

Males and females behaved similarly except for their use of middens, where males defecated significantly more often at border middens while females did so more frequently at internal middens. When pooling the frequencies for the two sexes, adult aardwolves pasted significantly more often at border middens and at internal dens. They used internal dens for sleeping significantly more than expected than border dens.

Distribution of Dens and Middens in a Territory

The distributions (internal versus border) of all dens and middens in territory J (pair Joseph & Calypso) that were active in each season are shown in Table 5.6. In both seasons there were significantly more active dens in the interior and this was also true for middens in season 91. Middens in season 92 were distributed in proportion to what would have been expected by the areas of the two zones. There was a significant increase in the number of middens used by the pair in their borders in 1992 relative to 1991 ($\chi^2 = 4.79$, d.f.= 1, $p < 0.05$).

Table 5.6 Distribution of dens and middens in territory J and the surfaces of internal and border areas of the territory in 1991 and 1992. * expected is derived from the ratio of the two areas' sizes.

		Territory			**J**		
		Number		Areas (ha)		observed versus expected *	
	Season	Internal	Border	Internal	Border	χ^2	p
MIDDENS	91	27	15	125	148	5.79	<0.05
	92	11	18	99	147	0.07	n.s.
	Total	38	33	224	295	3.11	n.s.
DENS	91	19	2	see		16.88	<0.001
	92	26	5			24.56	<0.001
	Total	45	7	above		39.90	<0.001

Encounters with Intruders

Encounters with Intruders inside the Territories: It was tested whether the residents of the three northern territories encountered intruders inside their territories at different frequencies while they were followed in both non-mating seasons combined (Table 5.7). The residents of territory O encountered intruders (2.12 / 100 hrs) about twice as often as residents of territories J (0.87) and EC (1.11).

Table 5.7 Frequencies of encounters while following aardwolves inside their territories in non-mating seasons 1991 and 1992 combined.

Territory	Name	Encounters	Hours followed	Encounters / 100 hours
O	Orion	5	194	2.58
O	Electra	2	239	0.84
O	Echo	3	87	3.45
Totals		11	520	2.12
J	Joseph	1	199	0.50
J	Calypso	2	147	1.36
Totals		3	346	0.87
EC	Eclipse	1	43	2.33
EC	Nike	0	47	0
Totals		1	90	1.11

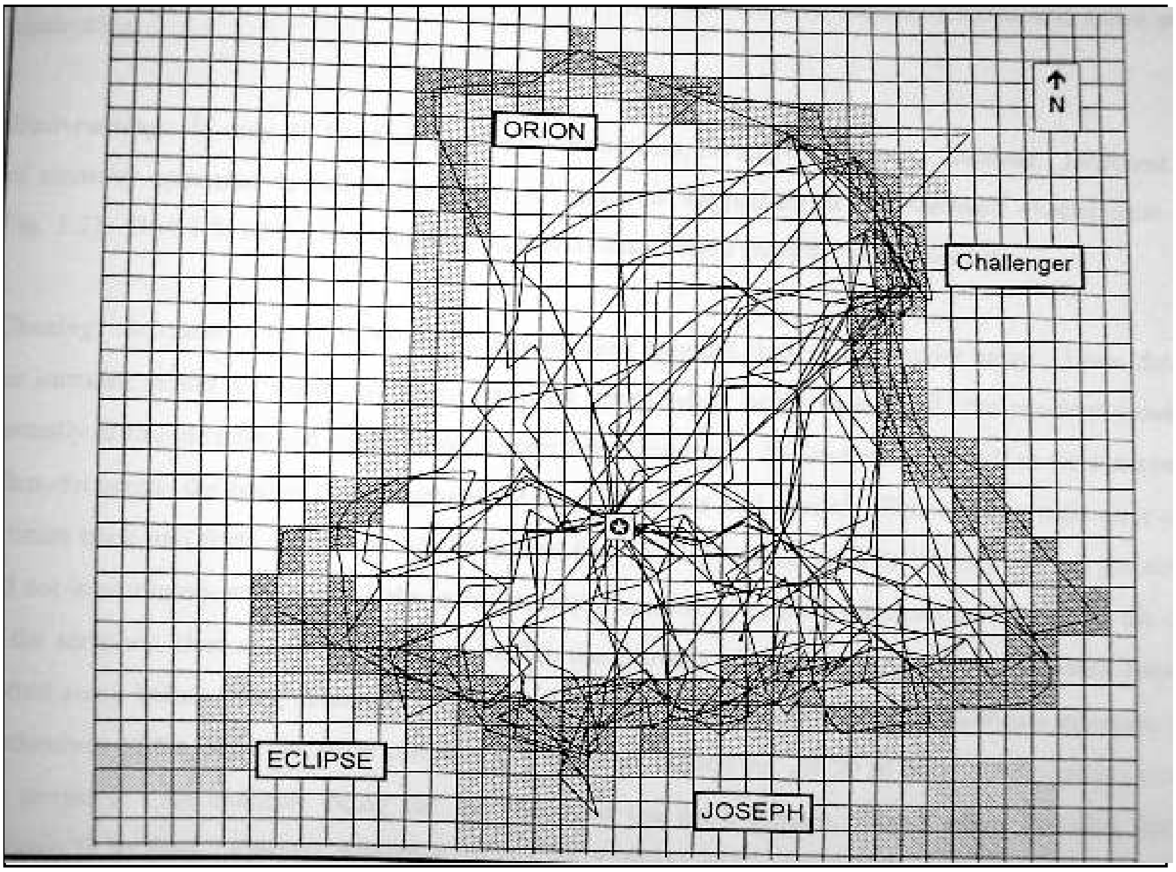
Seasonal Variation in Intruder Pressure

The observed seasonal differences in the scent marking behaviour and the pasting and use of dens and middens between season 91 and 92 is compared with intruder pressure in the three northern territories.

'Simulated Intrusions': The most significant difference between the two seasons was through the conducting of just four translocation experiments in season 91 compared with 19 in season 92 in two of the northern territories (Chapter 9). This is nearly a fivefold increase in 'simulated' intrusions, which maybe posed a serious challenge of territorial take-over through scent marking of simulated intruders.

Focal Animal Intrusion: The frequency of nights with intrusions of more than 100 m across the shared border into a neighbouring territory by the focal animal versus nights with no intrusions was investigated. To reduce the influence of counter-intrusions stimulated through 'simulated intrusions' the nights when translocation experiments were conducted (Chapter 9) and the two nights after the experiments were not included in this data set. The five adults of territories J and O, where all the translocation experiments were conducted, decreased their frequencies of intrusions from season 91 (18 out of 50 nights, 36 %) to 92 (10 out of 54 nights, 18.5 %) ($\chi^2 = 4.03$; df = 1; $p < 0.05$).

Intrusion with scent marking: A male intruder was observed to enter and to scent mark the large territory O repeatedly at the start of the non-mating season 92. In response Orion patrolled and marked his north-eastern border along the point of intrusion (along a 1 km long stretch) heavily for one week and often lay down for several hours a night in this area (Fig. 5.15). He seemed to wait for the challenger to come past. Finally he tracked him down and defeated him in the interior of his territory in a serious fight lasting for seven minutes.



▬	Path followed	☐	Internal or Outside cell		
▨	≥ 1 mark / cell	▢	Border cell	✪	Den

Figure 5.15 Map showing Orion's movements and scent marking patterns in his borders during one week in September 1992 in response to an intruding male from the east who scent marked in his territory.

Aardwolf Interaction

The frequency of interaction types observed during 178 aardwolf interactions during both non-mating seasons are summarised in Table 5.8, showing the frequency of interactions between males and females with members of their own territories and with neighbours and unidentified aardwolves. I included the behaviours from the focal animal only, not taking into account the reactions of the addressee. The four interaction types, described in General Methods (Chapter 2), in the order from friendly to increasingly aggressive were:

Greeting: Parents and cubs greeted usually longer than partners. In contrast to Richardson (1985) I could observe on many occasions that aardwolves sniffed each other's anal region. These were always cubs sniffing their parents anal pouch and vice versa, and the two females Electra and Echo sniffing each other.

Hair-raising: In only 40 % of all aardwolf interactions, no hair-raising was involved. Different levels of intensity appeared to reflect the extent of alarm or aggression of the aardwolf (Richardson 1985, Fig. 1.2). On 51 % of the hair-raisings both individuals were from the same territory.

Chasing: *Intruders:* In 41 % of the chases an adult resident chased an intruder away. Upon detecting the intruder, either by sight, but more often by smell when being downwind, the resident would run instantly at the intruder and chased it to the territory boundary. When both aardwolves were males they often ran across the border then reversing the roles of chaser and chased. This chasing went on a couple if times back and forth across the border before they retired to their own territories. When the resident did not immediately start chasing the intruder, it circled around it until it had its back towards the centre of the territory, then ran at the intruder. Often the intruder discovered the territory resident first, and trotted away before being detected. Vigorous chases were mainly restricted to same sex animals, while aardwolves of the other sex were sometimes ignored or chased for 20-50 m only, not necessarily out of the territory. An example being the behaviour of the male Joseph, whom often intruded far into territory O to feed. Despite detecting Electra or Echo he did not leave, or just ran 50-100 m when chased by them, to start feeding again, remaining in their territory. The females did not always give chase when detecting him. His reaction was markedly different when detecting, or being chased vigorously by Orion, though he still returned sometimes on the same night. The female Nike often intruded into territory O to her north. When detected on several occasions and nipped by Orion she ran a couple of metres only, then stood her ground, but did not leave his territory, while he moved on without involving her in a fight. In contrast Nike was chased immediately back into her territory by Electra, but despite this returned half an hour later on two occasions.

Residents: A high proportion of the chases (59 %) were accounted for residents chasing each other, but then for 10 - 50 m only. It often involved a feeding animal chasing away another resident (partner, or cub) from a termite column. Away from the breeding dens, and while feeding and patrolling their territory all adults were highly anti-social animals and intolerant of each other' close company.

Fighting: Fighting occurred rarely, usually when the resident involved in the chase caught the intruder. This was the situation in 6 of 9 fights (67 %) observed during the non-mating seasons. Males were more often involved in fights than females, though they had the same number of fights with intruders.

Table 5.8 Interactions (n = 178) during the non-mating season of male (n = 82) and female (n = 96) aardwolves followed as focal animals with members of their territories and with intruders.

	Behaviour	**Residents**		**Non-Residents**				**Total**
			Own	Neighbouring			Uniden-tified	
		Mate	Cub	Cub	Male	Female		
Males	Greet	7	20					27
	Raise hair	4	5	2	1		4	16
	Chase	8	8	4	10	2	1	33
	Fight	1	2		3			6
Females	Greet	11	33					44
	Raise Hair	10	4	6	4	1	1	26
	Chase	15	2		3	2	1	23
	Fight			1	1		1	3

Males behaved generally more aggressive than females with more fights and chases than raising of hair and greeting interactions observed. In both sexes greeting was restricted to territory residents and more so to the parents' own cubs with females showing less aggression both to their cubs and their male partners than males towards them and their cubs. Non-resident cubs of neighbouring territories, usually about 8 - 10 months old were mainly chased away or just intimidated by raising hairs. Both sexes found and thus involved neighbouring males in more agonistic interactions (13 chases and four fights) than neighbouring females (four chases).

DISCUSSION

The aim of this chapter was to test how the resident aardwolves deposited their scent marks in order to ensure the most effective maintenance of their territories. It was further examined if this was achieved by means of intimidation via scent marks backed up by physical aggression (Richardson 1991).

Scent marks charcteristics seemed to be consistent with maximising their advertising power (see Alberts 1992). The amount of secretion used by an aardwolf during an average non-mating season night of marking with 150 pastes would be about 0.26 g dry matter secretion, and thus should represent a negligible energetic loss in comparison to the energy spent walking to strategic places for scent marking (Richardson 1991). About 40 % of all marks of an individual were deposited close to landmarks probably enhancing the ease of visual localisation (Eisenberg & Kleiman 1972) whilst aardwolves seemed to scent mark at land marks in proportion to their availability in their territory.

Many studies on carnivore scent marking behaviour (Peters & Mech 1975; Rothman & Mech 1979; Macdonald 1979, 1985; Bowen & McTaggart Cowan 1980; Gosling 1981, 1982; Erlinge *et al.* 1982; Kruuk *et al.* 1984; Gorman & Mills 1984; Clapperton 1989; Smith *et al.* 1989; Richardson 1990, 1991) assumed that scent marking is directed towards an intruder and scent marked areas correspond to defended areas. Aardwolves of this study marked rarely outside of their territories. Those marks outside were mainly due to some animals still marking part of their previous territories or were an artefact of the problem that territories cannot be defined over long periods perfectly (Richardson 1993).

The mark-rates of aardwolves in border and internal areas varied considerably during this study. Neither males nor females singly marked with significantly higher rates in either border or internal areas. Therefore variations could not be simply explained by the large range in defended territory sizes, in males a sevenfold difference and in females a threefold. However a significant inverse correlation was found for males when plotting relative density (corrected for observation time) of marks for border cells relative to territory size. This was not significant for females which contrasts with Richardson (1991). Females during this study seemed to concentrate more on leaving higher relative densities of marks in the interior the smaller their territory size, while this pattern was not significant for males. So males and females seemed to emphasise marking the two areas differently. Thus with increasing territory size males deposited lower relative densities in the border and females lower densities in the internal areas of their territories. Marking dimorphism has been reported for coyotes organised in pairs or groups where males and females showed different marking frequencies (Bowen & McTaggart Cowan 1980) and has also been suggested to have different functions in the two sexes (Wells & Bekoff 1981).

Contrary to the predictions higher relative densities of scent marks were deposited inside than in the borders of the smallest territories under observation. The second smallest territory, already greater than 200 ha showed the ‘bowl’-type for relative mark densities and this mark distribution was then maintained through to the biggest territories. Thus territory sizes, in the range of observed territories, were not big enough to create a ‘hinterland’ marking pattern yet. Richardson (1991) suggested a threshold territory size of 200 hectares in which aardwolves would not decrease their relative densities of marks in border cells with increasing territory size any further. Too few scent marks in an area would no longer be effective in territory maintenance. This characteristic for aardwolf territories was confirmed in the non-mating seasons 91 and 92.

Variation in mark-rates and mark densities in border and internal territory areas could possibly be interpreted as a reaction to a perceived increase in intruder pressure. An almost fivefold increase in scent marks translocated between territories (Chapter 9) in non-mating season 92 may have been perceived as serious challenges and therefore a threat with attack to territory holders. The marking activity of all afflicted animals increased from season 91 to 92 displaying their readiness to defend their territories. Similar increases in marking activity has recently been documented for male coypu due to growing intruder pressure (Gosling & Wright 1994). Additional support for this tendency came from the increased use and marking of border middens by males in season 92.

The scent matching hypothesis proposes that the territory owner will present himself to be smelt so that the intruder can match his scent with that of his scent marks (Gosling 1982, 1990). Aardwolves during this study gave chase immediately and from long distances away, thus performed no scent matching ritual when they met intruders. This is in accordance with the intimidation hypothesis (Richardson 1991, 1993). Territorial disputes occurred relatively rarely taking into account that just 29 chases and fights involving neighbours and strangers were observed while following adult aardwolves for 1409 km, giving one interaction about every 50 kilometres. When the average distance adult aardwolves walked on a summer’s night was eight kilometres for the present study, this would result in an average of one interaction every six days. This is less than half the interaction rate calculated by Richardson (1991) which fits the pattern of aardwolf pairs defending territories of approximately double the size of these in his study. Whilst in 1982/83 eleven adults defended five territories in the same northern study area ten years later seven adults defended merely three territories.

The comparatively few chases and fights observed demonstrate that physical agression seems to be actively avoided by intruders. This would give support to the intimidation hypothesis (Hediger 1949; Geist 1965; Johnson 1973; Gorman & Stone 1990; Richardson 1991, 1993), with scent marks acting as a threat with physical damage to the intruder should he get caught by the territory owner (Wallace 1973; Zahavi 1977; Dawkins & Krebs 1978; Richardson 1993). When a resident encounters an intruder in its scent marked area it must be prepared to defend this area by chasing or even fighting the intruder, in order not to loose credibility. “If after a week of trespassing in a territory and utilising its resources, an intruder is threatened with only a ritualised display and retreats without injury, this will clearly be a very minor deterrent against trespassing and the territory maintenance will be ineffective” (Richardson 1991, page 22). With the present larger than previous territory sizes chances of meeting intruders were lower and chases and fights should thus have been carried out even more persistently. Most intruders during this study were neighbours that avoided fighting with the owner and fled after using the resources for some time already. In fact during both seasons Joseph intruded frequently and was observed to feed for a total of 33 hours without being found by Orion the territory owner. On the occasions he was chased out he sometimes returned shortly afterwards. One could argue that in the large territory (480-630 ha) defended by Orion territorial maintenance becomes ineffective, due to diminished encounter rate and punishment of intruders.

Richardson (1991) showed that the rate, density, and relative density of scent marking increased with diminishing territory size, assuming a relatively stable marking frequency for all individuals. During this study this was found for relative density of marks only due to a larger variation in territory size as well as in individual marking effort. Some males were marking on average half as often per night as others, independently of territory size.

Aardwolf territory size seems to reflect the often-observed pattern of being inversely related to the density of resources (Myers *et al.* 1979; Schoener 1983; Davies & Houston 1984). Thus the smallest territories should have the highest densities of food resources (Richardson 1987a) and should also attract the highest intruder pressure (Richardson 1991) as has been found for other species as well (Myers *et al.* 1979; Hixon 1980; Schoener 1983). This could be applied to this study’s territories, though not quantified by food resource data. A special case was provided by the largest territory of this study which was defended by Orion with two females supporting double the number of cubs. The higher number of intruders encountered by the three residents than in the other two territories would also hint to an even higher number of undetected intrusions. In this much larger territory intruders would be less likely discovered by the residents than in the other territories. Still Orion succeeded in defending the territory from take-over while keeping both females inside of it for the study period. The food resource of this territory were likely sufficiently large since all the cubs born survived the winter to the age of dispersal.

Scent mark density advertises to intruders the degree of occupation of a territory, level of commitment of the owner to defend it and thus the chances of encountering the resident (Gosling 1982; Clapperton 1989; Smith *et al.* 1989). At exactly what size a territory becomes undefendable depends probably on individual marking effort and thus readiness of the owner to defend it aggressively. Territories are defendable at intermediate resource densities only, as a decay in golden-winged sunbird territoriality was observed when resource densities were too high or low for defence (Gill & Wolf 1975). Defensible territory size is also dependent, in the light of the observed seasonal differences in marking effort, on intruder pressure (Hixon 1980, Schoener 1983, 1987). In years of favourable environmental conditions when all neighbouring aardwolves have sufficient resources in their defended areas there should be less intruder pressure than during years of adverse conditions. These frequent intrusions could trigger a further increase in marking effort of the large territory owner. However if an individual is already marking at the maximum capacity one may expect a reduction of his or her area, with a higher density of marks resulting and a higher probability for escalated encounters.

The assumption of the intimidation hypothesis that intruders are intimidated by scent marks and thus should cross over well-marked borders for shorter periods received support from observations in territory O. Both neighbouring males and females frequently crossed over into the large territory O. Maybe territory O was at the threshold of the maximum size for effective maintenance. Intruders possibly realised that the chances of meeting the residents were rather low because of the large territory size and lower density of marks. Though Orion was a high quality male and able to defend such a large territory with a high mark-rate his territorial defence was not as effective in maintenance as that of other aardwolves in smaller territories. The intimidation message seemed to apply more strictly to same-sex individuals as members of the other sex were chased or punished only lightly, despite their plundering of food resources. Most commonly intruders were neighbours with the sole purpose of feeding and not challenging the owners to take over their territory with scent marks. Challenges were possibly perceived by territory owners through translocated scent marks (Chapter 9) from non-residents signalling their preparedness for physical escalation. In the single ‘natural’ challenge observed a male intruder scent marked the large territory O at the start of non-mating season 92 for one week. In response Orion patrolled and marked the border along the point of intrusion heavily and finally tracked down and defeated the challenger in the interior of his territory in a serious fight. This selective marking strategy was possibly shown by all aardwolves after numerous translocation experiments in season 92 (Chapter 9). An interesting addition to the argument that scent marks seem to intimidate the sniffer is that both sexes preferred to sleep in dens situated in the interior of their territories, where they would be more secure from intruding challengers. Aardwolves have been shown to lower their metabolic rate by dropping their body temperature for several degrees (Anderson 1994). The concurrent lethargy would make them more vulnerable to attack from a challenger finding them at their den.

Food-based accounts of territoriality predict that territorial defence should be shared by all members of a territory, and should if anything be most marked in females, since female reproductive success is primarily food limited (Trivers 1972; Wrangham 1982). In males however territoriality may be a mechanism to monopolise access to females. By defending a territory males are attempting to prevent neighbours from gaining reproductive access to resident females (Wrangham 1982; Roper *et al.* 1986, 1993). The observed male-female differences in marking the border and interior of territories at different rates and densities as well as their usage of middens may reflect such divergent motivations for territorial marking. Males may mark more and use more middens along the borders to intercept challenging males and possibly to advertise to neighbouring females for future mating opportunities (Chapter 6). In contrast females may be most concerned in defending sufficient termite food resources for herself and her cubs. These hypotheses would also explain, though not precisely measurable during this study, why interactions of males with solely feeding intruders of the opposite sex were less aggressive than with same-sex intruders. Still they offer no explanation for the mild female reactions to feeding male intruders, which are exploiting their all important food resources. The hypotheses are however quantifiably backed by the sexes' reactions to serious challenges in scent mark translocation experiments (Chapter 9), where the female reaction may have been always stronger due to their suggested greater dependence on food resources.

The results of the present non-mating season marking patterns suggest that a scent mark seems to function as a representation of an aardwolf's claim to a territory area and its readiness to resort to physical escalation. The intimidation hypothesis is likely to function successfully in the territorial system of aardwolves as physical escalation was observed rarely with one "natural" challenge and resulting fight for territory ownership observed in two non-mating seasons only.

CHAPTER 6

SCENT MARKING OF THE AARDWOLF DURING THE MATING SEASON

INTRODUCTION

In many carnivore species scent marking by both sexes increases markedly in the breeding season, and particularly during courtship as the female approaches oestrus (Ewer 1973). Such increases involve marking with scent organs (Rasa 1973; Kruuk *et al.* 1984), but in particular token marking with urine (Macdonald 1979; Wells & Bekoff 1981). The pungency of both dog and vixen red fox urine increases during the breeding season (Jorgenson *et al.* 1978; Henry 1980). For the European otter seasonal changes in urinary oestrogens have been documented (Trowbridge 1983 in Gorman & Trowbridge 1989). Beagle males were able to distinguish between urine and vaginal secretions collected during oestrus and during dioestrus (Doty & Dunbar 1974) and many other carnivores.

The aardwolf is considered a socially monogamous species (Richardson 1985) on account of one pair holding a perennial territory and male parental care. Sexually however the aardwolf is polygamous, with numerous extra-pair copulations (EPCs) occurring during the short winter mating season (Richardson 1987b, Chapter 7). Territories are maintained by both the male and female partners of one territory, but the opportunity to mate with a female is not exclusively available to the resident male, but appears to be determined by open competition with neighbouring males.

Paired males attempt to father more offspring by engaging in EPCs with neighbouring paired females in addition to copulating with their own female partner. At the start of the mating season adult males begin to make ‘scouting’ excursions into neighbouring territories, initially without scent marking there. As the season progresses a few of the more aggressive males start pasting outside their territories. In the pro-oestrus period, about a week before the female allows copulation, several males are visiting her territory during which time their pasting reaches a peak. By the time the female comes into oestrus they may be pasting more intensively outside their territories than inside (Richardson 1987b). The scouting males will often revisit the same areas to paste, especially dens and middens, gauging the resident male’s response to their scent marks by checking if they were overmarked. It will be tested whether especially border dens and middens are in fact visited more frequently, serving as noticeboards, during the mating season. The scouting behaviour together with pasting should firmly familiarise the males with their neighbour’s individual scent and to gauge their commitment to defend their females from

EPCs (Richardson 1987b). Concurrently the male territory holder receives a measure of quality of the scouting and pasting male. The energy spent for extensive extra-territorial pasting, by walking long distances, involves considerable costs at times of lowest food availability, that high quality males are able to afford only. Richardson (1987b) has hypothesised that the male partner is intimidated by this while he advertises to the females his prowess as a male (Zahavi 1977; Richardson 1987b).

Likewise paired females may employ a selection of strategies to obtain EPCs with neighbouring males. The advantages for males are that the more mating opportunities (EPCs) he has, the greater his chances for propagating his genes (Trivers 1972) while females could aim to improve her reproductive success in less obvious ways. Her offspring may gain the higher quality genes of the intruder (Gladstone 1979); she may produce 'sexy' sons - with the cuckolding tendencies of their father (Weatherhead & Robertson 1979); if she is fertilised by several males, she will increase the genetic variability of her offspring (Maynard Smith 1978).

About a month after the start of the mating season the females are coming into oestrus, and most will mate over the following month. Females seem to paste more extensively than normal in pro-oestrus and do so especially along their borders and on neighbouring territories (Richardson 1987b). It was suggested that it is particularly those females pasting at length which are paired with males marking less aggressively (Richardson 1987b). This is hypothesised to encourage visitations by extra-pair males. Within her oestrus, lasting for up to three days, a female will often mate with her partner and an aggressively marking neighbour (Richardson 1987b). Females may also facilitate the finding of their advertising scent marks by extra-pair males by visiting border area dens and middens more frequently for pasting during the mating season.

Female aardwolves possibly try and attract as many suitors as possible to ultimately mate with the most dominant male. When not in visual contact on their large territories this goal may be achieved by the deliberate placing of scent marks. The aim of this chapter is to test whether or not scent marks are used to attract the opposite sex and if male scent marks intimidate other males.

METHODS

The mating season was defined to start when males showed interest through following, sniffing, and the flehmen grimace towards females and their scent marks the first time (Richardson 1985). It was considered to end when the last female of the study population was mated. This period generally extends from May until the end of July. The term anoestrus is applied to each female singly as the time when her reproductive apparatus is inactive, corresponding to the time before the start of the mating season. In pro-oestrus, usually a week before the female permits copulation (Richardson 1987b), her reproductive apparatus becomes active. During oestrus, which may last up to three days, the female permits copulation (Richardson 1987b; Richardson & Coetzee 1988). Metoestrus follows after each female was mated, being gravid. However, if a female is not fertilized during oestrus she may cycle again about two weeks later (Richardson & Coetzee 1988)

In order to establish a measure of the frequency with which males and females were pasting outside their territories a pasting index was calculated for each individual (Richardson 1985, 1987b). This was determined by multiplying the percentage distance travelled outside the territory with the pasting rate, that is the number of marks left per 100m travelled while outside of the territory (PI = [% outside of total distance travelled] x [Marks / 100m when outside]). The pasting index (PI) ensures that the data are independent of sample size and takes into account the relative density of pastes to which aardwolves in neighbouring territories would be exposed. Animals with high PI indexes were considered as aggressive and of superior quality since they risked being chased or even injured in fights with competitors. In many species high pasting activity has been linked with dominance (Ralls 1971; carnivores: wolf, Peters & Mech 1975; African wild dog, Frame & Frame 1976; stoats, Erlinge *et al.* 1982; European badger, Gorman *et al.* 1984; Kruuk *et al.* 1984), though this is not conclusive for spotted hyaenas (Mills & Gorman 1987), and brown hyaenas (Mills 1990). Male aardwolves with low overall mark-rates during both non-mating and mating season together with a low PI index were considered inferior, or at least ranking lower relative to their neighbours. No social hierarchy could be determined as aardwolves defended separate territories.

RESULTS

Scent Marking: Mating versus Non-Mating Season

The numbers of scent marks left and the distances travelled during the three mating seasons together with the calculated mark-rate of individual male and female aardwolves outside, in the border and internal areas of their territories are displayed in Table 6.1. The mark-rates (marks per 100m walked) and numbers of pastings left are compared between mating and non-mating season in Fig. 6.1.

Males' individual mark-rates were not consistently higher in the mating (Table 6.1; n = 8) than non-mating seasons (Table 5.2; n = 9)(Mann-Whitney U (MWU)-tests: border versus border: Z = -0.579; internal versus internal: Z = -0.481; n = 17). Though the male mating season outside rate of marking

(1.08 marks / 100 m) was six times higher than that of the non-mating season (0.18; Table 5.2) the difference for individual males was not significant between the seasons (Z = -1.3, n = 17).

Individual females marked at significantly lower rates over the whole mating (Table 6.1; n = 11) than non-mating seasons (Table 5.2, n = 9) in both border (Z = -2.85, n = 20, p < 0.005) and internal areas (Z = -2.39, p < 0.05) but not outside their territories (Z = -0.305, p > 0.05; Fig. 6.1).

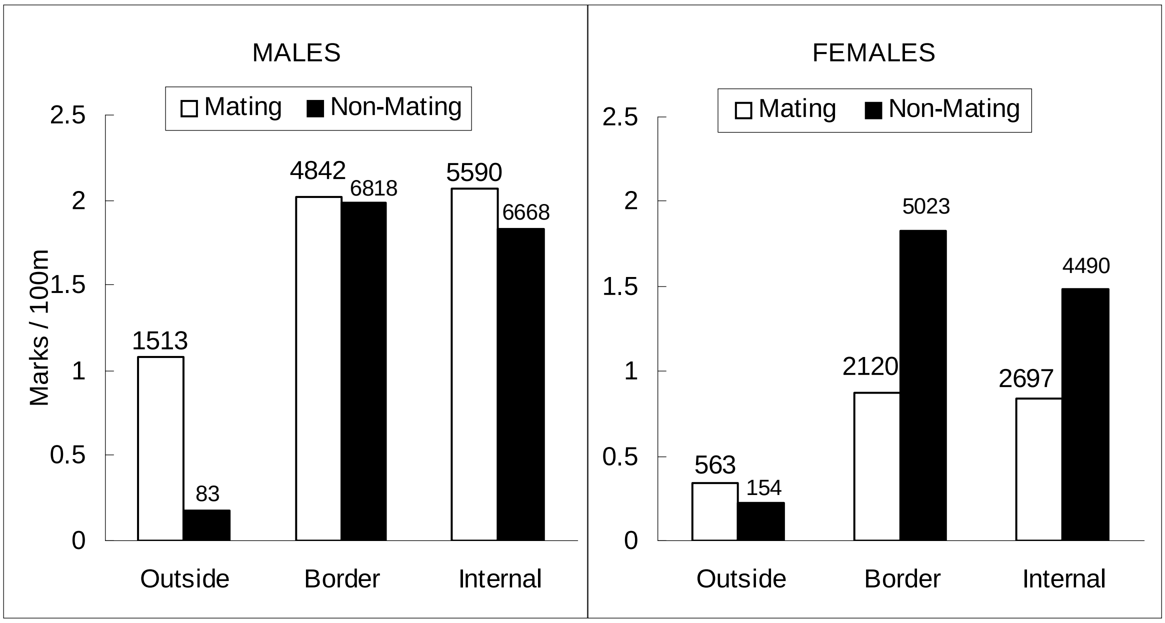
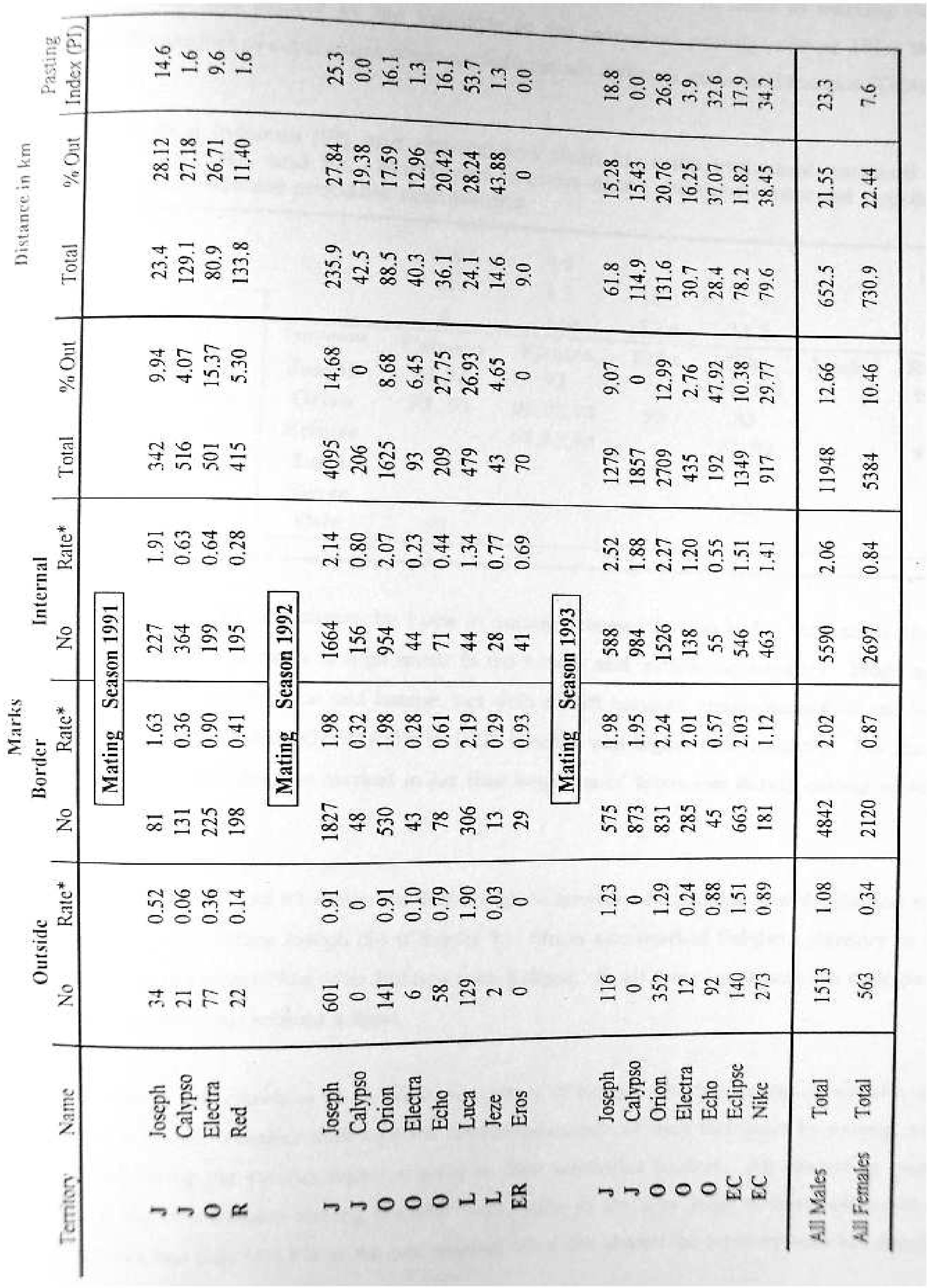


Figure 6.1 Total numbers of male and female scent marks pasted and mark-rates (marks / 100 m walked) during the mating seasons and non-mating seasons.

Males versus Females during the Mating Seasons

Males showed higher mark-rates than females in the different areas (MWU-tests, n = 19; outside: Z = -2.57, p < 0.01; border: Z = -2.98, p < 0.005; internal: Z = -2.97, p < 0.005) during the mating seasons. The male mark-rates comparing border and internal areas were similar to each other (Z = 0, n = 16, p > 0.05). Their mark rate dropped to about half of that when they would mark in border and internal areas whilst walking outside their territories. Males deposited 12.7 % of all their marks outside of their territories. Females left on average less than half as many marks as males in the same zones, and similarly showed no differences in marking their border and internal areas (Z = -0.33, n = 22, p > 0.05). Their mark rate while travelling outside of their territories was less than half of the rates they were marking when walking in the internal and border areas. Females deposited 10.5 % of all their scent marks outside of their territories.

Table 6.1 Number of marks deposited, mark-rates, and distances travelled by adult aardwolves within the internal, border area, and outside their territories, during mating seasons 91, 92, and 93. * Rate = Marks / 100 m travelled



		Marks								Distance in km		
		Outside		Border		Internal						
Territory	Name	No	Rate*	No	Rate*	No	Rate*	Total	% Out	Total	% Out	Pasting Index (PI)
				Mating Season 1991								
J	Joseph	34	0.52	81	1.63	227	1.91	342	9.94	23.4	28.12	14.6
J	Calypso	21	0.06	131	0.36	364	0.63	516	4.07	129.1	27.18	1.6
O	Electra	77	0.36	225	0.90	199	0.64	501	15.37	80.9	26.71	9.6
R	Red	22	0.14	198	0.41	195	0.28	415	5.30	133.8	11.40	1.6
				Mating Season 1992								
J	Joseph	601	0.91	1827	1.98	1664	2.14	4095	14.68	235.9	27.84	25.3
J	Calypso	0	0	48	0.32	156	0.80	206	0	42.5	19.38	0.0
O	Orion	141	0.91	530	1.98	954	2.07	1625	8.68	88.5	17.59	16.1
O	Electra	6	0.10	43	0.28	44	0.23	93	6.45	40.3	12.96	1.3
O	Echo	58	0.79	78	0.61	71	0.44	209	27.75	36.1	20.42	16.1
L	Luca	129	1.90	306	2.19	44	1.34	479	26.93	24.1	28.24	53.7
L	Jeze	2	0.03	13	0.29	28	0.77	43	4.65	14.6	43.88	1.3
ER	Eros	0	0	29	0.93	41	0.69	70	0	9.0	0	0.0
				Mating Season 1993								
J	Joseph	116	1.23	575	1.98	588	2.52	1279	9.07	61.8	15.28	18.8
J	Calypso	0	0	873	1.95	984	1.88	1857	0	114.9	15.43	0.0
O	Orion	352	1.29	831	2.24	1526	2.27	2709	12.99	131.6	20.76	26.8
O	Electra	12	0.24	285	2.01	138	1.20	435	2.76	30.7	16.25	3.9
O	Echo	92	0.88	45	0.57	55	0.55	192	47.92	28.4	37.07	32.6
EC	Eclipse	140	1.51	663	2.03	546	1.51	1349	10.38	78.2	11.82	17.9
EC	Nike	273	0.89	181	1.12	463	1.41	917	29.77	79.6	38.45	34.2
All Males	Total	1513	1.08	4842	2.02	5590	2.06	11948	12.66	652.5	21.55	23.3
All Females	Total	563	0.34	2120	0.87	2697	0.84	5384	10.46	730.9	22.44	7.6

Pasting outside of Territories

There were however considerable differences in individual behaviour. In terms of marking outside of their territories this was evident by the variation in the individual pasting indexes (PIs) tabulated together with the number of copulations observed between the different males and females (Table 6.2).

Table 6.2 Pasting indexes (PI) and copulations seen for each individual aardwolf during mating seasons 91, 92, and 93. Boldfaced season dates indicate observed copulations, italic season dates indicate probable copulations.

PI-91				1.6	9.6				1.6
	PI-92			0	1.3	16.1			
		PI-93		0	3.9	32.6	34.2		
			Copulations	**Calypso**	**Electra**	**Echo**	**Nike**	**Jezebel**	**Red**
14.6	25.3	18.8	**Joseph**	**92,93**	**92**		**92, 93**		**91**
	16.1	26.8	**Orion**	**92, 93**	*91,92,***93**	**93**	**93**		
		17.9	**Eclipse**		**91,92,93**		*92*, **93**		**91**
	53.7		**Luca**						
			Silver				**93**		
			Otis	**93**					

The highest overall male PI was shown by Luca in mating season 92, who had a very small territory (69 ha) and thus was able to mark at high levels in the border and outside his territory. High indexes were also shown by the males Orion and Joseph, but with a shift between mating season 92 and 93. In 1992 Joseph had a higher PI than Orion while in 1993 Orion's was higher than Joseph's. The scouting movements of Joseph and where he marked in his four neighbours' territories during mating season 92 are displayed in Fig. 6.2.

In both mating seasons 92 and 93 Orion marked Joseph's territory extensively and fought and mated with his partner Calypso before Joseph did (Chapter 7). Orion also marked Eclipse's territory in 1993 and copulated with his partner Nike after fighting with Eclipse. In all these incidences the male partner did not give their partners up without a fight.

The highest female PI was shown in 93 by Nike the partner of Eclipse. In this mating season she mated with four different males. Females with high PIs advertised outside of their territories by pasting, which was verified by plotting the various nights relative to their territorial borders. An interesting contrast existed between the two females staying together with Orion in the very large territory (490-630 ha). The mother Electra had low PIs in the two seasons when she shared the territory with her daughter, whilst Echo showed very high PIs. In the first mating season (91), while Electra lived alone, she had a higher PI (Table 6.2).

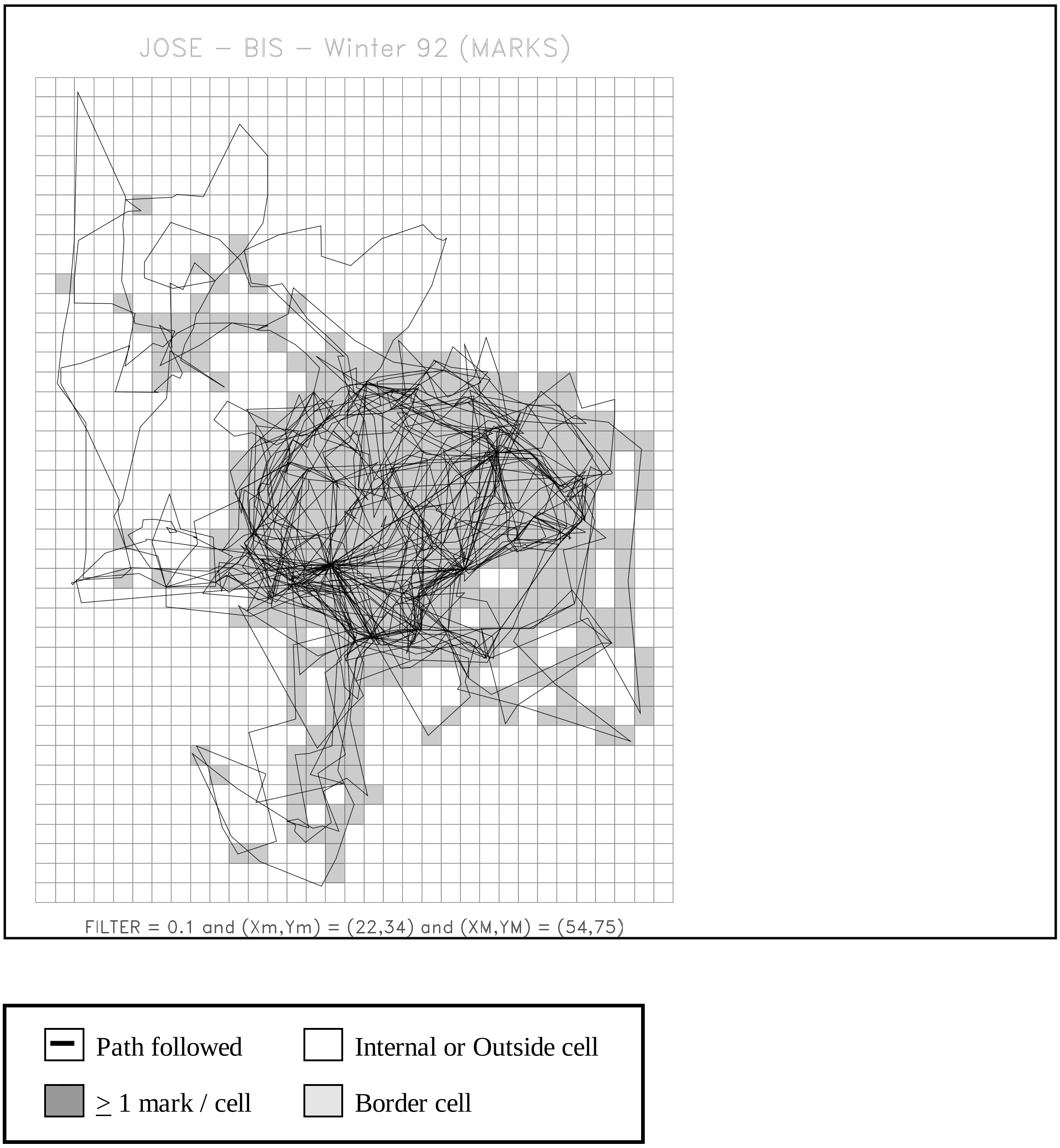


Figure 6.2 Map illustrating the paths followed and the scent marking activities of Joseph during the mating season 92. He was followed for 236 km over 117 hours over 35 nights and deposited 4095 pastings.

Rank Assignment

The assignment of the terms superior or inferior for the three northern male aardwolves, Orion, Joseph , and Eclipse, was attempted taking values for scent marking and copulation characteristics (Chapter 7) into account. These were border and outside of territory mark-rates during mating seasons, pasting indexes (PI), the average time they copulated per female mated, and the number of EPCs their female partners engaged in during mating season 93. The values averaged for the two mating seasons (92 + 93) were sorted for the three males and ranked. The respective ranks for the four males are presented in Table 6.3.

Table 6.3 Male scent marking during the mating seasons and copulation characteristics ranked. The largest value received Rank = 1. * fewest EPCs of partner = Rank 1.

Name of Male	Border Mk-rate	Outside Mk-rate	PI	Time copulated per Mating	EPCs partner engaged in 93*	Sum of Ranks
Orion	1	2	2	1	1	7
Joseph	3	3	1	2	2	11
Eclipse	2	1	3	3	3	12

The ranks of the measurements changed for the males for all but one correlation; longest copulation time with the fewest EPCs engaged in by the partner (Table 6.3). It was thus difficult to associate a particular marking characteristic with a superior and an inferior male. The summed ranks of the measurement for each aardwolf however showed that Orion had the lowest sum of ranks and thus highest overall values. The two other males had similar summed ranks, though Joseph had a slightly lower sum of ranks than Eclipse. So one could assume that Orion was the most aggressively marking male, who also copulated most frequently with other females. He was thus the superior male, which was consistent with my impression in the field and during fights with the other two males. He even chased other intruding males while scouting in Eclipse's territory.

Changes in Male Mark-Rates over the Mating Season

The mark-rate (marks/100m walked) of individual aardwolves underwent changes during the scouting period, pro-oestrus, oestrus, and after mating. It was thus critical during what period the observer followed the particular aardwolf. Due to the nature of the field work it was just possible to follow one aardwolf at a time during periods with frantic mating and fighting activity. So naturally the data is biased due to unequal sampling of individuals during these short periods.

Male mark-rates, derived from taking the total marks left that night divided by the total distance walked irrespective of where the aardwolf travelled were plotted relative to the matings of the females for mating seasons 92 and 93 (Fig. 6.3 a,b). In season 92 Orion and Joseph were observed extensively and marked at about two marks / 100 m walked throughout already four weeks before the first mating took place. These marking rates gradually increased until reaching a peak two days before Electra, Orion's partner, the first female of the season, accepted copulations. Both males mated with her and their mark-rates dropped to the same level as at the start of the mating season. Then Nike, the partner of Eclipse, became receptive. Both Orion and Joseph scouted into her territory and Joseph was seen to mate with her. Two days later Joseph's female Calypso accepted copulations and was mated by Orion first. On this day Joseph increased his mark-rate. In contrast Orion decreased his mark-rate, possibly in order not to advertise his presence to Joseph while leading Calypso into his territory for mating. On the following day Joseph mated with Calypso and, like Orion the day before, decreased his rate of scent marking (Fig. 6.3).

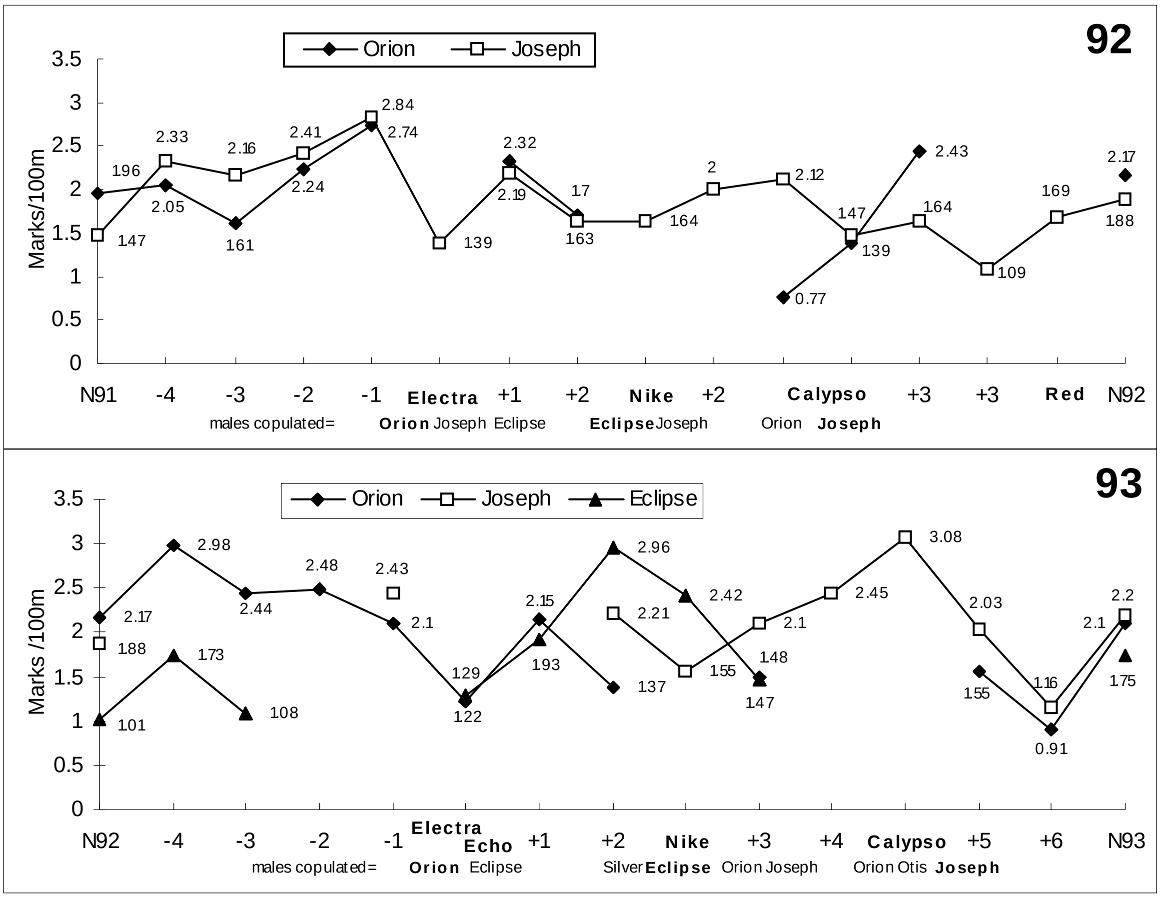


Figure 6.3 Daily mark-rates (marks/100m) of males for the mating seasons 92 and 93. Mark-rates are displayed within the weeks before (-) and weeks after (+) relative to the first female's oestrus (Electra). The oestrus of Echo, Nike, Calypso, Red are also displayed. Territory partners are boldfaced. N91, N92 are average mark-rates for non-mating seasons, N93 are the mark-rates in late August 93, after the mating season.

In the 93 mating season four weeks before Electra (the first female) came into oestrus Orion marked at close to three marks / 100 m walked throughout. He decreased his mark-rate on the two days prior to mating with his partners Electra and Echo, whilst his rate was lowest the day he copulated. Orion's marking increased again when searching for his females while probably trying to guard them from mating with other males. Despite his effort Electra was seen to copulate with Eclipse. Eclipse in 1992 also showed a peak in marking two days before mating with his partner Nike - who subsequently engaged in EPCs with three other males. Finally Joseph increased his marking rate as his partner Calypso came into oestrus though she copulated with Orion first. The next day when Joseph mated her his mark-rate dropped as well. A general decrease in mark-rates was observed for all males after all neighbouring females were mated. This was probably due to the unavailability of mating partners and termite food.

Male Marking relative to Partner's Oestrus

To test for the increase in mark-rate before each male's own partner came into oestrus their different mark-rates were arranged on a time scale and overlaid on the day of her first accepted copulation (Fig. 6.4). It was possible to overlay the different mark rates arranged by weeks before and after the mating day only, since not all males could be followed and their mark-rate recorded on the same days relative to their partners mating. In three out of the five cases where an intrapair copulation was observed in the two seasons, the first copulation accepted by the female was not with her partner.

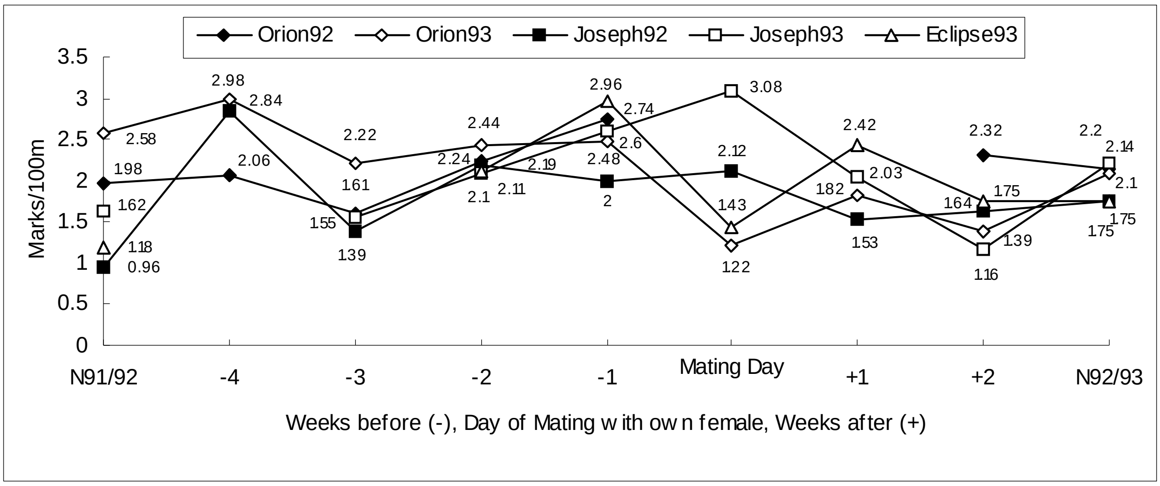


Figure 6.4 Changes in daily mark-rates within the weeks before (-) each male mated with his own female partner (Mating Day) and the weeks after (+). Their different mark-rates are arranged on a time scale and overlaid on the day of her first accepted copulation. Non-mating season mark-rates are given for comparison at the left and right extremities of the graph.

In the week prior to their partner's oestrus males generally had mark-rates greater than two marks / 100m. An exception was Joseph in 92 who scouted Eclipse's territory, thus marking at lower rates, and subsequently mated Nike the day before his own female Calypso accepted copulation with Orion first. Though differences in mark-rates were not clear-cut a gradual increase towards the week before oestrus is discernible (Fig. 6.4). The mark rates one week before were significantly higher than three weeks before (MWU-test, $Z = -2.205$, $n = 9$, $p < 0.05$). Orion and Eclipse decreased their mark-rate on the day of mating their partner, while Joseph increased it. During the week after mating, males either increased their mark-rate when other males still showed interest in their partners or dropped their mark-rate when females were already in metoestrus. Within the second week after mating the males' mark-rates were significantly lower than during the week before mating (MWU-test, $Z = -2.402$, $n = 10$, $p < 0.05$).

Changes in Female Mark-Rates over the Mating Season

Female daily mark-rates were calculated like those of males. Rates were plotted relative to the first day they accepted copulation, the second day of copulation, and the first day after the last copulation (Fig. 6.5). Mark-rates showed a very large variation and clear-cut patterns are difficult to discern when looking at them in Fig. 6.5. In the 91 and 92 mating seasons mark-rates were fairly low prior to mating (Fig. 6.5), while two females advertised after being mated by their partner on the border of their territory to that of their chosen cuckolding male. In season 93 (Fig. 6.5) females already displayed high mark-rate in the week prior to their mating, and then decreased their marking on the day of mating.

When pooling the three mating seasons females marked at significantly lower mark rates at the start of the mating season, four weeks before their copulation, than within the week before oestrus (MWU-test, $Z = -2.382$, $n = 16$, $p < 0.05$; Fig 6.5). Their mark-rates within one week before oestrus was also higher than within the second week after oestrus (metoestrus) (MWU-test, $Z = -2.143$, $n = 13$, $p < 0.05$). Females dropped their mark-rates on their first mating day relative to the week before their oestrus, though this was not significant at the 5 % level (MWU-test, $Z = -1.868$, $n = 12$, $p = 0.06$).

My impression of females in their pro-oestrus was that they advertised their reproductive condition with higher mark-rates when walking alone than when they were courted by males was tested. On eleven days mark-rates of females walking alone were compared with those when a male courted them on that same day. Mark-rates of females followed by males (mean = 0.84 mks / 100 m) were always lower than when walking alone (mean = 1.39 mks / 100 m) (Wilcoxon signed-ranks test: $Z = -2.93$, $p < 0.005$). Some of the females stopped even marking altogether when a male was courting them.

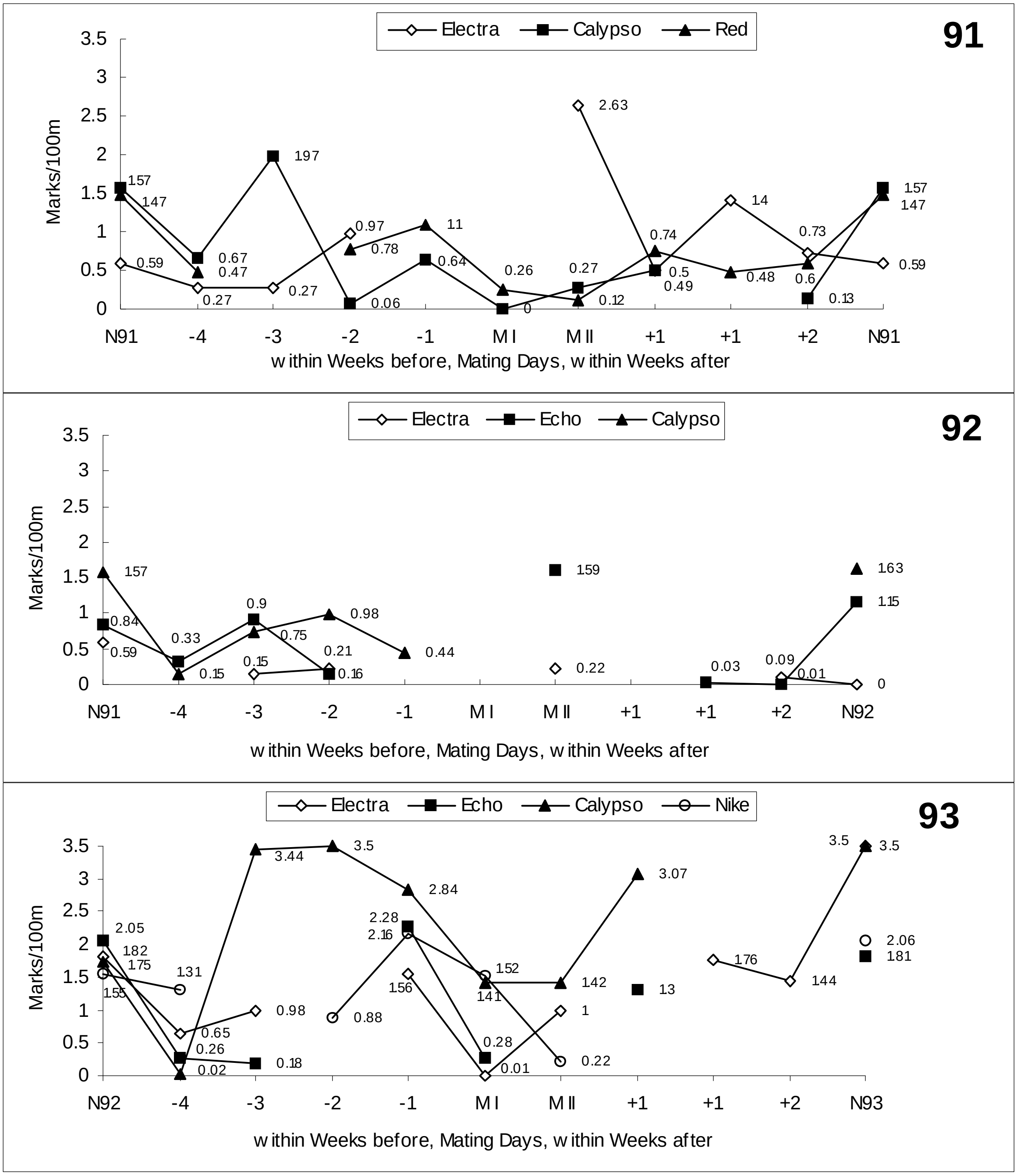


Figure 6.5 Female daily mark-rates for the mating seasons 91, 92, and 93. Mark-rates from within four weeks before (-), on their first Mating Day (MI), on their second Mating Day (MII), and within the weeks after (+) the last copulation. N91, N92 are individual mark-rates for March and September of non-mating seasons. N93 are the mark-rates in late August 93, after the mating season.

After copulating with their own partner some of the five northern females were seen to increase their mark-rates relative to their first or second mating day presumably to continue advertising their oestrus to suitors by scent marking (Fig. 6.5). Echo's scent marking behaviour relative to the territory of the neighbouring male to the north-east is shown for the night following her presumed mating with her partner in 1992 (Fig. 6.6). She concentrated to mark heavily in the territory of the chosen male outside of her territorial borders, leaving 50 scent marks there. However high mark-rates by a female within her territory (both in border and internal areas) could also signal her receptivity likewise. One example was Calypso in season 93 who for weeks before her oestrus showed mark-rates at around three marks / 100 m walked (Fig. 6.5) without ever leaving scent marks outside of her territory (PI = 0; Table 6.2). She continued to mark on the days she mated, though reduced, but increased her pasting once more after mating with her partner, whilst again not leaving her territory.

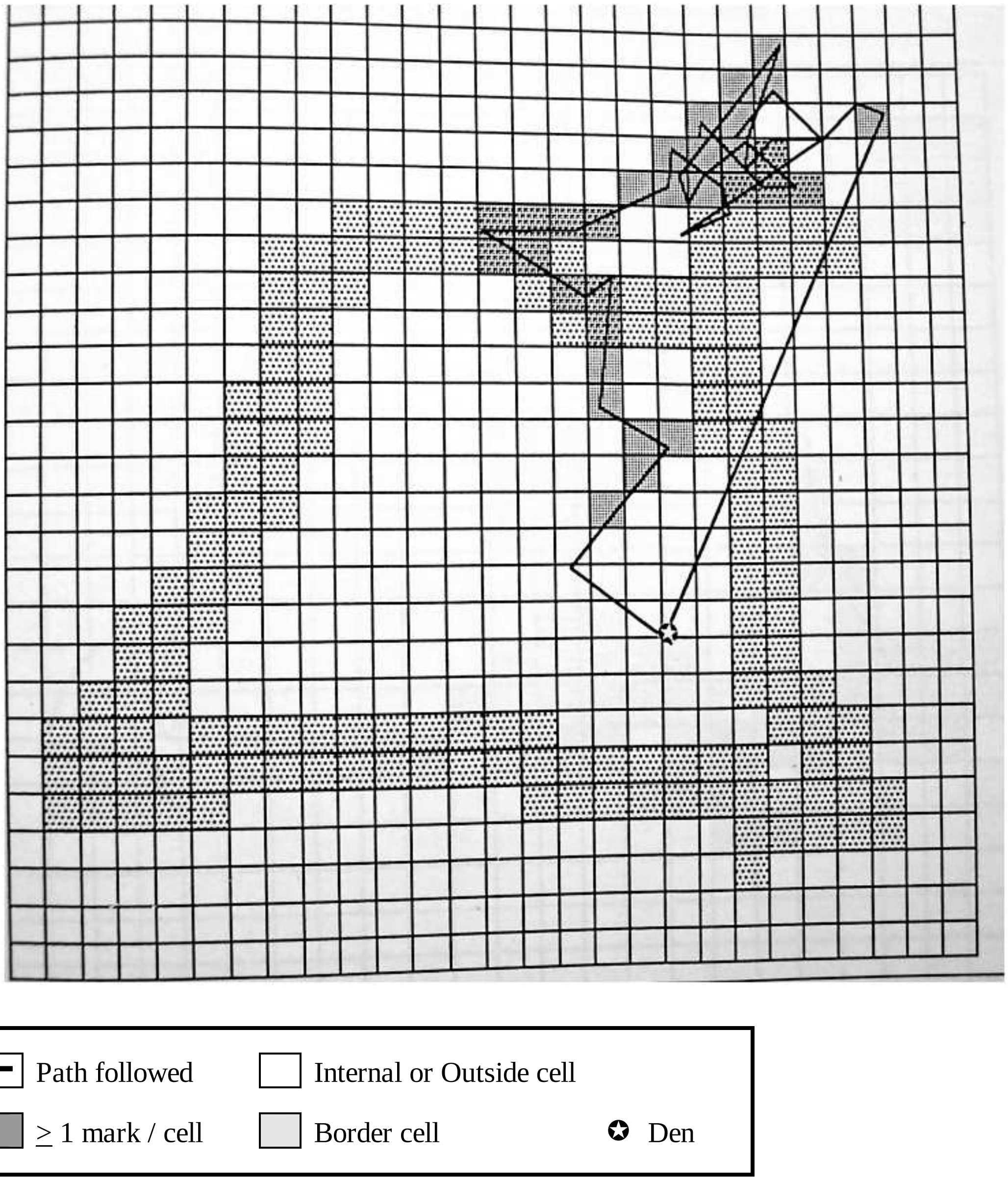


Figure 6.6 Path taken by female Echo and the 1-ha cells where she scent marked in the night after her presumed mating with her partner in mating season 92.

Response of Male to Female Scent Marks

A few well placed scent marks by the advertising female may be effective in attracting EPCs from a neighbouring male (Fig. 6.7). After having mated with three other males (including her partner) Nike presumably marked inside of Joseph's territory. He found the first mark sniffed and showed flehmen, then trotted straight into her territory, after 830 m found a second mark, flehmened and sniffed for 20 seconds and galloped on. He found Nike one minute and 170 m further upwind. So within 20 minutes and travelling 1000 m he presumably found her through her scent marking. They walked together for 1 100 m while Nike left 13 pasting and Joseph none, then started to copulate.

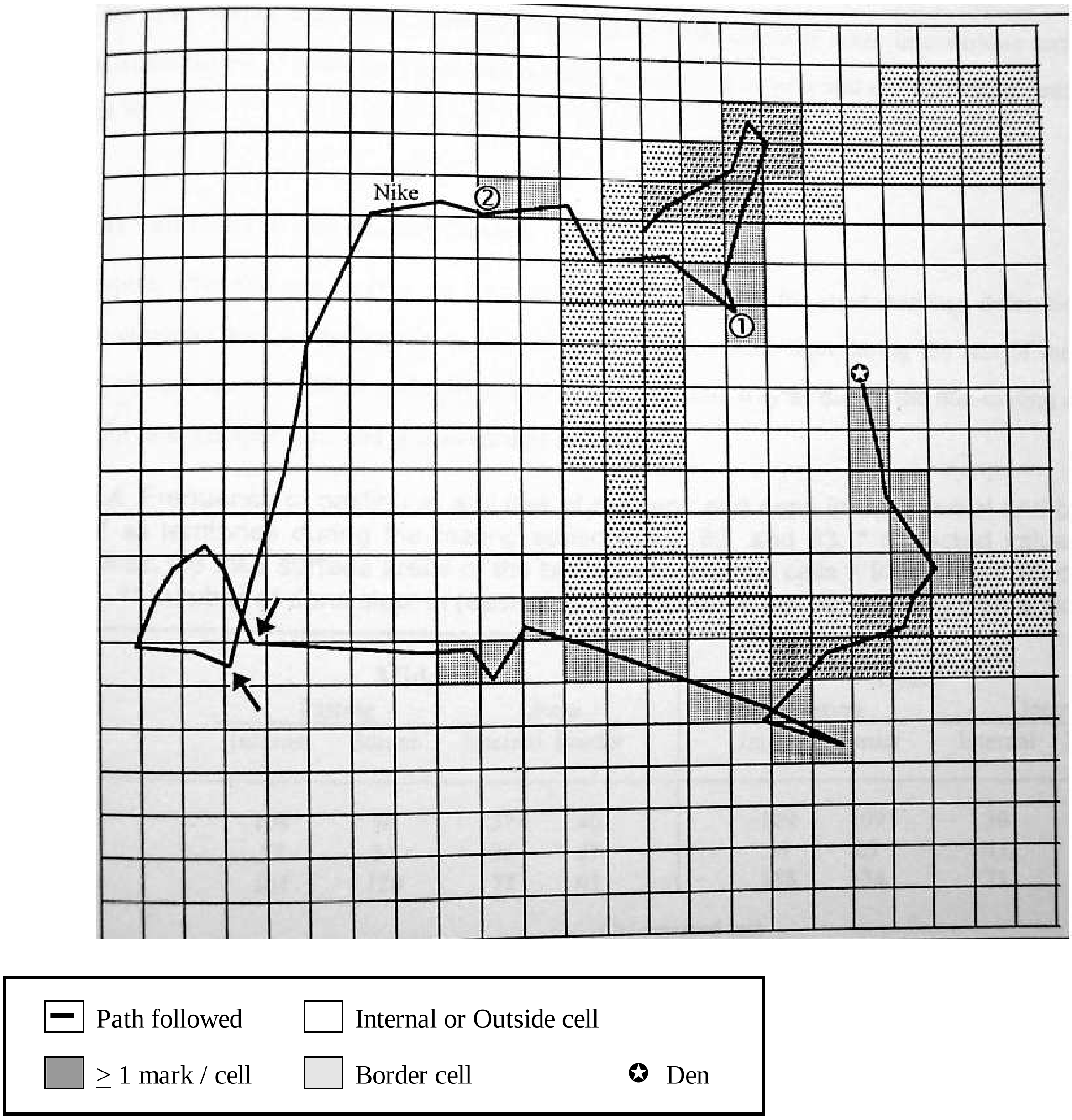


Figure 6.7 Path followed and scent marking by Joseph leaving his territory on the night he found scent marks (①②, presumably deposited by Nike) and mated with Nike. The start and end of their copulation is indicated by arrows.

Redefining Territory Borders

After the hectic mating activity in late July was over both aardwolf sexes were less actively walking, feeding, and marking. Correspondingly their mark-rates dropped significantly in relation to those showed in the days around oestrus (Wilcoxon signed ranks test; Z = -3.3, n = 14 (pairs), $p<0.001$), to pick up towards the end of August when reinforcing previous territory borders or defining the outlines of their territories anew (Fig. 6.3; Fig. 6.5). The mark-rates during September, when territories were presumably redefined were significantly higher than those in late July and mid August (Z = -3.3, n = 14 (pairs), $p < 0.001$; Fig. 6.3; Fig. 6.5). This pattern was especially evident after the mating season 93 after having simulated numerous intrusions by both aardwolf sexes into various territories through translocation of scent marks in the preceding non-mating season and during mating season 93 (Chapter 9).

Middens and Dens in the Mating Season

It was hypothesised that aardwolves use dens and especially middens for scent marking, defecation and urination in border zones significantly more during the mating season than during the rest of the year. The marking and use of middens and dens is analysed in the same way as during the non-mating season to allow for later comparisons and is summarised in Table 6.4.

Table 6.4 Frequency of pasting at and use of middens and dens in the internal and border areas of all territories during the mating seasons 91, 92, and 93. * expected values are derived from the total surface areas of the two areas, internal cells = 938 ha, border cells = 817 ha). ** number of dens slept in (each den counted once per season and animal only).

	Middens				**Dens**			
	Pasting		Usage		Pasting		Usage**	
	Internal	Border	Internal	Border	Internal	Border	Internal	Border
Males	104	96	37	40	129	109	30	9
Females	57	24	36	21	59	25	41	10
All adults	161	120	73	61	188	134	71	19
	Chi-squared test							
	χ^2	p	χ^2	p	χ^2		χ^2	
Males vs. females	7.95	s.	3.01	n.s.	6.57	s.	0.16	n.s.
Adults: observed vs. expected*	1.44	n.s.	0.05	n.s.	2.67	n.s.	22.36	s.

Males pasted at border middens significantly more often than females, which pasted proportionately more often at internal middens (Table 6.4). This suggests that males concentrate their effort more in the borders than females, possibly for defending their females via scent marking or advertising to neighbouring females visiting border middens. Both sexes jointly marked border and internal middens at the same rate as the relative sizes of the two zones predicted.

Midden usage for defecation and urination was not statistically different comparing the sexes, though males used border middens slightly more often than internal (Table 6.4). Females alone used internal middens significantly more than border middens ($\chi^2 = 3.94$, d.f = 1, $p < 0.05$). The overall usage by both sexes was again not different from that expected from their distribution.

Scent marking of border dens was significantly more pronounced in males relative to females, though they still pasted more often at internal dens (Table 6.4). Like for the marking of middens this shows that males and females emphasise marking dens differently. This was also evident when combining the data for the sexes and comparing it to that expected from their distribution, but was not significant.

Both males and females used significantly more dens for sleeping in the interior than in the border (Table 6.4). The sexes did not differ in this behaviour.

Middens and Dens: Mating Season versus Non-Mating

Taking the frequencies each behaviour was seen during each seasons whilst pooling sexes, aardwolves used border and internal middens for defecation and urination similarly during both seasons ($\chi^2 = 0.08$, d.f. = 1, $p > 0.05$). Females alone marked significantly fewer times at border middens during the mating than non-mating season ($\chi^2 = 9.9$, d.f. = 1, $p < 0.05$).

Aardwolves slept in internal and border dens at a similar ratio during the mating and non-mating season when combining the sexes ($\chi^2 = 0.18$, d.f. = 1, $p > 0.05$). Significant differences were however found in males visiting more border dens for pasting during the mating season ($\chi^2 = 3.86$, d.f. = 1, $p < 0.05$), though still fewer times than internal dens.

It was tested how intensively males and females pasted at middens and dens in the mating and non-mating season (Fig. 6.8) relative to the distances they walked. Males and females walked respectively 653 km and 731 km in the mating, and 755 km and 654 km in the non-mating seasons. Males left significantly more pastings at internal and border middens and internal and border dens during the mating season (internal middens $\chi^2 = 35.4$, d.f. = 1, $p < 0.001$; border middens $\chi^2 = 8.9$, d.f. = 1, $p < 0.005$; internal dens $\chi^2 = 51.3$, d.f. = 1, $p < 0.001$; border dens $\chi^2 = 72.1$, d.f. = 1, $p < 0.001$). This suggests that dens and middens were visited more frequently by males specifically for pasting during the mating season. In contrast females left significantly fewer pastings at border middens

($\chi^2 = 30.9$; d.f. = 1, $p < 0.001$) and at border ($\chi^2 = 10.3$, d.f. = 1, $p < 0.005$) and internal dens ($\chi^2 = 9.6$, d.f. = 1, $p < 0.005$) than in the non-mating season. Differences between the seasons for females were not significant for internal middens ($\chi^2 = 3.5$, d.f. = 1, $p > 0.05$). This suggests that females pasted at dens and middens, serving as focal points for aardwolf communication, less frequently per distance walked in the mating season.

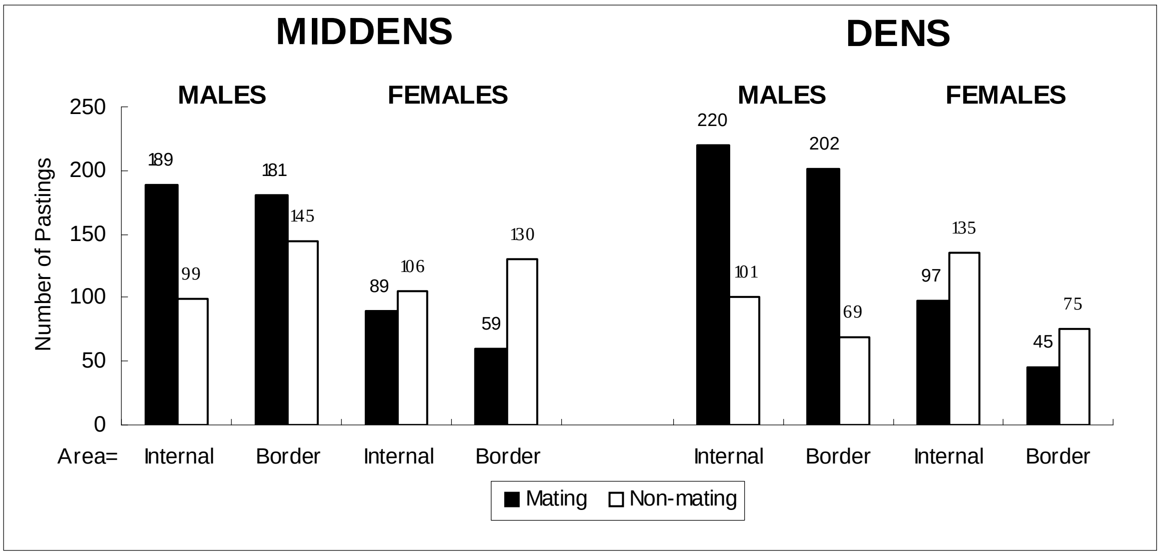


Figure 6.8 Numbers of pastings left at internal and border middens and dens by males and females during the mating and non-mating season.

DISCUSSION

The aim of this chapter was to test what role scent marking plays in the mating system of the aardwolf. The sexes in fact seemed to advertise to the opposite sex by increasing their rates of marking and strategic placement of scent marks in order to bring about EPCs. Males scouted and scent marked neighbouring territories to engage in EPCs and placed their scent marks more frequently on middens and dens in borders. The reactions of males suggested that they could determine by sniffing female scent marks when they came into oestrus and thus to time their own scouting trips.

Over the whole mating season males' scent marking activity increased just slightly in the border and internal areas of their territories in comparison to the non-mating season. The contrast between the two seasons resulted from the increase in rate of marking outside of their territories. This is in accordance with Richardson (1987b) although his observed outside mark-rate by males was nearly the same as the inside of the territories. During this study the outside mark-rate was always about half that of the inside mark-rate. Still EPCs were common during this study (Chapter 7) and all observed males marked outside of their territories and engaged in the same number of observed EPCs.

A reason for the moderation of the rate of marking outside of their territories in comparison to Richardson's (1987b) study could be that males were pursuing two different advertising strategies. A male might not have to mark aggressively outside of its territories and to fight physically to engage in EPCs. Alternative breeding strategies, while trying to sneak copulations without overt threat and fighting has been shown to be successful in silent as opposed to calling amphibian males (American bullfrog: Howard 1978; green tree frog: Perrill *et al.* 1982; natterjack toad: Arak 1988). Otherwise it was of importance which animal I was following at any one time since differences in mark-rates varied strongly over the season for one individual and between individuals. Another argument would be that territories during the present study were larger (see Chapter 5) and thus males were more limited in their ability to mark outside their territories. Almost all females marked outside of their territories but their PI value was again no indication to the frequency they were seen to engage in EPCs (Chapter 7). One can however suggest that this outside of territory marking functions as an attempt to attract neighbouring males.

Advertisement and Intimidation through Scent Marks

The male with the smallest territory had the highest PI probably since he could afford to leave many scent marks outside of his territory. This hypothesis would support the above argument that small territory size allows for higher outside of territory mark-rates, while large territory owners would still be busy defending the borders of their large territories (Richardson 1991; Chapter 5).

The small sample of individuals observed during this study made the classification of males into the two categories 'inferior' and 'superior' difficult. However considering several criteria for copulation and scent marking identified Orion as a high quality male. The two other males, contrary to my impression, were similar in ranking. The higher pasting index (PI) of Orion the superior male was not necessarily in accordance with securing the most EPCs, as was found by Richardson (1987b). Even the lowest ranking male Eclipse was observed to engage in equally as many EPCs. The PI indexes were anyway rather similar in the three northern males so the PI index alone would not allow a good ranking of males. One could however classify males by the number of EPCs their females were able to engage in, which could be due to both the males' inability to defend his female through fights but also the females' influence.

During this study two male pasting tactics may have been employed to achieve EPCs. One is through early and frequent scouting, scent marking neighbouring territories at high rates, advertising to females and intimidating their male partners (Richardson 1987b), ultimately fighting with other EP-males and the female's mate. This tactic received support through observations of Orion's behaviour. The concept of intimidation is however subjective and therefore difficult to prove. That an intimidating challenge is in fact transmittable through the deposition of scent marks will be shown in Chapter 9. Intimidation to the point that male partners gave up their females to the EP-males without a fight was never observed and bloodshed was frequent. The other tactic was employed by Eclipse who scouted and scent marked less. He did not fight with the resident males for their partners, but still engaged in EPCs as frequently. At this point female influence may be important. Since aardwolves are long-lived and some territories remained relatively stable in time female preferences for certain neighbours can evolve.

An alternative function of male outside territory scent marking could be to lure the courted female towards the border of the intruding neighbours territory. The odour of male scent marks has also been suggested to have a physiological role, to familiarise and increase the readiness of the female to respond sexually to this particular male and to synchronise their activities (Soderquist & Ealey 1994; Storey *et al.* 1995).

Females with high PIs could advertised to other males outside their territory borders to solicit EPCs. They mainly scent marked outside her territory to attract males, when no courting males were around. In some cases a few female pastings were effective to produce the desired EPCs when deposited during important periods and at precise locations. High mark-rates inside territories could also attract visiting males and signal the females' oestrus, without females having to leave their territories. Females with extra-pair male attention whilst marking just inside their territories would ensure that solely bold neighbours, intruding and scent marking in the females' territories would find their marks. Aardwolf males were capable of distinguishing female from male scent marks and to sense when a particular female was approaching oestrus (Chapter 9) to time their intrusions. This testing of scent marks was indicated by showing flehmen after sniffing scent marks. Male dik-diks were also observed to show flehmen after smelling female pre-orbital marks (Brotherton 1994) and this behaviour is usually associated with testing oestrus (Estes 1972). It has been well documented that urine of female mammals contains reproductive hormones which provide a reliable indicator of oestrus (Eisenberg & Kleiman 1972; Doty & Dunbar 1974).

The outside of their territory marking pattern of Electra and Echo sharing one territory is open to speculation. The older Electra had a higher PI value whilst living alone in the first season, then in the following two mating season she had lower values, whilst Echo scent marked frequently outside her territory. Although I assumed in mating season 92 and observed in season 93 that Orion mated them both, he could not prevent EPCs with their neighbours. He copulated in 93 for more than three hours with each female and guarded them afterwards (Chapter 7). However since he could not guard both females effectively at the same time Electra copulated with Eclipse and Echo advertised to the north-eastern neighbour. Therefore a high PI value of Echo did not necessarily mean that she was paired to a inferior male. However she was not seen to copulate with another male which might have been due to Orion's superior quality in keeping competitors from copulating with her.

Changes in Mark-rate over the Mating Season

During the scouting period, up to four weeks before the first female came into oestrus, mark-rates of all males were generally high, increasing for each resident to a peak one or two days prior to the day of mating with their partner. This could be seen as a form of guarding their females, by leaving scent marks at high rates throughout their territory they signalled their determination to defend their partners to scouting males. High marking rates together with urinating over oestrus females' scent with their own urine has been widely reported in male ungulates (pronghorn: Moodie & Byers 1989; African buffalo: Sinclair 1977; dik-dik: Hendrichs 1975; Brotherton 1994; warthog: Radke & Niemitz 1989) but also in male canids (bat-eared fox: Lamprecht 1979). The decrease in mark-rate on the day of copulation was probably owing to the mating activity which kept males from maintaining high rates. In addition they were probably trying to avoid advertising their whereabouts to EP males while copulating. An extra-pair male following the female ready to accept copulation into her territory stopped scent marking as well. This could likewise have been to avoid detection by her male partner, and thus the resulting disturbance or even disruption of the copulation (Chapter 7). After the last female of neighbouring territories had mated there was a decrease in general activity including scent marking of males, probably to endure this time of low termite activity, to pick up again at the start of summer with warmer weather conditions (Richardson 1987a; Anderson 1994).

Female scent marking strategy was even more variable than that of males. At the start of May with increasingly cool temperatures and resulting reduced termite availability (Richardson 1987c; Anderson 1994), scent marking decreased in females. With approaching oestrus marking rates increased reaching a peak in the week before oestrus advertising their reproductive status. Their rate of marking though depended on the attention females received from scouting and courting males. When males were present they marked at lower rates, to increase their marking when males were not courting. They were trying to receive attention by both their partners and EPC males. Higher mark-rates were also displayed by dik-dik females in the absence of their partners (Brotherton 1994). Since male partners always tried to overmark or at least marked close to their female's pastings during the mating pair run (Chapter 7) or when following them around in pro-oestrus, her higher mark-rate whilst alone could aim to attract selectively EP males when her partner could not overmark their pastings.

I had the impression that when females approached oestrus they scent marked increasingly along their borders or in the territory of their neighbours of choice to advertise their reproductive state and encourage visits from them. In fact all females strove to receive EPCs (Chapter 7). In one case though, in the third year of habitual ‘planned’ yearly EPC, Electra met Eclipse at the same time and place even without prior extensive border or outside of her territory marking.

While walking together with a EP-male prior to copulation the female continued pasting leaving a trail for other males including her partner to follow. This could be seen as female incitation of male-male aggression, and will be more extensively discussed in the following chapter of the sexes mating tactics.

When females were in metoestrus their rate of marking dropped to low rates within the next day, to pick up again by the end of winter. This was probably like in males to save energy when neither food nor mating opportunities were available and thus worth defending. Both sexes increased their mark-rates towards the end of August, presumably to redefine territorial borders so often transgressed in the hectic female oestrus periods. Re-establishment or first establishment of territories has been reported to coincide with high mark-rates especially for seasonally breeding ungulates (pronghorn: Gilbert 1973; Thomson’s gazelle: Walther 1978) but also wolves (Rothman & Mech 1979).

In accordance with their prolonged scouting activity males marked at both border middens and dens more than females over the mating season. Both sexes retired much more frequently in dens in the interior of their territories not different from frequencies observed in the non-mating seasons. So aardwolves seemed to always considered it safer to sleep in the interior of their territories (see also Chapter 9). In comparison to the non-mating season males visited and marked all dens and middens more often per distance walked in the mating season while females showed the opposite pattern. The male’s tendency of treating dens and middens as focal points for olfactorial communication (Richardson 1990) even more so in the mating season thus was confirmed. Assuming further that border middens and dens serve an important territorial function (Richardson 1990) the reduced activity of females there hints to a reduced territorial defence of the feeding territory during the mating season with low termite availability. The main resource defended by males however switched from food in the non-mating to the even more valuable resource of female mating partners in the mating season. Males therefore increased their scent marking efforts correspondingly to defend their females.

CHAPTER 7

MATING TACTICS IN THE AARDWOLF

INTRODUCTION

Given their physical and ecological diversity, it is not surprising that carnivores exhibit considerable variation in social organisation. The majority of species (85-90 %) are solitary outside of mating periods (Creel & Macdonald 1995). Individual adults mostly hold territories excluding members of the same sex, but with extensive overlap with territories of the opposite sex (Ewer 1973, Powell 1979, Erlinge & Sandell 1986). Monogamous pairs are the basic social units among canids (Kleiman & Malcolm 1981), with a tendency to larger groups at the two extremes of body size (Moehlman 1986). Breeding groups are the general rule among smaller herpestids and larger hyaenids (Rood 1986, Mills 1989). Descriptions of mating systems are complicated as observations and genetic studies disclose that extra-pair (and off-territory) copulation may be commonplace (aardwolf, Richardson 1987b; European badger, Evans *et al.* 1989; grey wolf, Lehman *et al.* 1992; Ethiopian wolf, Gottelli *et al.* 1995).

Both brown and spotted hyaenas live in social groups, varying in size between one female adult with her cubs to 80 individuals called clans (Kruuk 1972, Mills 1989). The female members of a clan are related and nomadic or immigrant males accepted into clans by the females seem to perform most of the matings (Mills 1982, 1983, 1990, Frank 1983; Owens & Owens 1996). Whilst in brown hyaenas no dominance hierarchy was apparent in small clans (Mills 1989) a separate linear dominance hierarchy within each sex was observed in larger clans (Owens & Owens 1996). Regardless of clan size a dominance hierarchy exists among adult females of spotted hyaenas, and they and their offspring are dominant to the generally lighter built immigrant adult males (Mills 1989). Mating has been rarely witnessed in wild hyaenas but in the spotted hyaena the oestrus female attracts the attentions of a number of males already up to two months before she is ready to mate (Deane 1962, Frank 1983). The largest and most dominant male drives the others away and after varying periods of consorting with and courting the female copulation continues for several hours with bouts of 5 - 10 minutes, repeated 3 - 4 times per hour (Frank 1983). While the mating male seems remarkably tolerant of interference by young males, he drives away older males who approach and even attempt to disrupt the mating. After the dominant male mated other males have persistently attended females for up to 40 days later (Frank 1983). The available evidence for spotted hyaenas suggests a highly polygynous uni-male mating system, with the behaviourally dominant male fathering most of the cubs in the clan during his tenure (Frank 1983).

In contrast to the brown and spotted hyaenas the aardwolf is considered a socially monogamous species (Richardson 1985) because a male and a female share a perennial territory with the male showing extensive parental care. Sexually however the aardwolf is polygamous, with numerous extra-pair copulations (EPCs) occurring during the short winter mating season (Richardson 1987b). Territories are maintained by both the male and female partners of one territory, but the opportunity to mate with a female is not exclusively available to the resident male, but also appears to be determined by open competition with neighbouring males. As a result of an EPC a resident male may invest unknowingly in guarding the cubs (Richardson 1987b) that another male fathered (Power *et al.* 1981).

Paired males try to maximise their breeding success by engaging in EPCs with neighbouring paired females in addition to copulating with their own female partner (Richardson 1987b). The strategic marking of neighbouring territories by males during ‘scouting’ excursions has been detailed in the previous chapter.

Courtship is initiated by the aardwolf male following the female around, testing her receptivity through short attacks or by prancing past her with his tail raised in the air, described as ‘flirting’ (Richardson 1985). She tries to bite him and frequently gives chase for short distances. This testing of the female can continue for about ten days (Richardson 1985), until she comes into oestrus and shows interest to follow the courting male herself. The pair then walks around together for various distances, while the male makes short mounting attempts, lasting often a couple of seconds only. During these short mounts no intromission takes place, and after dismounting the female follows the male who walks on. After various time spans and distances covered permanent copulation is initiated. Copulation in aardwolves lasts from one to four and a half hours, depending on whether it is disrupted by the female, another male, or the male dismounts voluntarily. The penis remains inserted for the entire period, but with no copulatory tie as found in canids (Ewer 1973; Richardson 1987b). Initial thrusting just after permanent mounting is followed by more thrusting sequences at approximately hourly intervals, presumably indicating multiple ejaculations (Richardson 1987b).

Competing males tried to disrupt the copulation but also females terminate prolonged copulation by entering a den (Richardson 1987b). Males attempt to counter early termination of copulations by females by leading the female far away from her den. She then has to walk back with him clinging to her back, having to take several rests and thus prolonging copulation time and increasing the possible number of ejaculations. This introduces the subject of sperm competition, and which of the males is most likely to sire the most cubs (Parker 1984; Huck *et al.* 1985; Richardson 1987b; Birkhead & Møller 1992).

Some paired females seem to aim for EPCs with neighbouring males (Richardson 1987b), though the advantages to her appear less obvious. When she succeeds to attract (Chapter 6) and ultimately mate with a superior male her offspring may gain the higher quality genes of the intruder (Gladstone 1979). She may produce ‘sexy’ sons - with the cuckolding tendencies of their father (Weatherhead & Robertson 1979) and if she is fertilised by several males, she will increase the genetic variability of her offspring (Maynard Smith 1978). Within her oestrous period, lasting for up to three days, a female will often mate with her partner and an aggressively marking neighbour (Richardson 1987b; Chapter 6). A disadvantage to her is that a cuckolded resident male might defect from guarding her cubs (Richardson 1987b). Given mixed paternity is possible she may avoid defections by copulating with her mate as well as with the intruder (Richardson & Coetzee 1988). Multiple paternity within litters has been found in many of the carnivores for which genetic tests of paternity have been conducted (lions, Packer *et al.* 1991; dwarf mongooses, Keane *et al.* 1994; Eurasian badgers, Da Silva *et al.* 1993). There is some circumstantial evidence of mixed paternity in the aardwolf but conclusive evidence is still missing (Richardson 1987b).

Female choice has rarely been documented in mammals (Trivers 1972; Kleiman 1977; Emlen & Oring 1977) but there is growing evidence that females in highly polygynous species are able to exert considerable choice in determining their mating partners (e.g. Jamaican anole lizard, Trivers 1976; northern elephant seals, Cox & Le Boeuf 1977; fiddler crabs, Zucker 1983). Aardwolves females can choose males and can influence the duration of copulation by terminating it by entering a den (Richardson 1987b). This is hypothesised to allow for more copulations with other males (Richardson 1987b).

These observations made on aardwolves suggest that there may be considerable sexual conflict between the partners of one territory. The aim of this chapter is to test whether females solicit EPCs with neighbours or non-resident males. It will be determined whether females do influence the course of the copulation and whether they treat their resident male differently from extra pair males. Further I want to look at males and their ability to prevent their females from copulating with other males and the tactics they may employ to prolong their own copulations. With more copulations seen during the present study I will try to determine in greater detail the extent of the conflict between males and females during mating.

METHODS

The start, duration, and end of the mating season is taken as defined in the previous chapter. It was recorded when males first showed interest in each individual female. Suitors were defined as all males showing interest in a particular female, including her partner. Extra-pair males had to be observed scouting into her territory and courting her. The terms of anoestrus, pro-oestrus, oestrus including ovulation, and then metoestrus were defined in Chapter 6. It is not known whether ovulation is spontaneous or induced in the aardwolf. Induced ovulation has been reported for the Felidae and does not occur until after the last copulation (Burke 1975; Eaton 1976).

Several behaviours during copulation were recorded by continuous sampling (Altmann 1974). These were brief mounting attempts, permanent mounting, duration of thrusting movements of the male while inserted and the date and time intervals when these behaviours occurred. In addition the total mount time of a male and the distance the pair moved while copulating was recorded. Previously it was suggested, that merely the second thrusting sequence after an hour of intromission represented an ejaculation (Richardson 1987b). Here I will treat the first thrusting sequence also as an ejaculation. Additional information was collected on whether the male guarded the female from other males before or after his copulation. Guarding was defined as the time the male stayed within visual contact of the female, which was ready to accept males, and attempted to chase away all other competitors.

RESULTS

Timing of Mating

The duration and onset of the mating season started at slightly different times in the three winters. The different dates of copulations of the females are displayed in Fig. 7.1. The copulations that were observed between individual males and females have been listed previously in Table 6.2. The mating seasons lasted between 7 and 11 weeks from May through to the end of July with all copulations observed (n=18) within one months time from late June to late July. A further three unobserved copulations were expected to have taken place assuming that the female always mated with her resident male. This would take the minimum number of copulations analysed to 21. A shift in the timing of copulation of three females from the 92 to the 93 mating season was noticeable although the duration and onset of the two seasons were similar. Electra and Nike shifted their dates of matings forward by one week while Calypso delayed it by 12 days (Fig. 7.1). The fact that the majority (n = 12) of observed copulations occurred in July shows that breeding was synchronous in the female aardwolves of the study area.

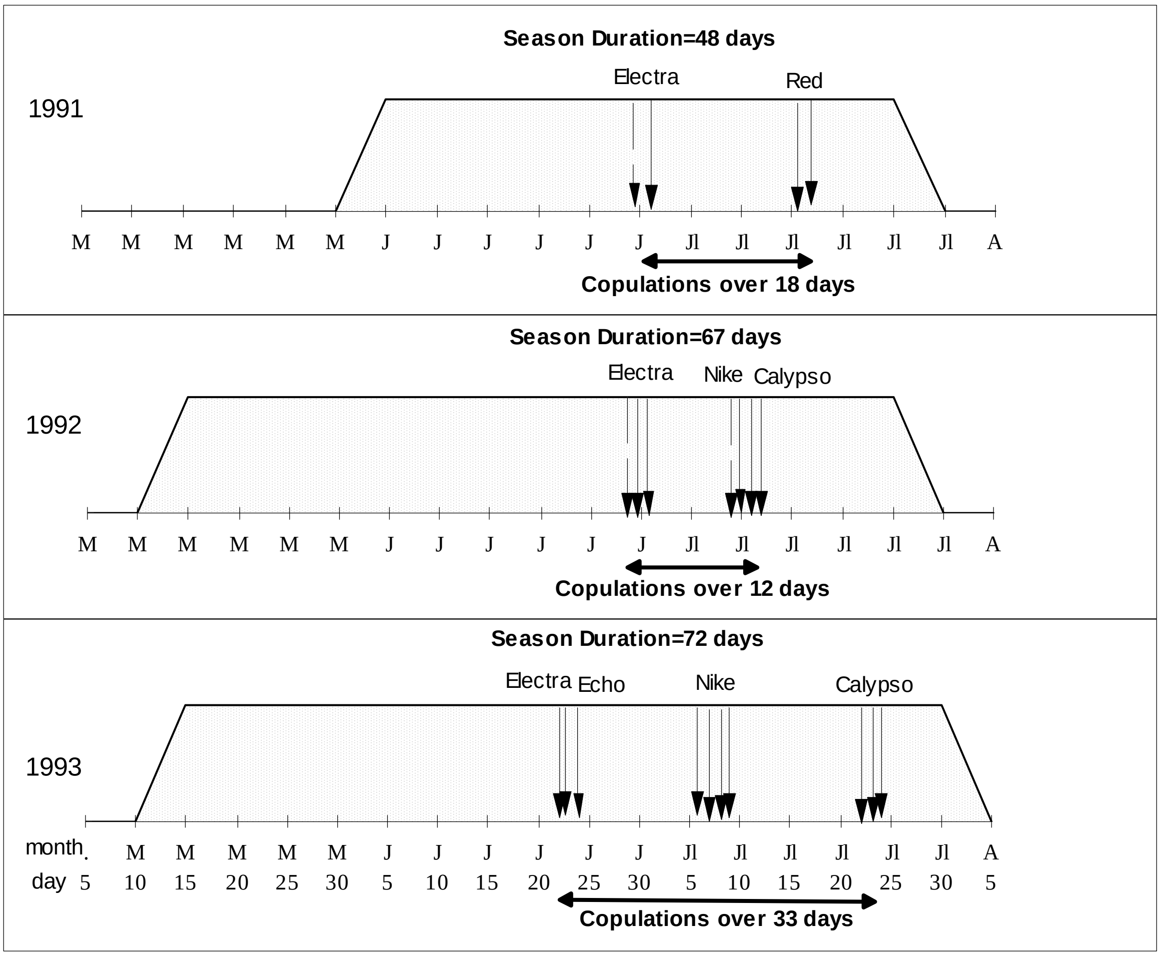


Figure 7.1 Timing of the mating season in 1991, 1992 & 1993 with observed and expected copulations. X-axis is segregated into 5 day segments from May to August. Solid lines indicate copulations seen, dotted lines copulations expected.

Pre-copulatory Behaviour

Males showed interest in a particular female for widely different time periods prior to their respective mating (Table 7.1). The number of suitors varied between two and five and was on average greater than three. Male partners showed interest in their partners associating with them frequently for a mean of more than a month before their females came into oestrus (Table 7.1; range 10 - 57 days before oestrus). They followed the females around their territories for up to two hours at a time courting them by ‘flirting’ (prancing past them) while sniffing their scent marks and showing flehmen repeatedly towards them. This was continued until the female became receptive and was ready to accept copulation. Males tried to chase competitors away from their female. This male behaviour of associating and testing the receptivity of the females may be seen as a form of pre-copulatory guarding.

Table 7.1 Summary of events observed during the mating seasons 91, 92, and 93. N/A - not known. * number of copulations each female was assumed to have received.

Year	Name of Female	Interest of Males in Days before	Number of courting Males	Copulations observed (probable*)	Total Copulation Time (hours)	Total Ejaculations received	Total Time (min) Males thrusted
91	Electra	N/A	2	1(2)	2	2	19
91	Red	12	4	2	6	4	32
92	Electra	30	3	2 (3)	4	3	33
92	Nike	14	3	1 (2)	3.5	3	28
92	Calypso	58	4	2	8	5	49
93	Electra	55	3	2	5.5	6	55
93	Echo	45	2	1	3	4	24
93	Nike	10	5	4	13	11	81
93	Calypso	71	5	3	6	6	57
Mean ± S.D.		37 ± 23.65	3.4 ± 1.13	2 (2.3) ± 1 (0.86)	5.7 ± 3.31	4.9 ± 2.66	42 ± 19.98

Three of such pre-copulatory guarding incidences observed during two seasons are hereafter described in more detail below. Since the aardwolf pair moved around together extensively it is termed the ‘mating pair run’ (MPR). On two occasions the female was mated before by an extra-pair male and her male partner succeeded in disrupting the copulation. On the third occasions the resident tried to disrupt the EPC but was defeated by the extra-pair male. After the disruption by the resident male or after the EPC was over the male resident stayed close to his female, who was ready to accept copulation from him. The often lay down together sometimes even touching each other. The pair would also walk fast together and on several occasions even ran around the perimeter of their territory while both were scent marking. The female was marking at a lower rate than the male (Table 7.2).

During this MPR male suitors tried to run in on the pair and challenged the resident male, who gave chase (Table 7.2), the female partner often accompanying him, possibly to watch the outcome of fights between the males. The pair often sniffed each others scent marks, showed flehmen and overmarked directly or within 0.5 m of each other. While walking together shifts in the lead were frequent, each partner possibly trying to lead the other in its interest. In order to avoid aggressive disruption of their copulation by other males the resident male might have tried to avoid detection by leading the female into areas of the territory seldom used for feeding and where trespassing seldom occurred. He may have simply tried to lead the female away from her den as far as possible. Females seemed reluctant to follow the male too far away from her den. When the female stopped following her partner he made short mounting attempts several times without intromission. After these she usually seemed to follow him more eagerly again. The male finally mated after a mean of 16 hours (Table 7.2) of being together with the female who had stood still and been receptive from the start of the association (MPR).

Table 7.2 Summary of observations of partners staying together and the ‘Mating Pair Run’ (MPR, n = 3). * distance a pair walked together excluding chases by the male of other male suitors.

Pair male/ female	Season	Time together (hours)	Time (hours) on MPR	Distance on MPR* (km)	Male Marks	Female Marks	No. of fights (chases) with EP-males	Copulation after No. of hours together
Joseph / Calypso	92	10	2	3.5	76	44	3 (3)	6.5
Joseph / Calypso	93	45	3.5	7.8	159	126	4 (20)	25.5
Eclipse / Nike	93	19	7	8.8	170	70	2 (10)	16
Total		74	12.5	20.1	405	239	9 (33)	48
Mean		24.67	4.17	6.7	135	80	3 (11)	16

The female on the MPR appeared to encourage other suitors to find them by scent marking, leaving a ‘scent mark trail’ for other males to follow. In mating season 93 Nike left significantly less numbers of scent marks than Calypso (Table 7.2) in proportion to those left by Eclipse and Joseph over a similar distance of MPR ($\chi^2 = 12.6$, d.f. = 1, $p < 0.001$). Females often ran towards the male challengers when her partner did not react immediately. He then had to follow in order not to loose her and give the other males a mating opportunity. In 1993 Joseph found Orion mating with Calypso after 1.5 hours and disrupted the copulation. Joseph then stayed together with Calypso for 24 hours without copulating. At this time, the male neighbour Otis repeatedly ran towards them and was chased by Joseph, who subsequently lost Calypso. Otis found Calypso and they succeeded in mating for one hour whilst Otis ejaculated once, when Joseph managed to disrupt the copulation. Joseph then immediately mounted Calypso for prolonged copulation. They copulated for nearly 3.5 hours and he continued guarding her from more suitors for 16 hours afterwards. Calypso was aggressive towards Joseph guarding her and continued scent marking at a high rate when walking. By this date she was the last female of the study area in oestrus, so all the suitors’ attentions were focusing on her.

Although the sample size for MPRs is small there seemed to be a difference in energy spent by Joseph during the two seasons (Table 7.2). In 1992 Orion enticed Calypso out of her den and when they just started prolonged copulation Joseph found them. Orion won the fight with Joseph and copulated with Calypso for 4.5 hours afterwards. The next day Joseph found Calypso and they stayed together. However Joseph’s scent marking and chasing of suitors as well guarding Calypso for 3 hours after their copulation only seemed less energetic than in the 1993 mating season. During 1993 he defeated Orion copulating with Calypso after 1.5 hours.

Copulation

Females copulated with between one and four different males with a mean of more than two (Table 7.1). Thus the total time each female was observed to copulate each season varied accordingly between two and 13 hours. Likewise the number of ejaculations received varied between two and 11 with the mean close to five. The total recorded time females received stimulation through thrusting by the different males varied between 19 and 81 minutes, with a mean of 42 minutes (Table 7.1). The duration males thrusted just after mounting permanently was always longer than when thrusting the second time (MWU-test: $Z = -4.65$, $n = 33$, $p < 0.001$), while the second lasted longer than the third ($Z = -2.69$, $n = 23$, $p<0.01$).

There was a significant correlation between the number of ejaculations and copulation time during matings (Spearman Correlation coefficient; $r_s = 0.588$, $n = 18$, $p < 0.05$). Likewise the number of ejaculations was correlated with the duration of thrusting movements ($r_s = 0.849$, $n = 18$, $p < 0.0001$) and the latter with the copulation time ($r_s = 0.583$, $n = 18$, $p < 0.01$).

Termination of Copulation

The number of times females terminated copulations are summarised in Table 7.3. In most of the IPCs (80 %) the female terminated the copulation by going down a den, leaving her partner at the entrance, whilst in the EPCs nearly half the copulations ($n = 6$) were ended by the male dismounting voluntarily or the copulation was forcefully disrupted (23 %) by another male. Females walked significantly further with her mate on her back, to go down a den ending the copulation, than in EPCs (MWU-test: $Z = -2.42$, $n = 8$, $p < 0.05$). Taking the distance they walked back to their den as a measure for their eagerness to mate they walked nearly 2.5 times the distance with their mate than with an EP-male (Table 7.3).

It was tested if there were differences in the copulatory behaviour between IPCs and EPCs. Pooling all mating seasons and matings observed in the intensively studied four northern territories, it was apparent that the male resident (IPC) copulated for longer than neighbours during EPCs though not significantly so (MWU-test: $Z = -0.7$, $n = 18$, $p > 0.05$; Fig. 7.2). However partners thrusted significantly longer ($Z = -2.37$, $n = 18$, $p < 0.05$; Fig. 7.2) and ejaculated more frequently ($Z = -2.01$, $n = 18$, $p < 0.05$; Fig. 7.2) per mating than neighbours during EPCs. This pooling of the behaviours of the three males however conceals the fact that at least in one incidence Orion as an extra-pair male copulated longer than the resident male Joseph with his female afterwards.

Table 7.3 Termination of observed copulations.

Copulation type	Female ends copulation (n)	Male ends copulation (n)	Other Male forces termination (n)	Totals	Mean ± S.D Distance (m) moved while copulating
IPC	4	0	1	5	1080 ± 440
EPC	4	6	3	13	442 ± 200
Total	8	6	4	18	619 ± 400

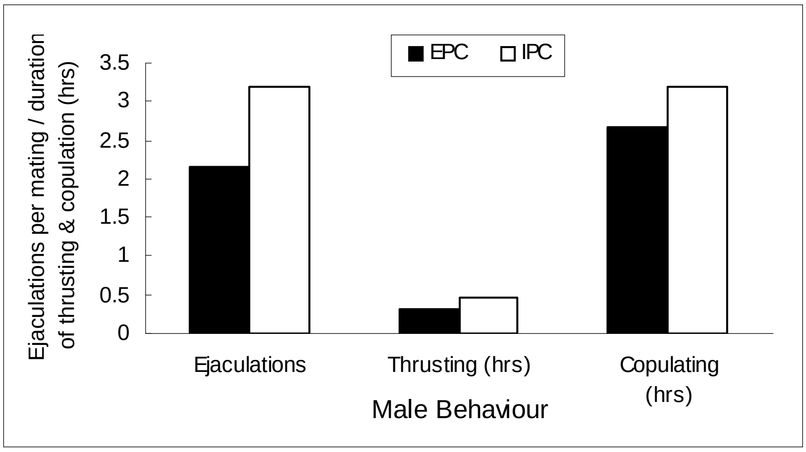


Figure 7.2 The mean number of ejaculations observed and the mean duration of thrusting and mean time copulated in hours during IPCs and EPCs.

Post-copulatory Mate-Guarding

In four out of five observed IPCs the male partner and in a sixth case one of the competing extra-pair males guarded the female after they had copulated themselves. They guarded their females for between 3 - 16 hours (mean = 10.8 ± 5.4 hours, n = 5). In one case of an IPC the male did not guard his partner after the copulation due to disruption by another male. After a long MPR Eclipse had been copulating with his partner Nike for 2.5 hours when Orion came and disrupted the copulation. Eclipse seemed to have won the fight since Orion ran away. Nike ran after Orion, but Eclipse made no attempt to follow, and Nike and Orion later mated for 3.5 hours.

Individual Strategies

There was considerable variation in the behaviour of the three females which each were observed to copulate five times in the three mating seasons. Electra being the largest aardwolf of the study population, at 13 kg being one kilogram heavier than the largest male, followed her mating partners just for short distances and moved a mean 367 ± 162 m when mounted by a male back to her den. She ended the copulation four times (80 %) actively. Nike the smallest female (7.5 kg) followed males for much further (794 ± 412 m) and never ended a copulation on her own. The differences in distance these females carried were statistically significant (MWU-test: $Z = -1.98$, $n = 10$, $p < 0.05$). Nike advertised extensively outside of her territory (Chapter 6, Table 6.2) and during season 1993 copulated for 13 hours with four different males carrying them for almost 4 km. Calypso was intermediate in these respects, moving 648 ± 537 m and terminated her two IPCs by entering a den.

There is evidence to suggest that one female may repeat her EP mating tactics from year to year (Chapter 6). In all three mating seasons of this study, after mating with her partner (once observed, twice assumed), Electra was observed to mate with the male Eclipse of the neighbouring territory after meeting him close to the same den at the border of their territories at sunset. She also always terminated the copulation by entering that same den after 1-2 hours and 1-2 ejaculations.

There is evidence to suggest that a female may choose whether or not to leave her den to start copulation with a particular male. In mating season 92 Joseph courted his mate Calypso intensively by flirting, following her, and by visiting her den, where she spent long periods inactive. On these occasions he stood at the entrance, whilst whining and sometimes scratching in mounting agitation to entice her out of the den. This was also the case on the first day of her oestrus. Calypso did not leave her den when Joseph came past. Two hours later Orion came to her den and she left her den to follow him. At first Calypso seemed hesitant in following Orion who appeared to be trying to entice her across the border into his territory. Just after the Calypso and Orion started prolonged copulation, still within her territory, Joseph disrupted the copulation. Orion won the fight and Calypso then followed him willingly for 500 m into his territory. They copulated for 4.5 hours after which he dismounted voluntarily.

The three northern males were each observed to engage in EPCs and IPCs three or four times during each of the three mating seasons (Table 7.4). Due to the unpredictable nature of copulations both in space and time I probably have missed some of them e.g. Orion’s IPCs in seasons 91 and 92. However males were copulating for a different mean duration per female (Table 7.4). When considering the distance each male was carried by females during EPCs Joseph was carried for significantly further than Eclipse (MWU-test; $Z = -2.02$, $n = 8$, $p < 0.05$).

Table 7.4 Mean durations males copulated and distances they were carried by females in EPCs and IPCs.

Male	EPCs: Duration copulated in hours (occasions)	EPCs: Range of Distances carried by females	IPCs: Duration copulated in hours (occasions)	IPCs: Range of Distances carried by females
Orion	3.17 (3)	190-530 m	3.5 (2)	350-1140 m
Joseph	3.06 (4)	420-780 m	3.38 (2)	1070-1330 m
Eclipse	2.00 (4)	230-550 m	2.25 (1)	1500 m

The incidence of EPCs during this study was very high with 13 (62%) observed versus eight IPCs assuming that the resident male always mated with his female (n = 3 not observed) (Fig. 7.1). When observed copulations (IPC = 5) were considered only the percentage of EPCs from a total of 18 observed copulations increased to 72 %. In just one out of 18 matings (5.6%, from three mating seasons) am I reasonably certain that the female mated with her partner only.

Whilst attempting to assess the three northern males' reproductive success a number of parameters are considered. Male bodymass, the number of observed EPCs by his partner, his cub-guarding effort in the following season, and the survival of his female partners' cubs to the age of dispersal in both September 1992 and 1993 are summarised in Table 7.5.

Table 7.5 Parameters relevant to male reproductive success in 1992 and 1993. * Orion had two females (EPCs and cubs surviving per female).

Male Name	Summer Body mass (kg)	Female partners' EPCs	Intensity of cub-guarding in 1992	Cubs surviving to dispersal
Orion	8.5	3 (1.5)*	very diligent	8 (4)*
Eclipse	9	4	less diligent	4
Joseph	12	3	no guarding-	1

Though the males' partners engaged in similar numbers of EPCs they guarded their partners' cubs differently and correspondingly the survival of these cubs was different. The body mass of the males during the guarding period was inversely correlated to their cub-guarding effort.

DISCUSSION

Despite the difference in length of the three mating seasons all copulations occurred within a period of one month. The effect of such a concentrated period of female oestrus may influence the extent of guarding mates, seeking EPCs, and changes of the sexes' mark-rates over the mating season (Chapter 6). In a year of drought the onset of mating in the aardwolf was hypothesised to be delayed by low termite availability (Richardson 1985). Similarly, a low level of nutrition has been reported to delay the onset of oestrus in impala (Fairall 1983). Calypso may have delayed her oestrus in 1993 by almost two weeks due to her being food stressed. After a gestation period of about 90 days (Richardson & Koehler 1990) cubs were born in October and she was both guarding her cubs without support from her mate Joseph and suckling them until February. Sustained lactational effort of female aardwolves (Van Jaarsveld *et al.* 1995) would further influence loss of condition. As a result just one of Calypso's cubs survived to dispersal during the study period. In contrast Electra's and Echo's simultaneously shifted their oestrous forward by one week. This could have been a result of their shared cub-guarding and suckling duties in the previous non-mating season. This left them with more time to feed likely improved their nutrition level. Also Orion was guarding their cubs very diligently. An effect of this spreading of female oestrus periods over a longer time span could be that males could concentrate on each female separately. They would not have to give up post-copulatory guarding of their own females to engage in EPCs when other females come into oestrus soon after their females.

The incidence of EPCs was very high, accounting for between 62-72 % of all copulations, although most male partners guarded their females after copulation. Almost all females copulated with more than two males. Attempted cuckoldry was thus the prominent strategy used by the aardwolves during this study. EPCs occurred in a greater proportion of instances than observed by Richardson (1987b), despite much higher outside of territory mark-rates recorded during his study. This might have been due to a larger discrepancy in male quality during his study. Some males were marking very strongly and engaged in EPCs frequently, while some of his observed males scent marked little outside of their territories and did not achieve EPCs (Richardson 1987b). During his study top males may have been more successful in preventing EPCs. In my study all three males may have been of more similar quality. All scouted and scent marked in neighbouring territories and engaged in similar numbers of EPCs. The fact that Orion had two females also may have weakened his ability to guard them from EPCs. Ultimately aardwolf males during the present study may have achieved their goals without high outside of their territories marking and / or females were more willing to accept EPCs.

Male Incentive for EPCs and Chances for fathering cubs

The courtship of spotted hyaenas resembles that of the aardwolf with prolonged association between the pair, copulations bouts stretching over several hours and one male monopolising access to the oestrus female by guarding her (Frank 1983). In contrast to the aardwolf the social dominance hierarchy in spotted and brown hyaenas is determined in the clans prior to mating and the dominant male seems to perform most of the matings (Frank 1983; Mills 1990; Owens & Owens 1996). Due to the pairs' territoriality aardwolf males do not maintain a social dominance hierarchy (Richardson 1987b). Male quality is advertised to their neighbours by means of scent marking (Chapter 6) and in fights over mating rights by scramble competition between males.

The more mating opportunities a cuckolding male has the greater his chances for propagating his genes (Trivers 1972). However he may lose some, or all paternity of his partner's offspring to another extra-pair male mating with his female while he was courting a second female himself (Hanken & Sherman 1981; Alatalo *et al.* 1984). There is evidence for the aardwolf (Richardson & Coetzee 1988) and other species (hoary marmot: Barash 1975) that a cuckolded male will spend less time or even defect completely from investing in his partners cubs. In dunnocks (Davies 1986) a male helps rear chicks only if he too copulated with the polyandrous female. Mixed paternity in one litter has been suggested in the aardwolf (Richardson 1987b) and was recorded in several carnivores species (Packer *et al.* 1991; Keane *et al.* 1994; Da Silva *et al.* 1993). This would leave the cuckolded male with a chance of paternity provided he has copulated with his partner. He should not defect from cub-guarding unless he has an alternative female with which he can breed exclusively, or if he affected his future reproductive output negatively by devoting energy into raising the cubs (Richardson 1987b).

In some bird species paired males attempt to prevent EPCs by mate-guarding, chasing off suitors during most, and sometimes her whole fertile period (bank swallow: Beecher & Beecher 1979; mountain bluebird: Power & Doner 1980; pied and collared flycatchers: Alatalo *et al.* 1984). But also mammals practice mate-guarding (Gilbert 1973; Sinclair 1977; Richardson 1985, 1987b; Brotherton 1994; Storey *et al.* 1995).

The adaptiveness of copulation behaviour of mammals has been extensively studied (rodents: Dewsbury 1972, 1984; carnivores: Ewer 1973; lion: Bertram 1975). Potential strategies for siring success in male aardwolves may be: (1) prolonged copulation: could act as a form of mate-guarding, would allow the sperm to move closer to the ova after ejaculation and consequently have a better chance of fertilisation than sperm introduced by a second male. It may also serve to displace previous ejaculates back down the vagina, for the second male. (2) multiple ejaculation: by increasing the total volume of his ejaculate, a male dilutes the relative concentration of another male's sperm, whether introduced before or after his own sperm. (3) stimulation: prolonged stimulation of the female vagina through thrusting would make ovulation more likely in induced ovulators (Burke 1975). Prolonged copulation and multiple ejaculation may serve the interest of either the first or the second male (Hanken & Sherman 1981; Huck *et al.* 1985). Induced ovulation and the timing of, and between, copulations are also of great significance to siring success (Dewsbury 1984; Huck *et al.* 1985). No data exist for these aspects of aardwolf reproduction, though the behaviours observed during matings allow for speculation.

EPCs were observed both before and after IPCs. If there was a first-male mating effect this should have affected the male's cub-guarding activity when cubs were born. Joseph's lack of guarding Calypso's cubs may indicate this. An argument against this effect would be that some males spent considerable time and energy during the MPR, after another male had already mated their female. The male partner then copulated after spending many hours guarding his female, which was eager to accept copulation from him from the start. Males may aim for the most favourable point in time when their partners' ovulation was most likely. This may have been indicated by their frequent sniffing and flehmen of females' scent marks. Joseph may have sensed that in season 1992 Orion's EPC with Calypso was more effective since his MPR and post-copulatory mate-guarding of Calypso was shorter than in 1993.

Another function of the MPR may be that the male receives cues of the female's motivation to copulate with him. After her EPC she may strive to secure his commitment to cub-guarding. This part of courtship may thus allow the male to assess his certainty of paternity, before investing in offspring by cub-guarding. Male ring doves rejected females willing to accept copulation prematurely, those females having courted with another male beforehand (Erickson & Zenone 1976).

Aardwolf females may be spontaneous ovulators and thus may have a short critical period for fertilisation (Huck *et al.* 1989). The fact that Eclipse did not guard Nike from EPC despite that he apparently defeated Orion may indicate this. He may have been confident that he had fertilised Nike and further fighting was unnecessary. The risk of further injuries through fighting with Orion while trying to prevent the EPC may have been higher than Orion's chances for fertilisation. The fact that almost half the EPCs were terminated voluntarily by the male, and therefore likely happened during a sub-optimal time for fertilisation, add further weight to this hypothesis. Dominant males of spotted hyaenas were observed to lose interest in a female after having copulated even when other males were still interested in her (Frank 1983). The timing of copulating with the spontaneously ovulating female may be the main function of the mating pair run (MPR).

Striving for EPCs must however still pose a potential reproductive benefit to males, even when mating at an unfavourable time during oestrus only. The risk of injury when detected by the male partner and cost involved in scouting to neighbouring territories may be offset by the chance to achieve at least partial fertilisation of a litter. Many EPCs remained undetected by the resident male and occurred mainly after the IPC. The sole male that was not challenged aggressively for his partners was the superior quality Orion who despite guarding his females could not prevent EPCs in his absence. Another reason male partners were failing to prevent EPCs altogether could be due to their changing motivation. There may be behavioural trade-offs between the optimum period to guard and when to leave to find other mates (Parker 1974). However a male could have reduced the probability of being cuckolded by guarding his female at least for the critical time around ovulation.

The number of ejaculations and total time of stimulation while copulating would be of importance if sperm competition is happening, thus the male copulating the longest should have the greatest chance for fertilisation. Males tried to prolong copulation by leading the female away from her den and seemed to keep her interested to follow him through short mounting attempts. However copulation time alone might not be sufficient to ensure fertilisation. Joseph copulated with Calypso for 3.5 hours, though after Orion mated with her beforehand for 4.5 hours. He defected from cub-guarding that season but did not desert his territory to move into that of another female as reported by Richardson and Coetzee (1988).

Considering all of the above arguments and observations Orion was likely the most successful male in both not being interrupted in his copulations with his two females, in possibly achieving several prolonged EPCs at the critical time for fertilisation by fighting aggressively and the number of cubs that he guarded to survive until dispersal. Since no conclusive data is available on mixed paternity in aardwolf litters Joseph's and Eclipse seemed similarly successful in their frequency of mating, though more cubs survived in Eclipse's territory than in Joseph's.

I hypothesise that a mixture of all the above arguments is likely to determine success of fertilisation of a female's offspring. A resident male would maximise his chances of fathering most of his female's cubs when copulating with her for a long time depositing large volumes of sperm. He may increase his siring success by copulating at the most favourable time for ovulation, or by inducing ovulation through prolonged stimulation. Meanwhile the number of EPCs achieved and even the duration of copulations alone seems inappropriate to indicate a male's success of fertilisation since even lower quality males were able to achieve numerous EPCs. Preliminary results from DNA fingerprinting of blood samples collected from Electra's cubs failed to record mixed paternity (Richardson, Sliwa, Wiid, in prep.). So although Electra after mating with Orion engaged in two EPCs in season 92 on her second day of oestrus, her cubs were all sired by her partner Orion.

Female Incentive for EPCs and their Influence on Copulations

The genetic advantages a female may gain from EPC (Maynard Smith 1978; Gladstone 1979; Weatherhead & Robertson 1979) may be offset by the disadvantage that her cuckolded partner might defect from guarding cubs (Richardson 1987b). However she can avoid defection of cub-guarding by resident male by granting both males some chances of paternity and copulate with her mate as well as with the intruder.

Females may encourage sperm competition (Knowlton & Greenwell 1984) by (1) soliciting EPCs through advertising with scent marks outside her territory (Chapter 6) and leaving a scent mark trail for other males to follow when on the MPR (2) by becoming available for a particular male when leaving her den at the critical time of her ovulation (3) by terminating copulations through entering her den a female can make herself available for mating with other males. (4) by incitation of male-male aggression by running towards another male when with her partner on the MPR. Some female ungulates in pro-oestrus initially flee the bull’s mounting attempts, the ensuing chasing attracting the attention of other males and often leads to the replacement of a smaller by a bigger bull (African buffalo: Sinclair 1977; eland: Hillman 1979).

Aardwolf females may differ in their motivation to influence the course of their EPCs, dependent on the quality of their male partner. Their influence was likely also dependent on female size and thus strength to terminate a copulation. A female with a high quality male guarding her cubs diligently would be expected to terminate her EPCs more readily. Electra followed her unchallenged high quality male Orion further away from her den than she followed the extra-pair males Joseph and Eclipse. However in the incidences when IPCs were disrupted by EP males the female partner did not hesitate to follow the interrupting male. All females seemed eager to copulate with their mate. This was likely to secure their partners’ commitment for parental care to her cubs.

The question however still remains why Electra and Echo with their superior quality partner Orion aimed for EPCs with lower quality males like Eclipse. Although Eclipse was apparently of lower quality than Orion Electra still allowed him to copulate, however probably at an unfavourable time for fertilisation, for shorter periods, and all copulations were terminated early by Electra. It has been observed that dominant female Ethiopian wolves appear to mate only with the dominant male within their own group, but mate with males of any status from neighbouring groups (Sillero-Zubiri *et al.*, in press). The emphasis in this case of female aardwolf mating behaviour may to increased genetic variability of her offspring (Maynard Smith 1978) in a closely related population. Some evidence for inbreeding has been found for the aardwolves of this study area (Richardson, Sliwa, Wiid, in prep.). Many aardwolves died due to locust poisoning in 1986 (Richardson & Coetzee 1988) and several subadults were observed to remain in the territory or established in neighbouring territories increasing the chances of inbreeding in the local population.

Although conclusive evidence from a genetic study of paternity in aardwolf litters is still outstanding the hypotheses discussed in this chapter suggest that all males aim to improve their siring success by engaging in EPCs. All females seem to solicit EPCs either to gain increased genetic variability or superior genetic quality of their offspring. Male mate-guarding was not completely successful in preventing EPCs. Both males and females seemed to pursue their mating tactics at least in part against the interests of their partner by trying respectively to prolong or terminate copulations. Females treated their copulating partners differently from EPC males with the likely purpose to avoid their defection from cub-guarding duties.

CHAPTER 8

THE USE OF URINE AND FAECES AS A MEANS OF COMMUNICATION IN THE AARDWOLF

INTRODUCTION

When urine and faeces are used for scent marking by carnivores, one is faced with the difficult problem of distinguishing between excretion and communication (Gorman & Trowbridge 1989). One distinction is that signalling with the two excretion products usually involves small, token volumes placed at specific objects, that are reanointed frequently (Kleiman 1966; Macdonald 1980, 1985). This token marking is common in all carnivore families, with the possible exception of the Hyaenidae (Gorman & Trowbridge 1989). In many carnivore species, including the hyaenas, faeces accumulate at discrete sites, known as latrines or middens, over long periods. These middens are often situated along the borders of territories and serve an important territorial function as scent marking sites (Kruuk 1972; Peters & Mech 1975; Mills *et al.* 1980; Gorman & Mills 1984; Richardson 1987a, 1990).

The functions and techniques of scent marking with faeces and urine are well documented in carnivores (Kruuk 1972, 1976; Peters & Mech 1975; Mills *et al.* 1980; Macdonald 1985; review in Gorman & Trowbridge 1989; Vila *et al.* 1994). How striped hyaenas use their middens is not yet clear (Kruuk 1976; Macdonald 1978). In the other two hyaena species faeces are left exposed on middens frequently situated on the border of clan territories, thus serving a territorial purpose. The smell and white colour of the faeces serve as conspicuous olfactory and visual signals (Kruuk 1972; Gorman & Mills 1984; Mills & Gorman 1987; Mills 1990). In contrast to this aardwolves treat their elimination products differently. Most defecations are deposited on middens and scratched over with soil possibly to avoid olfactorial confusion of faeces, smelling of terpene, with *Trinervitermes* feeding columns (Kruuk & Sands 1972; Richardson 1990). Scent marking through pasting with secretion from the anal pouch onto grass stalks is the primary means of delimiting an aardwolf pair’s territory (Kruuk & Sands 1972; Richardson 1990, 1991; Chapter 5). The preference for defecating and scent marking at middens along the territory borders, particularly in male aardwolves, suggests however a territorial function (Chapter 5 & 6). When urine is not excreted together with the faeces on a midden it appears to be voided at totally random positions in the territory, wherever the aardwolf happens to forage or walk (Richardson 1991). This is in accordance with studies on other hyaena species (Kruuk 1972; Mills 1990). Richardson

(1990) suggested that urine might play some role in scent marking during the mating season, when males left small deposits of urine at frequently used and visited middens and dens.

The purpose of this chapter was to investigate if urine and faeces could serve a communication purpose in aardwolves to complement the more obviously communicative pasting with fatty secretions from the anal pouch. One way of testing this was to see whether there were differences in the use of the different elimination behaviours and where faeces and urine were voided during the mating and non-mating season. This would indicate a potential reproductive function. Faeces and urine may even have a communicative function throughout the year, in which case one would anticipate no seasonal differences. Uncovered faeces away from middens and deposited along the borders or urine deposited specifically at dens and middens with pronounced scratching may be used for signalling.

METHODS

Defecations and urinations were continuously sampled as detailed in ‘General Methods’ (Chapter 2). Seasons were defined as non-mating season (September until April corresponding to summer) and mating season (May until August corresponding to winter). Mean number of times aardwolves defecated in the two seasons were calculated by including solely nights when the animal was followed for the entire activity period. Otherwise defecations and urinations left by the focal aardwolf after leaving the den or before retiring to its den in the morning would have been missed.

Six different types of elimination behaviours were distinguished:

a) defecation with scratching before and afterwards (DS)
b) urination and defecation with scratching before and afterwards (US);
c) defecation no scratching (DN);
d) urination and defecation no scratching (UD);
e) urination alone no scratching (UR);
f) urination alone with scratching (SU).

Further it was recorded if the defecations and urinations were at / on established middens or away from them and if deposited in the border areas of the territories defined by the seasons’ paste marking patterns.

Table 8.1 Frequencies of the different elimination behaviours recorded during the non-mating season, whether at middens or away, in the border or internal area of the territories, and for each sex.

	Non-Mating Season							
	At Middens				Away from Middens			
	Border		Internal		Border		Internal	
Behaviour	Male	Female	Male	Female	Male	Female	Male	Female
DS	21	14	8	20	2	5	1	2
US	83	57	22	77	10	7	2	5
DN	2	7	-	-	7	3	-	2
UD	12	12	5	1	12	3	1	1
UR	8	3	-	-	62	89	38	62
SU	1	1	-	-	-	1	-	-
Totals	127	94	35	98	93	108	42	72

Table 8.2 Frequencies of the different elimination behaviours recorded for the mating season, whether at middens or away, in the border or internal area of the territories, and for each sex.

	Mating Season							
	At Middens				Away from Middens			
	Border		Internal		Border		Internal	
Behaviour	Male	Female	Male	Female	Male	Female	Male	Female
DS	9	6	3	5	-	-	-	-
US	35	28	23	28	2	2	1	1
DN	1	1	-	1	4	5	3	2
UD	2	-	-	-	2	-	-	-
UR	19	5	-	1	30	36	13	26
SU	4	-	-	-	-	-	-	-
Totals	70	40	26	35	38	43	17	29

RESULTS

Frequencies of Elimination Behaviours

A summary of the frequencies of each elimination behaviour type recorded for non-mating and mating season, if at or away from middens, in the border or internal areas of the territories, and for the two sexes separately, is displayed in Tables 8.1 and 8.2.

Faeces were most commonly left together with urine and scratching (US) while urine alone was most commonly voided without scratching (UR), together counting up to more than 80 % of all elimination behaviours. Aardwolves defecated 2-6 times on a non-mating season night (mean = 2.87; S.D. = 0.97; n = 187). In the mating season they defecated less often due to fewer termite food available, between 1-4 times a night (mean = 1.4; S.D. = 0.65; n = 120). The number of single urinations (UR) varied between 1-7 times (mean = 1.99; S.D. = 1.25; n = 187) a night in the non-mating season, apart from the urine deposited together with defecations. In the mating season urine alone was deposited 1-3 (mean = 1.49; S.D. = 0.88; n = 88 nights). In the mating season urine was sometimes not voided alone during one activity period since it was left together with faeces on the midden. All elimination behaviours combined an aardwolf deposited faeces and / or urine up to nine times a night in the non-mating and seven times in the mating season.

Pooling of Behaviours

Sample size for many of the single elimination behaviours for seasons, sexes, whether at or away from middens, and deposited in border or internal areas were too small (expected < 5) for statistical treatment. Chi-square-tests to justify for subsequent pooling could just be performed for frequencies with which aardwolves deposited covered faeces (DS, US) at middens in their borders versus internal areas of territories. No differences were found, neither for the non-mating (Males: $\chi^2 = 0.58$, d.f. = 1; Females: $\chi^2 = 0.02$; Table 8.1) nor for mating season (Males: $\chi^2=0.91$, d.f. = 1; Females; $\chi^2=0.08$; Table 8.2) for the two behaviours. Frequencies of covered defecations away from middens were too small to be tested separately in the non-mating season or not recorded in the mating season. On this basis covered defecations were hereafter pooled (DS + US = Ds). Likewise frequencies for uncovered defecations with and without urine (UD, DN) were too small for testing so they were subsequently pooled as uncovered defecations (Dn).

Urinations alone (UR, Tables 8.1 & 8.2) were kept separate, while urinations with scratching (SU) were too few to allow for meaningful comparisons.

Defecation

Of a total 568 defecations 483 (85 %) were deposited at middens and just 85 (15 %) away from middens. At middens 439 (91 %) were covered while 44 (9 %) were left uncovered. Away from middens 40 (47 %) were covered while 45 (53 %) were left uncovered. Significantly more faeces were thus left uncovered away from middens than at middens ($\chi^2 = 105.1$; d.f. = 1; $p<0.001$).

Frequencies for the sexes are displayed in their percentages of being at and away from middens for border and internal areas during the seasons for covered (Ds = Fig. 8.1), for uncovered faeces (Dn = Fig. 8.2), and for urinations (UR = Fig. 8.3).

Covered defecations (Ds) showed no significant differences in their percentages deposited away from middens between non-mating and mating season, or border and internal areas, and even when comparing males and females, varying between 2.9 - 14.5 % (Fig. 8.1).

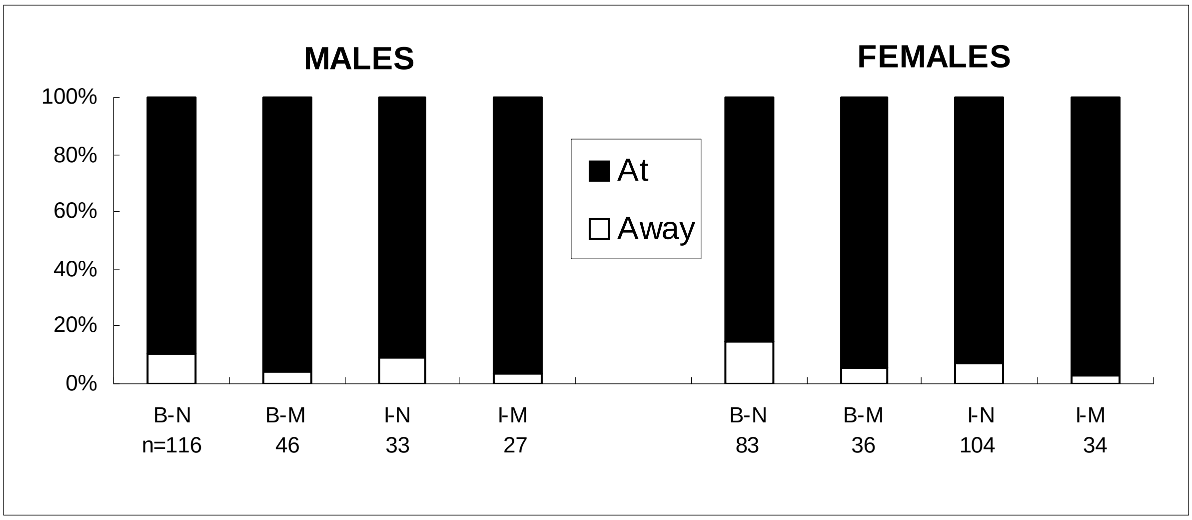


Figure 8.1 Percentages of covered faeces (Ds) in **B**(order) and **I**(nternal) areas, At and Away from middens during **N**(on-mating) and **M**(ating) season.

Uncovered faeces were left in varying percentages at and away from middens (Fig. 8.2). In the non-mating season males showed no significant differences in leaving uncovered faeces in border and internal area ($\chi^2 = 3.4$; d.f. = 1; $p>0.05$). Differences between season for males defecating in their borders were also not significant ($\chi^2 = 0.24$; d.f.=1; $p>0.05$). The other combinations could not be tested due to small sample sizes. The corresponding tests for females were however significant (border versus internal: non-mating, $\chi^2 = 4.19$; d.f. = 1; $p<0.05$; border: non-mating versus mating season, $\chi^2 = 7.44$, d.f. = 1; $p<0.05$). Differences between the sexes were prominent only when comparing uncovered defecation in borders during the non-mating season (B-N) ($\chi^2 = 6.54$; d.f. = 1; $p<0.05$) with males leaving more uncovered faeces away from middens than females. The other categories were again not testable due to small sample sizes.

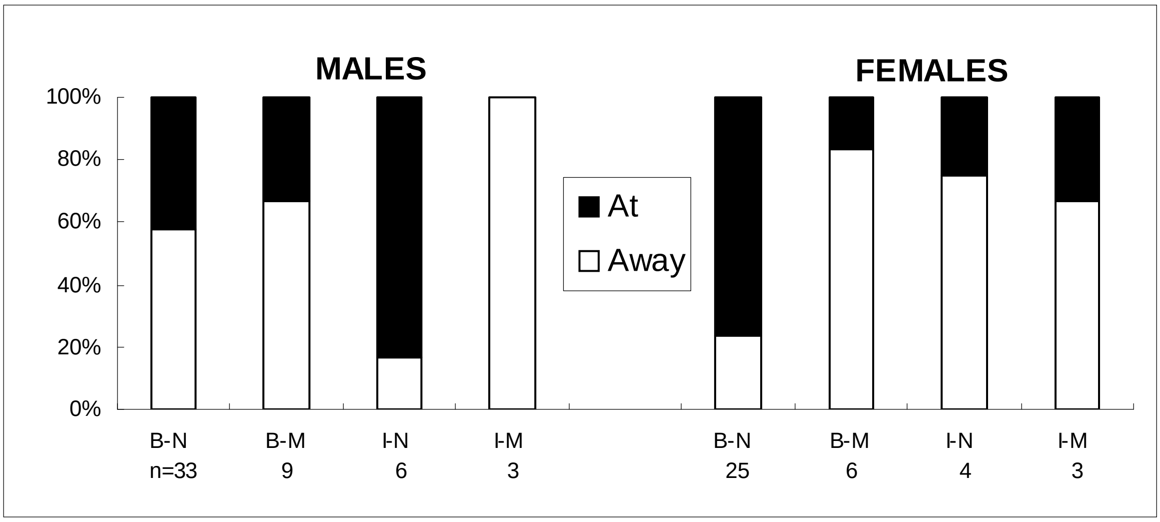


Figure 8.2 Percentages of uncovered faeces (Dn) in **B**(order) and **I**(nternal) areas, At and Away from middens during **N**(on-mating) and **M**(ating) season.

Further evidence for a territorial function of uncovered faeces came from observations of the male Orion. For one week in non-mating season 92 a male from the east was intruding every night into his territory. During this week Orion was followed for five nights and patrolled and pasted the eastern boundary every night, lying down there for long periods and leaving eight uncovered defecations away from middens. This is more than half of a total of 15 defecations he made. He did not feed in this area, which had low densities of termites (Richardson 1985) and few middens.

Aardwolves left significantly more uncovered defecations in the mating than during the non-mating season ($\chi^2 = 7.22$, d.f. = 1; $p<0.05$).

Uncovered faeces were placed distinctly more often in the border area than covered ($\chi^2 = 16.16$, d.f. = 1; $p<0.001$), when pooling he sexes.

Urination

The above tendencies were also tested for urinations at and away from middens. From a total of 392 single urinations without scratching (UR) 356 (91 %; Tables 8.1 & 8.2, Fig. 8.3) were deposited away from middens where the aardwolf walked or fed and just 36 (9 %) were at middens, where it would suggest a communicative function. Of the latter 25 were done during the mating season versus 11 in the non-mating season. Aardwolves deposited significantly more urinations at middens during the mating season compared with the non-mating season ($\chi^2 = 23.54$; d.f. =1; $p<0.001$). In the mating season 18.5 % were deposited at middens while in the non-mating season just 4.6 %.

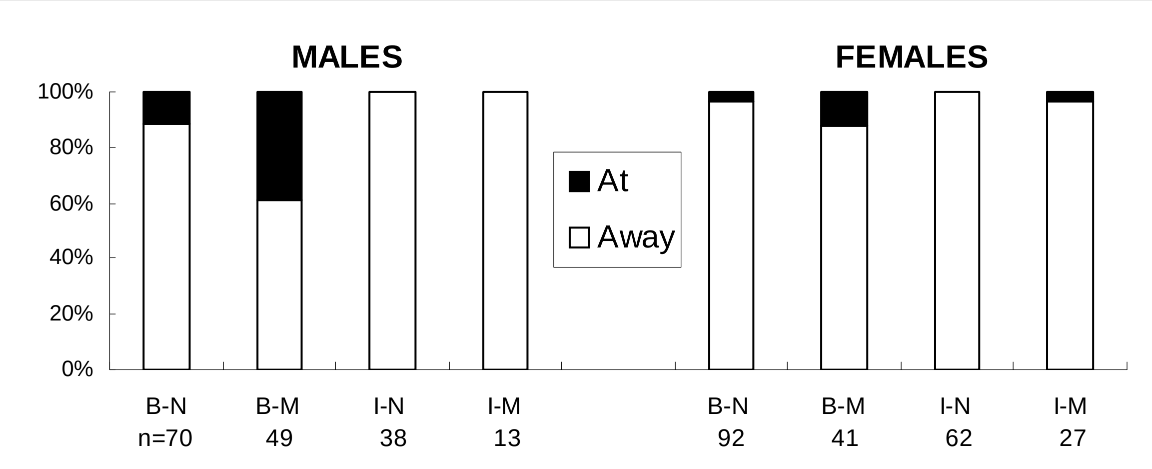


Figure 8.3 Percentages of uncovered urinations (UR) in **B**(order) and **I**(nternal) areas, At and Away from middens during **N**(on-mating) and **M**(ating) season.

Of the 36 urinations 27 (75%) were done by males and 9 (25%) by females ($\chi^2 = 9.0$; d.f. = 1; $p<0.005$). All except one midden (97.2 %) marked with urine were located in the border areas. Thus this marking of middens with urine was mainly performed by males during the mating season and almost always in the borders of the territories. There was too little data on single urinations with scratching (SU) for statistical treatment, but they reflect the patterns observed for UR.

DISCUSSION

Aardwolves defecated mostly at middens and the majority of those were scratched over or even completely buried, as was observed by Richardson (1990). Just a small proportion of covered faeces was deposited away from middens, with little variation due to season, sex, or position in border or internal areas. Thus it can be assumed that depositing covered faeces away from middens in aardwolves does not support a specific reproductive or territorial function and is done consistently by aardwolves regardless of sex. Uncovered faeces showed great variation in these measures. They were placed by both sexes distinctively away from middens, more often during the mating season, and more frequently in the border areas. They were likely used by a male in his border as additional, long lasting scent marks, to communicate his readiness to defend his territory to a specific intruder. Thus uncovered faeces were probably concentrated along the border of the territory to serve a communicative purpose to non-resident conspecifics.(Peters & Mech 1975; Gorman 1990; Richardson 1991, 1993).

In some instances the reason for leaving faeces uncovered away from middens could have been owing to the difficulty to cover faeces when no midden with loose soil was available close to the feeding site during the non-mating season. This would apply specifically to territory owners with extensive areas of hardbaked calcrete soil. In a study on European badgers single faeces deposited away from well established middens (latrines) were referred to as ‘temporary defecation sites’ (TDS) and suggested to simply serve the purpose of defecation pure with no additional communicatory function (Roper *et al.* 1986). The difference however, between these rather common TDSs (71 TDS versus 36 latrines), and uncovered faeces away from established middens in the present study is that in badgers they were not specifically located along territory boundaries.

Uncovered faeces were shown to be more prevalent during the mating season suggesting a certain role in reproduction. During the mating season both sexes scout along the outside or even intrude into neighbouring territories advertising through paste marking to seek extra pair copulations (Richardson 1987b; Chapter 6). In this special situation any bodily excretions are potential marks to the recipient (Dunbar 1978; Bekoff 1979). Another reason for more uncovered faeces during the mating season could be that in summer faeces smelling of terpene are mostly scratched over and deposited at middens possibly to avoid olfactorial confusion with foraging *Trinervitermes* columns. In the mating season the reduction of *Trinervitermes* in the aardwolves’ diet would then decrease the chance of confusion, and during this study aardwolves increased their defecation behaviour away from middens, often leaving the faeces uncovered. This allows faeces to be used as additional scent marking agents to communicate to territory neighbours and strange intruders passing through the borders during the mating season.

Urine deposited at border middens was probably used for scent marking (Gorman 1990) and its use showed an even more distinct seasonal pattern than defecations. Nearly one fifth of all urinations in the mating season were placed at border middens (Richardson 1990). Aardwolf males urinated at middens three times more frequently than females, suggesting that this marking behaviour might serve a sexual purpose in addition to pasting. Males were also the more active sex in the early phase of courtship (Richardson 1987b; Chapter 6). They may advertise both to other females and intimidate other males with their urine. The few scratched urinations (SU) observed seem to fit the same pattern.

The potential scent marking function of all elimination products, uncovered faeces (n = 89) and urinations at middens (n = 36), compared with the 42 000 paste marks recorded during this study, constitute 0.3 % of the total scent marking effort only. However faeces may have the additional advantage over minute paste marks of serving as long lasting visual signals and can be deposited in areas with little or no grass, as is required for paste marks. When there is no interference with the finding of food they could be used for supporting territorial paste marking and during the mating season for mate attraction and intrasexual intimidation. Urine might as well be a quicker agent than paste marks to signal physical condition, reproductive state, and social status through metabolites (McCullough 1969; Yahr & Thiessen 1972; Dunbar 1977; Rothman & Mech 1979; Ryon & Brown 1990) to conspecifics. The amount of urine available for aardwolves for scent marking may be limited during the mating season through the scarcity of termite food and the availability of open water for drinking (Richardson 1987a, Anderson 1994). Aardwolves could nevertheless reduce the amount voided to 'token' size as foxes do (Macdonald 1979).

I suggest that paste marking takes such a dominant role in the aardwolves' scent marking system that there would be little extra benefit, and thus tendency for additional use of elimination products for olfactory communication. When an aardwolf visits a specific area trying to communicate to non-residents it may as well void his elimination products as further support for his paste marking. While the role of faeces as additional agents in chemical communication of the Hyaenidae has been well documented (Kruuk 1972, 1976; Kruuk & Sands 1972; Mills *et al.* 1980; Gorman & Mills 1984; Mills & Gorman 1987; Richardson 1990) their use of urine has received little attention. In contrast other carnivores use faeces (otters: Trowbridge 1983; badgers: Roper *et al.* 1986, 1993) and urine (wolves: Peters & Mech 1975; foxes: Macdonald 1979; coyotes: Wells & Bekoff 1981; tigers: Smith *et al.* 1989) as their main scent marking agents despite their physiologically limited availability in comparison to paste marks in the hyaenas.

The results suggest that uncovered faeces away from middens and urine left at middens and dens, could function especially during the mating season as additional scent marking agents. They are however not used as prominently as scent marking with anal pouch secretion.

CHAPTER 9

RESPONSES OF AARDWOLVES TO TRANSLOCATED SCENT MARKS

INTRODUCTION

Numerous behavioural studies have demonstrated that biological odours serve as cues in animal communication (*e.g.* see Ralls 1971; Eisenberg & Kleiman 1972; Johnson 1973; Brown 1979; Müller-Schwarze & Silverstein 1983; Brown & Macdonald 1985; Halpin 1986; Alberts 1992). Scent marking through pasting with secretion from the anal pouch has been shown to be distributed in patterns consistent with expectations of territory advertisement for hyaenids (Kruuk 1972, 1976; Kruuk & Sands 1972; Rieger 1977; Macdonald 1978; Mills *et al.* 1980; Gorman & Mills 1984; Goss 1986; Tilson & Henschel 1986; Mills & Gorman 1987; Henschel & Skinner 1991; Richardson 1990, 1991; Chapter 5). However patterns show trends only, with no conclusive evidence. With the exception of a few paste marks translocated from one territory to another in studies on brown hyaena (Mills *et al.* 1980) and aardwolf (Richardson 1991) no such experiments have been conducted in the wild to demonstrate how hyaenids respond to known scent marks. The functioning of scent marks in territorial animals has been proposed in the 'scent-matching' hypothesis as a means for an intruder to assess the resource holder's quality in a direct confrontation (Gosling 1982, 1990; see Chapter 5). Further scent marks may be left by territory owners in order to create a 'wall of smell' to fend off intruders and as an individually distinctive signature of territory occupancy (Gorman & Mills 1984, Gorman 1990). Intruders may interpret scent marks as a threat with immediate physical attack if they are encountered by the resident, as has been defined in the 'intimidation hypothesis' (Richardson 1991, 1993; Chapter 5). All these hypotheses rely purely on observation of scent marking behaviour.

The capability for individual identification by scent has been tested in many mammals under controlled conditions (Bowers & Alexander 1967; Rasa 1973; Von Holst & Lesk 1975; Gorman 1976; Porter & Moore 1981; Clapperton *et al.* 1988). Most of these studies and the techniques applied to prove individual recognition were critically reviewed in Halpin (1986). In contrast a much smaller number of studies has attempted to test a species' discrimination abilities in its natural surroundings (Mills *et al.* 1980; Harris & Murie 1982; Blumstein & Henderson 1996). However apart from using artificial scent posts placed at a single location (Harris & Murie 1982; Meier 1991) no study has so far taken both seasonal differences and variations in response due to different positioning of scent marks in a wild animals territory into account.

The aardwolf is especially well suited for conducting translocation experiments with scent marks. A paste mark is often deposited singly on a grass stalk that can be collected and translocated much easier than, for instance, urine. Paste marking is clearly the predominant means of scent communication in aardwolves, apart from a limited possible function of urine in the mating season and uncovered faeces away from middens (Richardson 1990; Chapter 8). A territorial aardwolf pair defends a clearly delineated territory of 100 - 600 ha through overt aggression and pasting (see Chapter 5). Border areas can be defined by an observer through the concentration of scent marks in one area by neighbouring territory holders, and their reluctance to scent mark when trespassing across these borders (Richardson 1991; Chapter 5). During the mating season territorial boundaries are frequently trespassed as high-quality males embark on "scouting trips" in search of oestrus females in neighbouring territories. They seem to enter and scent mark neighbouring territories in order to advertise their presence to the resident pair. When the females come into oestrus these extra-pair males were observed to displace the resident males by fighting and subsequently mate with the females (Richardson 1987b; Chapter 6 & 7). During this time the shortage of termite food due to low ambient temperatures aardwolves of neighbouring territories have been observed to feed in close proximity without chasing and fighting each other (Richardson 1985, pers.obs.).

The aim of this chapter is to reinforce observational evidence from previous chapters (4 - 7) on the functions of scent marking in the aardwolf. By monitoring the reactions of aardwolves of known identity to translocated scent marks of different familiarity several of the scent marking hypotheses can be examined. Through translocation of scent marks it will be tested whether intimidation can be induced by scent marks alone. The reactions of aardwolves after sniffing the translocated scent marks may show if a scent mark can elicit an appropriate response in the absence of the marker, and thus if scent-matching is insignificant in the aardwolf. It is hypothesised that scent marks present a greater threat to the territory holder if they are placed in the interior of the territory or even at the residents' den than at the borders. It will be tested whether the responses will change seasonally parallel with a change in the governing resource being defended from food to mates.

METHODS

Translocation experiments were carried out in the three northern territories of the study area. While following "experimental" aardwolves colour-coded stakes were placed at regularly visited dens used for sleeping and breeding purposes, middens currently in use, and boundary roads and paths that they patrolled regularly. This was in order to find these places easily during the day. Subsequently the outlines of their respective territories were plotted as accurately as possible on hand-drawn and later computer-generated maps. After a territory was defined (General Methods; Chapter 2) a donor aardwolf was followed and its scent marks collected. The animal was followed closely until it marked on a grass stalk. The stalk was collected using a pair of tweezers and sterile scissors then inserted in thin holes drilled into a wooden block placed within a cooler box. Then the aardwolf was tracked again to collect the next scent mark. Only stalks that contained a single and clearly visible fresh secretion deposit were collected. The next day each stalk was marked at the bottom with a small piece (< 1 cm^2) of reflective tape, again taking care not to touch the tape or the stalk with bare hands. That afternoon an hour before the aardwolves became active, the marked stalks were inserted into small wooden blocks which were buried into the loose sand of dens, middens and along roads of the territory of the aardwolf to be tested. The aardwolf was then located at its den and followed from becoming active until it retired to its den while recording all its behaviours. Whenever the focal animal found a translocated stalk the following specific responses were recorded:

sniff time	- time (in seconds) the aardwolf's nose was within 10 cm of the stalk until it turned away.
overmarking (OM)	- after sniffing the aardwolf overmarked on top of the stalk once or after sniffing again overmarked it a second time.
'flehmen' (FL)	- curling up the lips while stretching the neck and head up.
searching surroundings	- searching in the immediate surroundings after sniffing the stalk.
visiting a den	- visits den where the stalk was placed.
changing its own den	- retired to different den from where it left earlier that evening.
scent marking trip	- embarking on a scent marking trip to a specific part or around the total territory border.
change in marking effort	- if the number of marks deposited per 100 m walked changed sharply after finding the first translocated marks of the experiment.
change of travel speed	- speed in km/h the tested aardwolf travelled changed sharply after finding the first stalk of the experiment
smell detection	- distance in metres the smell of foreign marks seemed to be detected by aardwolf before sniffing them directly.

Some of the parameters that were considered during the analysis of the responses to sniffed stalks included:

experiment type	- different sexes of the donor of experimental stalk and the tested animal: male-male, female-male, male-female, female-female, and null-experiments (testing an individual with its own translocated stalks).
familiarity	- how well acquainted the tested animal was assumed to be with the smell of the translocated scent marks from: stranger (scent marks were taken from a territory four kilometres away), neighbour, partner, self.
seasonality	- if the experiment was conducted in the mating season or non-mating season.
location	- where the translocated stalk was placed: - border midden (BM), often visited by neighbouring territory owners. - border road (BR) between territories. - midden (M) in the core (internal) area of the territory. - den (D) not presently in use in the core area of the territory. - own den (OD) the tested animal was using on the night of the experiment. - breeding den (BD), where cubs were reared during experiments

All experimental stalks were collected the next afternoon. The number of distinct secretion pastings that were found on the grass stalks in addition to those of the scent mark donor were counted. It was also recorded when the grass stalk was distinctively bend over or broken as an aardwolf would have done while attempting to overmark on it.

In two experiments male aardwolves were simultaneously presented with two stalks each of their female partners and those of a non-resident female positioned 0.5-1 m from each other. These stalks were positioned at the males' dens (OD) or breeding dens (BD) and the males' responses to the stalks recorded.

RESULTS

A total of 43 translocation experiments were carried out between November 1991 and June 1993. Altogether 617 stalks were translocated, collected from 11 different aardwolves (five adult males, one subadult male (20 months old), and five adult females). On 164 occasions stalks were observed to be sniffed by eight different aardwolves (four adult females, one subadult female (six months old), and three adult males) in the presence of the observer involving a total of 13 different aardwolves in experiments. An additional 147 overmarked secretion pastings were found when collecting the stalks back (Table 9.1). Some of the stalks that were investigated in the presence of the observer were again visited and overmarked by another aardwolf, either the partner of the tested aardwolf or a neighbour along the borders, on the night of the experiment. Those 147 pastings together with the 164 observed investigations gave a total of 311 examinations of 217 different stalks found. This means that more than a third of all the individual translocated grass stalks put out were found by aardwolves on the first night.

Experimentally translocated scent marks were found and overmarked at each location with significantly different frequencies ($\chi^2 = 20.92$; d.f. = 5, $p < 0.001$; Table 9.1). Marks deposited at border middens (BM) were investigated proportionately more often than those deposited at disused dens within the territory ($\chi^2 = 9.52$; d.f. = 1, $p<0.005$). Also marks at occupied dens, combining marks at the animal's own den and at the breeding den, were found significantly more often by aardwolves in proportion to their numbers translocated than marks put out for instance at internal middens and dens (M: $\chi^2 = 7.21$; D: $\chi^2 = 15.54$; data from Table 9.1). The experimenter could assume that the aardwolf would usually return to its den where it spent the day or a male would come to the breeding den for guarding the cubs.

After finding stalks at disused dens aardwolves seemed to check consecutively other dens, often going out of their way, possibly to see if there were other translocated marks.

Table 9.1 Number of translocated scent marks investigated by aardwolves at different locations. Total marks put out at each location, marks investigated in the observers presence, marks overmarked (OM) in observers absence, total marks investigated, and marks with no evidence of aardwolf investigation. * percentage of total marks put out.

LOCATION INVESTIGATION	Border Midden (%)*	Border Road (%)*	Internal Midden (%)*	Internal Den (%)*	Own Den (%)*	Breeding Den (%)*	TOTAL (%)*
Total Marks put out	216	35	109	219	26	12	617
Investigated - observer present	53 (24)	5 (14)	31 (29)	38 (17)	25 (96)	12 (100)	164 (27)
Investigated (OM) - observer absent	79 (37)	6 (17)	20 (18)	41 (19)	1 (4)	0	147 (24)
Total investigated	132 (61)	11 (31)	51 (47)	79 (36)	26 (100)	12 (100)	311 (51)
Not investigated by Aardwolves	84	24	58	140	0	0	306 (49)

General Response to Stalks

Only the 164 responses to stalks investigated in the presence of the observer were analysed further. For the following results the 13 sniffing incidences of the four null experiments were excluded, leaving 151. Although sample sizes were small, if some parts of the data were pooled certain patterns would emerge. The responses to all the sniffed marks for each location regardless of season and sex are summarised in Table 9.2.

Table 9.2 Reactions of all aardwolves to experimental stalks at different locations: seasons, and sexes pooled.

Reactions Number of sniffs (% of total)	Mean time sniffed in seconds	No. marks MO (%)	No. marks FL (%)
49 (32.3%) border middens (**BM**)	11.5	42 (85.7%)	5 (10.2%)
5 (3.0 %) border roads (**BR**)	16.4	5 (100%)	0 (0%)
28 (18.9%) middens (**M**)	15.1	23 (82.1%)	5 (17.9%)
35 (23.2%) dens (**D**)	13.5	24 (68.6%)	8 (22.9%)
22 (15.2%) own den (**OD**)	23.4	1 (4.5%)	6 (23.7%)
12 (7.3%) breeding dens (**BD**)	34.9	4 (33%)	5 (41.7%)
151 (100%) Total sniffs	16.4	99 (65.6%)	29 (19.2%)

To find the general patterns I categorised the experiments, and the responses to them, by the sexes of donors and finders, the season, and the familiarity of the donor's marks to the finder. The results are summarised in Table 9.3.

The most notable pattern found was that stranger's marks were sniffed for longer and flehmen was shown towards them more often than to neighbours marks. Neighbours' marks were sniffed for longer and flehmened more often than partner's marks (Fig. 9.1). The sniff time and the frequency aardwolves showed flehmen were thus negatively proportional to familiarity (Spearman Correlation coefficient, $r_s = -1.0$; $p < 0.05$; $n = 3$) when giving partners the highest, neighbours the second, and strangers the lowest rank. A higher percentage of partners stalks were overmarked than neighbours, and those more often than strangers. Overmarking was thus proportional to familiarity ($r_s = 1.0$; $p < 0.05$; $n = 3$). These patterns suggest that flehmen and sniffing have different functions from overmarking. Flehmen is inversely correlated to overmarking, though not significantly ($r_s = -0.387$; $p > 0.05$; $n = 15$, from % OM and % FL of experiment types in Table 9.3).

Table 9.3 Summary of reactions to different types of experiments with translocated marks considering season and familiarity of scent. Experiment type *e.g.* Female/Male = female donor and male finder. OM = overmarked; FL = Flehmen response, (% of total).

Experiment type (Donor / Finder)	Season	Familiarity	No. of Experiments	No. of stalks sniffed	Mean time a stalk was sniffed (sec.)	No. of OM (% of stalks)	No. of FL (% of stalks)	No. of experiments where mark rate increased after finding the first stalk (%)
Male/ Male	Non-mating	Stranger	2	12	13.8± 17.4	10 (83.3)	0 (0)	2 (100)
Male/ Male	Non-mating	Neighbour	4	16	21.8± 28.7	12 (75)	0 (0)	3 (75)
Male/ Male	Mating	Stranger	1	4	11.3± 5.3	2 (50)	1 (25)	0 (0)
Male/ Male	Mating	Neighbour	2	5	5.8 ±4.1	4 (80)	0 (0)	2 (100)
Female/ Male	Non-mating	Stranger	3	12	37.3±28.9	3 (25)	8 (66.7)	3 (100)
Female/ Male	Non-mating	Neighbour	7	22	11.2±13.2	10 (45.5)	6 (27.3)	4 (57)
Female/ Male	Non-mating	Partner	2	6	3.8±1.2	5 (83.3)	0 (0)	1 (50)
Female/ Male	Mating	Neighbour	4	12	30.5±27.0	4 (33.3)	8 (66.7)	2 (50)
Male/ Female	Non-mating	Stranger	2	6	28.0±33.4	5 (83.3)	1 (16.7)	1 (50)
Male/ Female	Non-mating	Neighbour	1	2	21.0±8.5	1 (50)	0 (0)	1 (100)
Male/ Female	Non-mating	Partner	1	1	5.0	0 (0)	0 (0)	0 (0)
Male/ Female	Mating	Neighbour	2	3	11.3±6.8	2 (66.7)	0 (0)	2 (100)
Female/ Female	Non-mating	Neighbour	6	26	12.5±14.9	22 (84.6)	4 (15.4)	5 (83)
Female/ Female	Mating	Neighbour	6	23	9.6±11.7	18 (78.3)	1 (4.4)	6 (100)
Female/ Female	Mating	Partner	1	1	10.0	1 (100)	0 (0)	1 (100)
Self Male	Non-mating	Self	2	7	9.3±14.1	0 (0)	0 (0)	2 (100)
Self Female	Non-mating	Self	2	6	5.5±4.4	0 (0)	1 (16.7)	1 (50)

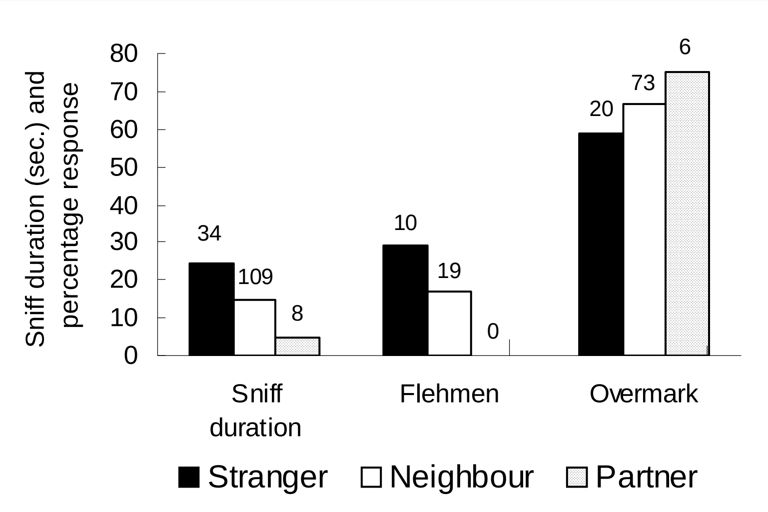


Figure 9.1 General response to scent marks of strangers, neighbours, and partners, regardless of sex and season. Sample sizes are given on top of columns.

Overmarking Response

Of all stalks that were sniffed in the observers presence 99 were overmarked (60.4 %). While overmarking aardwolves always seemed to try and hit the translocated stalk and often succeeded in covering the present secretion with their own fresh one. They occasionally turned around after the first overmark, sniffed the stalk as if to check whether they covered the foreign secretion, then overmarked it a second time. The amount of secretion left in these cases was especially large.

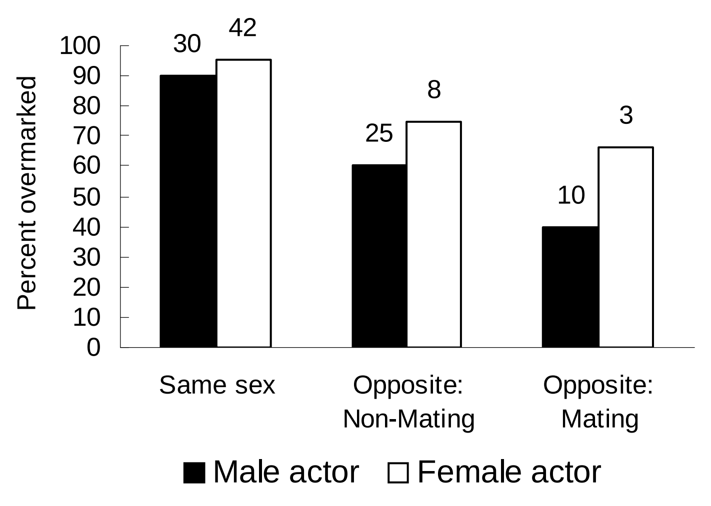


Figure 9.2 Overmarking towards scent marks of same and opposite sex away from occupied dens. Sample sizes are given above the columns.

Overmarking patterns to experimental marks at the tested animals own den (OD) were very different from those at other locations ($\chi^2 = 42.47$; d.f. = 1; $p < 0.001$; Table 9.2) with just one of 22 sniffed seen overmarked. In contrast 'away' from occupied dens (OD and BD) (Fig. 9.2) reactions to marks of the same sex (male - male or female - female) were always very strong (> 90 % overmarked, regardless of season). The overmarking of marks by the opposite sex were also high (> 50 %), though lower than to the same sex. Males appeared to overmark female marks less frequently during the mating than non-mating season ($\chi^2 = 3.3$; d.f. = 1, $p>0.05$). Females always overmarked a higher percentage of stalks of any sex than males regardless of season ($\chi^2 = 6.41$; d.f. = 1, $p<0.01$, Fig. 9.2). When testing this for the seasons separately this pattern was significant for the mating season only($\chi^2 = 9.04$; d.f. = 1, $p < 0.05$).

Overmarking at or away from occupied dens regardless of season was analysed while combining the data for males and females (Fig. 9.3). Reactions away from dens to marks of the same sex were high, with reaction to the opposite sex slightly lower. In contrast neither sex overmarked at its own den, with the exception of one case during the mating season where one female overmarked the translocated stalk of another female. The reaction at the breeding den was intermediate. The breeding den was simultaneously the females' own den whilst the males were guarding the breeding den for part of the night only. When males were inactive during the day they slept in another den.

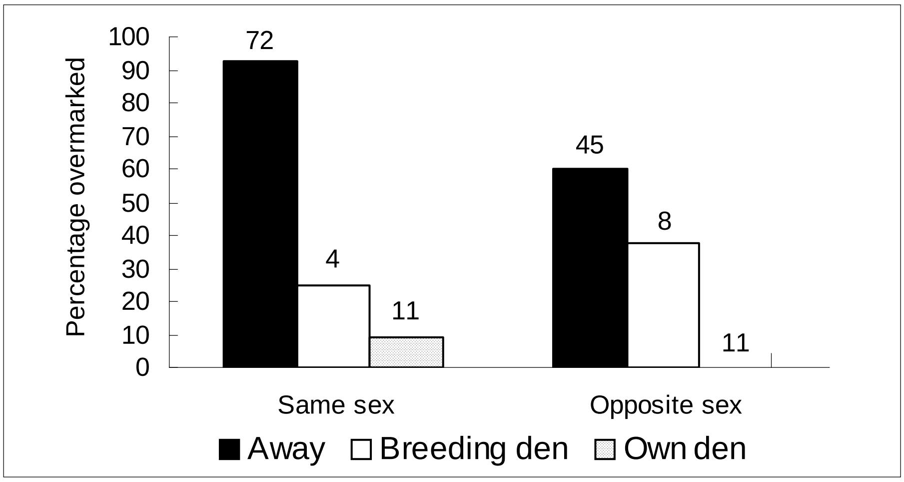


Figure 9.3 Overmarking at or away from occupied dens in response to marks of the same or opposite sex but regardless of season. 'Away' stands for reactions at all locations away from occupied dens (BM, BR, D, M). Sample sizes are given on top of columns.

Use of Den

The frequency tested aardwolves changed their dens in response to them being "scent marked" by a non-resident is shown in Fig. 9.4. Both males and females often moved their dens when it was marked by an intruder of the same sex during the non-mating season but the response to a mark of the opposite sex was much lower. In just one out of six cases the den was changed then. During the mating season, no dens were changed in response to any translocated marks at all. After leaving their old den and before going down the new den the tested aardwolves always checked and sniffed carefully, as if checking to see if this new den could have been visited by the simulated intruder as well.

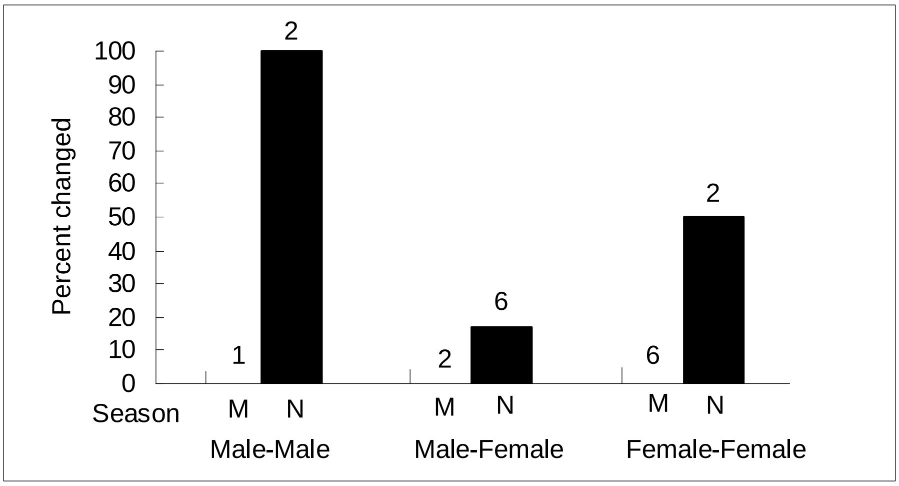


Figure 9.4 Frequency of changing own den (OD) in response to it being ‘scent marked’ by non-resident. Sample sizes are given above each column. (M)ating Season, (N)on-Mating.

Flehmen Response

The aardwolves’ flehmen (FL) response at different sites towards the same and opposite sex was examined. The reaction towards the same sex away from occupied dens was weak with just 3 of 72 stalks (4.2 %) flehmened. In contrast they showed flehmen to 3 of 11 stalks (27.3 %) at their own den. Males responded significantly more frequently to females’ stalks ($\chi^2 = 5.45$; d.f. = 1; $p < 0.05$), 22 of 52 stalks (42.3 %) flehmened, than did females to males’ stalks (1 of 12 (8.3 %)). The female flehmen response was so low that I solely looked at males’ flehmen behaviour for further patterns.

During the non-mating season males showed flehmen most frequently towards strange female stalks, less often to neighbours’ and they showed no reaction towards their female partners. Thus an inverse relationship of the frequency of flehmen to the degree of familiarity with the female’s scent was discernible (Fig. 9.5a). Flehmen was shown towards neighbouring females significantly more often during the mating season than non-mating season ($\chi^2 = 4.97$; d.f. = 1; $p<0.05$; Fig. 9.5b). Only six (20%) of the all stalks with the FL response were subsequently overmarked.

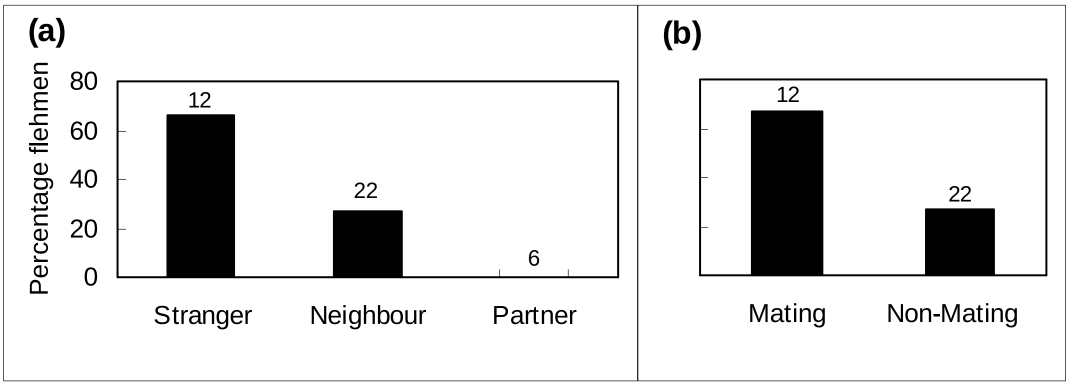


Figure 9.5 Flehmen response by male towards familiarity of **(a)** female and **(b)** neighbouring females during the two seasons. Sample sizes are given above each column.

First Stalk found

The first translocated stalk from a non-resident found during an experiment by the tested aardwolf was sniffed significantly longer than those found later that night. It was sniffed for a mean of 15 seconds (n = 26) compared with 9.1 seconds (n = 88) for the rest (Mann-Whitney U (MWU) -test Z= -3.402, d.f. = 1; p<0.001), when excluding the stalks with flehmen responses. In contrast the first stalks aardwolves found of residents (n = 6) were not sniffed for significantly longer than those found later that night (n = 14) (MWU-test Z= -0.865, d.f. = 1; p>0.05).

Including all experiments aardwolves flehmened significantly more frequently ($\chi^2 = 4.66$; d.f. = 1, $p < 0.05$) to the first stalks (28.9 %, n = 45) than to the rest (14.3 %, n = 119).

The duration flehmened stalks were sniffed by aardwolves was inversely proportional to their familiarity with the stalk donor (Fig. 9.6; see also sniff duration in Fig. 9.1). Sniffing times of neighbours' marks (mean = 37 sec., n = 19) were significantly shorter than to stranger's marks (mean = 54.3 sec.; n = 10; MWU-test, Z = -1.954; d.f. = 1; p = 0.05).

When one excluded stalks with flehmen responses the sniffing times became more similar in duration (Fig. 9.6). Despite this tendency, when responses of non-residents were pooled (strangers & neighbours, mean = 10.5 sec., n = 114) they were sniffed significantly longer than residents (partner & self, mean = 6.1 sec., n = 20) (MWU-test, Z = -2.357; d.f. = 1; p < 0.05). After the first sniffs of each experiment were excluded the durations non-resident were sniffed with a mean of 9.1 seconds (n = 88) and residents with 4.6 seconds (n = 14) were not significantly different any more (MWU- test, Z = -1.797; d.f. = 1; p > 0.05). When finally removing the sniffs at the tested animals' occupied dens from the data set differences became even less significant (average time non-resident sniffed: 6.0 sec., n = 71;

residents: 5.1 sec., n = 9; MWU-test, Z = -0.923; d.f. = 1; p > 0.05). It is apparent that whether the stalks were the first ones of the experiment nights sniffed and also if the stalks were found at the aardwolfs' occupied dens had a strong influence on the sniff duration.

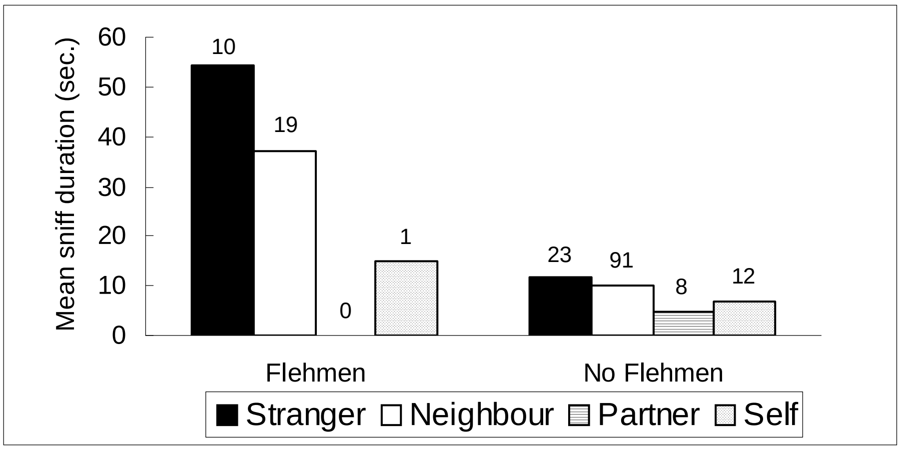


Figure 9.6 Mean duration stalks of markers of different familiarity were sniffed when the aardwolf showed flehmen and when these stalks were excluded. Data is presented regardless of sex and season. Sample sizes are given above each column.

When excluding stalks aardwolves showed flehmen to, the first marks of the experiments, and marks at occupied dens, aardwolves sniffed neighbours' marks significantly longer when finding them in the interior (n = 22) of their territories than those in the border areas (n = 11) during the non-mating season (MWU-test, Z = -2.214; d.f. = 1, p < 0.05).

Male Response towards Females

Male aardwolves investigated 34 stalks of females when excluding those at occupied dens. Females sniffed just 11 stalks of males during the non-mating season and were thus excluded form further analysis due to small sample size. The flehmen and overmarking responses of males towards females of different familiarity during the non-mating season were plotted in Fig. 9.7. As already shown in Fig. 9.5 flehmen seemed inversely proportional to familiarity ($r_s = -1.0$; $p < 0.05$; n = 3), while the frequency of overmarking increased with familiarity ($r_s = 1.0$; $p < 0.05$; n = 3). Consequently the flehmen response was inversely proportional to the overmarking response, suggesting different functions during this season ($r_s = -1.0$; $p < 0.05$; n = 3).

The tendency that males were more likely to overmark when finding marks of female neighbours in the border area (n = 11) than in the inside of their territories (n = 12) was not significant ($\chi^2 = 0.88$; d.f. = 1; $p > 0.05$). This could possibly provide an explanation for the males' intermediate overmarking response towards neighbouring females regardless of where they found their translocated stalks (45 % of stalks overmarked, Fig. 9.7).

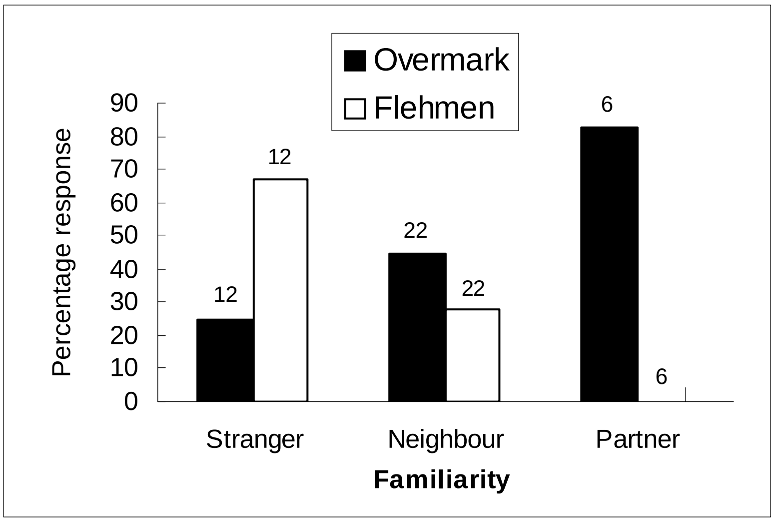


Figure 9.7 Overmarking and the flehmen response of males to translocated marks of females of different familiarity during the non-mating season. Sample sizes are given above each column.

The males Joseph and Orion were able to distinguish between simultaneously presented stalks of their female partners and those of non-resident females by showing markedly different treatment of the stalks in two experiments. They went straight to the non-resident females' stalks and sniffed them longer than their partners' stalks without overmarking them afterwards. After investigating the non-resident females' stalks they sniffed their partners' stalk, positioned 0.5-1 m away, briefly and overmarked them.

Null Experiments

In all four null experiments the translocated stalks, coming from the tested aardwolves themselves, were sniffed just briefly (Fig. 9.6) regardless of their position in the territory. The 13 stalks were sniffed for a mean of 7.5 seconds (Median = 2 seconds). None were overmarked after investigation. In the three experiments where I deposited stalks at their own dens the aardwolves did not change their dens or seemed otherwise perturbed, though they must have smelled my footsteps close to their dens. These null experiments also gave the impression that handling of stalks did not influence the reactions of the tested animals.

Scent marking Response

It was tested whether aardwolves changed their mark-rate (marks / 100m walked) after finding the first stalk of the experiment night of neighbours and strangers regardless of season and familiarity (Table 9.4).

Table 9.4 Changes in mark rate (Marks / 100 m walked) by tested aardwolves to marks from neighbours and strangers of different sex before and after finding the first mark of the experiment. Mean values pooling all (Total); male-male (MM); female-female (FF); female-male (FM); and male-female (MF) experiments.

Experiment Type (n = exp.) Measure	**Total**	**MM (9)**	**FF (8)**	**FM (13)**	**MF (6)**
Marks/100 m Before	1.68	1.81	0.93	1.88	2.09
Marks/100 m After	2.33	2.31	3.15	1.96	2.07

The mark-rate of all experiment types combined increased, though not significantly (Wilcoxon matched-pairs signed-ranks test, Z = -1.671; n = 36, p > 0.05). However in same sex experiments (MM and FF pooled) tested aardwolves showed a significant increase in marks deposited per 100m walked after finding non-residents' stalks (Wilcoxon, Z = -2.223, n = 17, p<0.05). The increase in scent marks in experiments with stalks of the other sex (FM and MF pooled) was not significant (Wilcoxon, Z = -0.201, n = 19, p > 0.05; Table 9.4).

Changes in the total number of marks deposited by the tested animal two days before the experiment, on the day of the experiment and in one of three nights afterwards were recorded. The independence of experiments from one another as well as familiarity of the tested animals with the scent of the donor had to be taken into account. Only experiments which were conducted at least a week after the previous ones and experiments with strangers and neighbours as scent mark donors were included in the analysis. In 18 of the remaining 21 experiments the number of marks tested aardwolves deposited increased on the same day of the experiment (χ^2 = 10.71, d.f.= 1, p<0.005). The increase was by a mean of 82 marks per night (S.D. = 63.7; n = 21; range = 373 to -118) or a 91 % increase relative to before the experiment. The percentage increase of marks on the experiment day for different experiment types is plotted in Fig. 9.8.

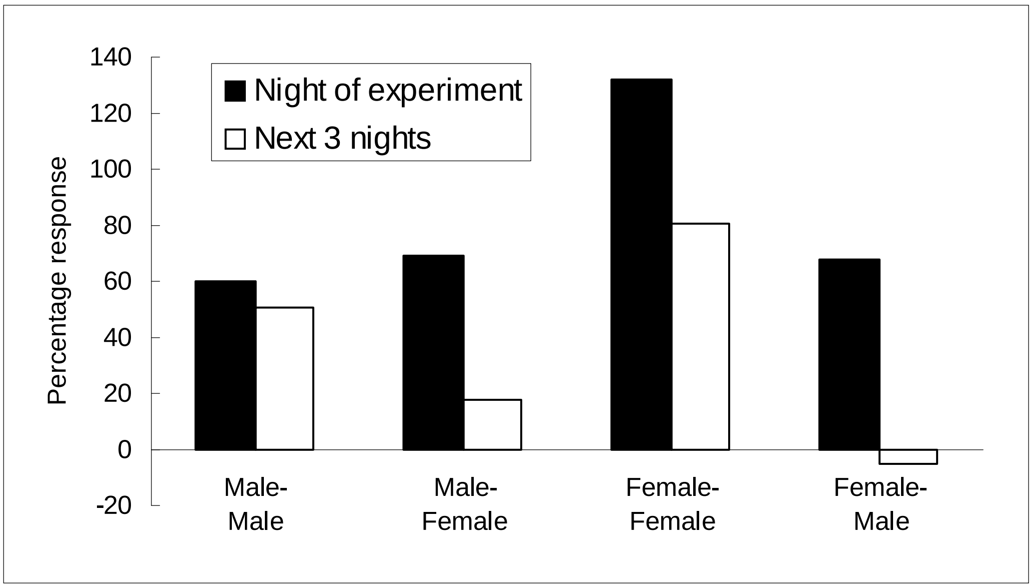


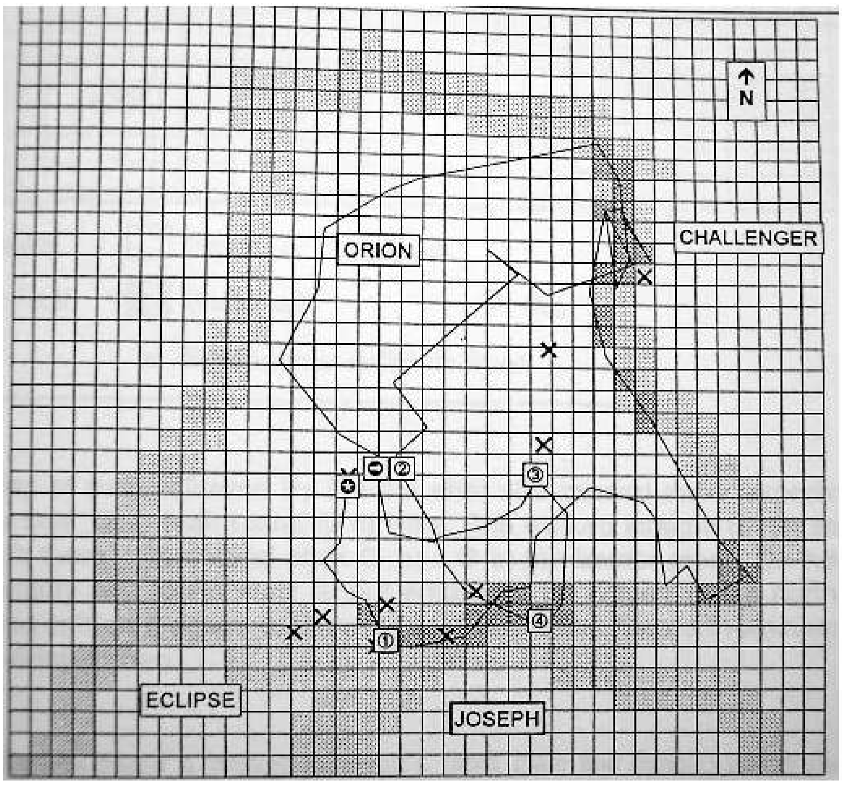
Figure 9.8 Percentage change in number of marks deposited per night on the night of the experiment and the average change to one of the next three nights relative to the average of two days before the experiment took place, regardless of season.

In 16 of 21 experiments the mark number per night dropped below that of the experiment day on the day after ($\chi^2 = 5.76$, d.f. = 1, $p < 0.05$). The number of marks decreased by a mean of 63 marks (S.D. = 68.9; n = 21; range = -80 to 235) from the experiment day level.

Three patterns seemed recognisable: (i) there was an increase in mark deposition on the experiment day in response to the opposite sex, though the increase in response to the same sex seemed stronger than to the opposite sex (ii) the decline in mark number deposited in the three days after the experiments was stronger in opposite sex experiments than same sex experiments (iii) the female-female response seemed stronger than the male-male response both in respect to an increase of marks on the experiment day in same-sex experiments and in the observed decline in marks deposited after opposite-sex experiments.

Scent Marking Trips

During the non-mating season both sexes went straight to the shared border area with their neighbour donors (Figs. 9.9, 9.10) after sniffing their translocated stalks and marked there (15 of 18 experiments (83%)). On three occasions when the shared border was not visited the first stalk was found just before the aardwolf was about to retire to its den. Orion found the stalk of his neighbour Joseph (Fig. 9.9), went straight to the their common border area to mark, then upon returning into the centre of his territory found a second translocated stalk to return directly for a second border marking trip. It was tested whether Orion marked proportionately more than expected in the shared border hectare cells with Joseph. The percentage of marks in the shared border cells to the percentage in the rest of Orion's border cells were compared relative to the percentages these cells take up from his total border area. Orion marked significantly more ($\chi^2 = 43.01$; d.f. = 1; $p<0.001$) in the relevant border cells with his neighbour Joseph than expected. A similar scent marking trip to the shared border was done by female Electra finding her female neighbour Nike's translocated stalks (Fig. 9.10). Electra marked significantly more in these shared border hectare cells ($\chi^2 = 67.53$; d.f. = 1; $p<0.001$) than expected. Thus Orion and Electra went straight to the correct shared border area probably matching the scent of the translocated marks and distinguishing between their different neighbours while marking there distinctively more than in the other border areas.



▬ Path followed
☐ Internal or Outside cell
⇩ Breeding Den
▨ $\geq$ 1 mark / cell
☐ Border cell
✪ Den
x Experimental stalks not found

Figure 9.9 Map of path followed by Orion after finding Joseph's experimental stalk (①) on their shared border. After patrolling his eastern border he returned to the breeding den to find ②, then he walked south-east, and found ③. He then walked south towards their shared border again to mark there again. He detected stalk ④ there and walked past the breeding den again and patrolled the western, and northern areas of his territory. Finally he lay down in his border area with the eastern male that challenged him during the past week.

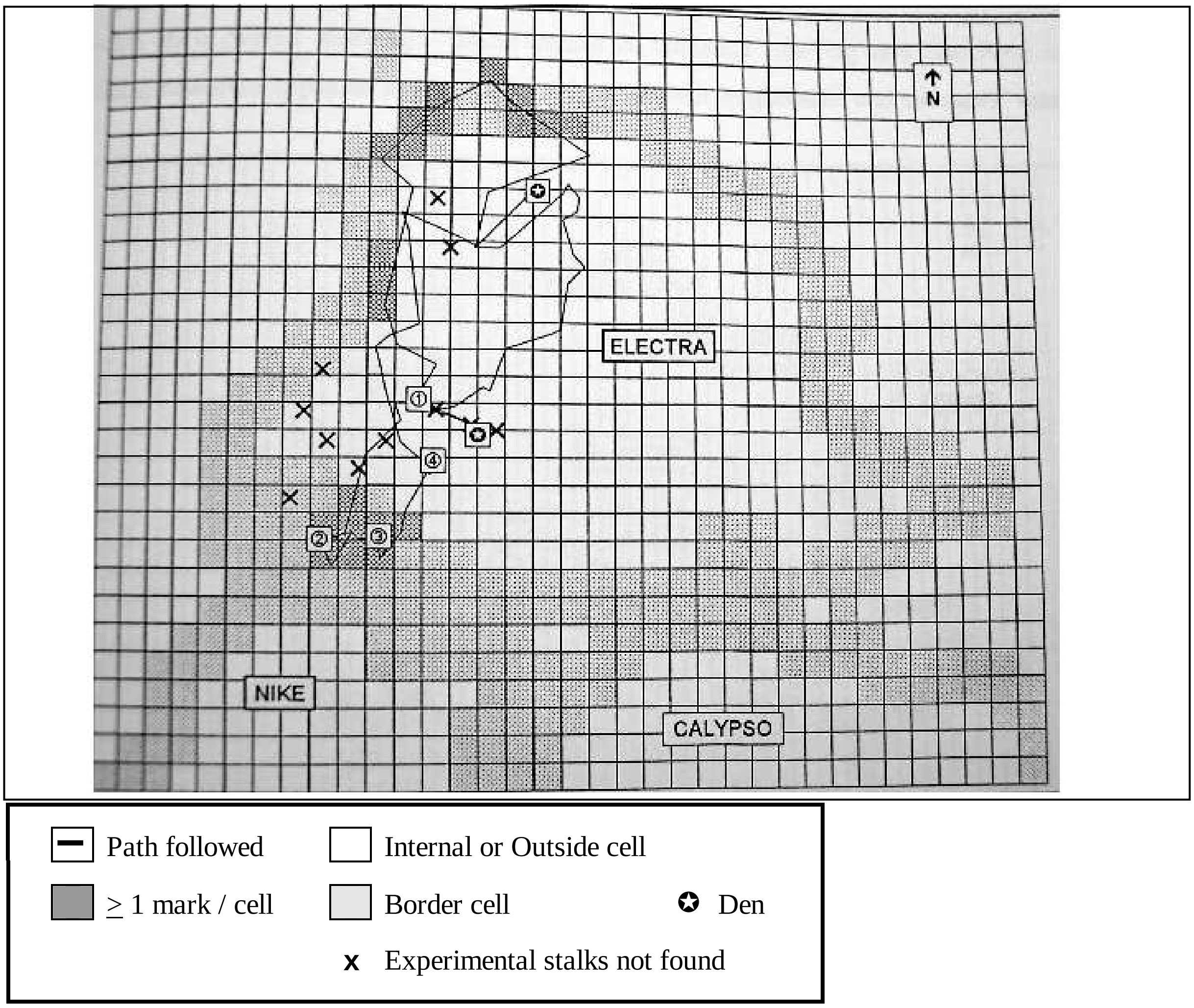


Figure 9.10 Map of path followed by Electra after she missed three experimental stalks after leaving her den. She then found ① of Nike. She walked straight to her shared border with Nike to mark there. She found stalk ② and ③ in the border area. On her way to the centre of her territory she found stalk ④ but embarked on a feeding trip north. Later she returned to ① and sniffed it again, then walked north to mark her north-western border and went to sleep in another den.

When tested aardwolves found a strange aardwolf's (both male and female) marks during the non-mating season both searched their territory for more translocated stalks, whilst not visiting a specific border area. This is illustrated in Fig. 9.11 for Electra who found the stalks of the strange male Luca. The shaded ha-cells where Electra walked and marked along her eastern border were neither in the relevant border area with Luca nor in the correct direction. He had a territory four kilometres to the south of her territory. It was tested whether Electra searched her territory without marking a specific border when finding Luca's marks. The comparatively lower chi-square values for the three shared border areas of Electra with neighbours (Calypso $\chi^2 = 9.22$; Nike $\chi^2 = 3.04$; Eastern Stranger $\chi^2 = 4.81$; d.f. = 1) in comparison to those found for the neighbour donors experiments given above could indicate such overall marking. These patterns of different marking and searching behaviour indicates that aardwolves appeared able to differentiate between neighbours' and strangers' marks.

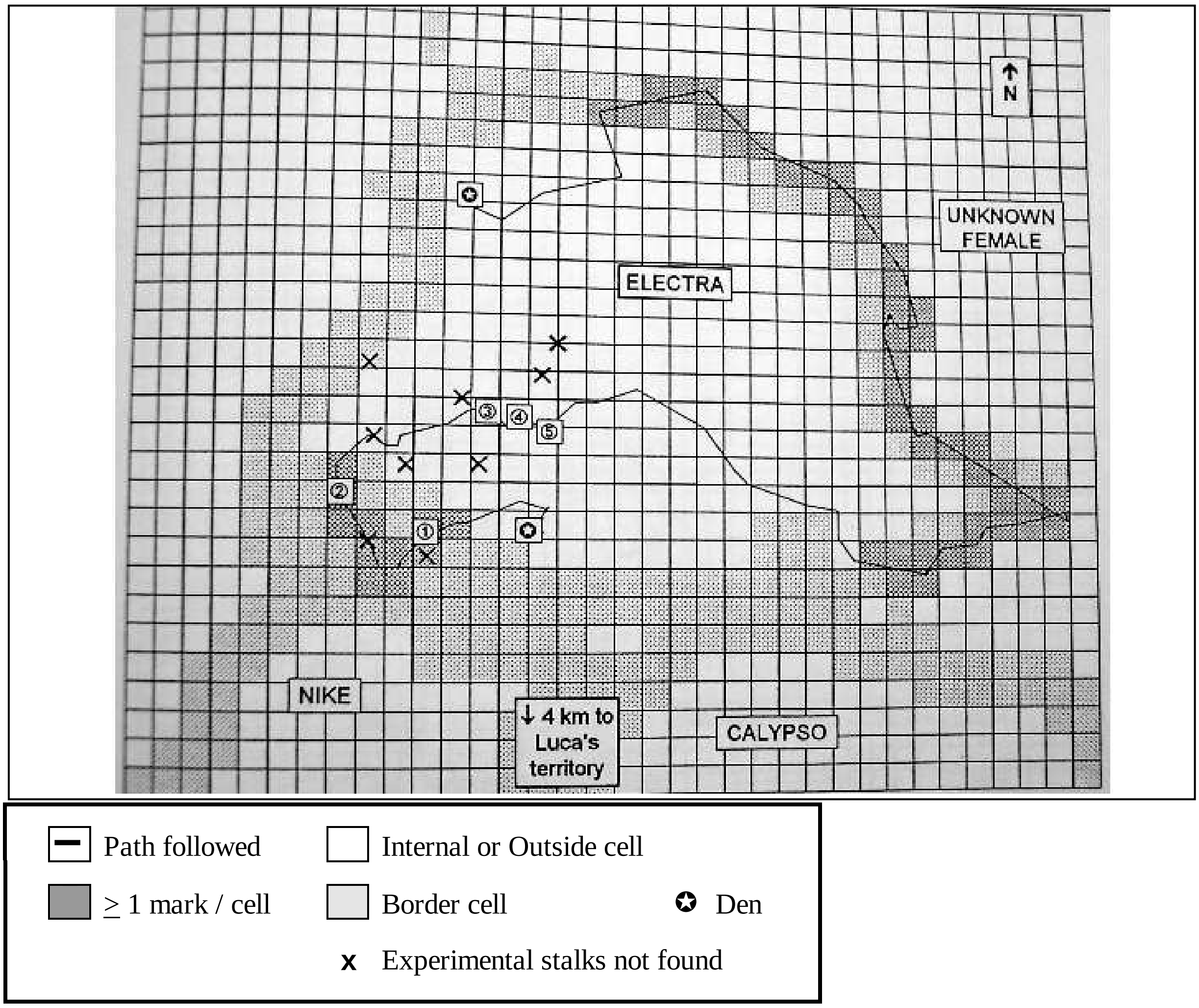


Figure 9.11 Map of path followed by Electra after she found ① of strange male Luca (lived 4 km south of her territory) in her south-western border. She found ② in the border then returned to the centre of her territory where she found ③ ④ ⑤. She went to mark her eastern and northern border extensively and went to sleep in a new den in the Northwest of her territory.

A different reaction to a strangers' translocated stalk was shown at the start of the mating season. Joseph found several translocated stalks of a strange male, and then embarked on the first scouting trip of the season into his neighbours territory whilst scent marking dens and middens and visiting the females there. In the mating season the reactions of males to translocated female neighbour stalks depended on her reproductive status. Four weeks before Nike was mated her translocated marks did not elicit any border visiting reaction of the neighbouring Orion. He simply showed flehmen once and went down his den when finding her marked stalk at his den. Three weeks later, one week before she came into oestrus, he sniffed very long, showing flehmen repeatedly and went straight towards their shared border (Fig. 9.12). He entered her territory for a scouting trip of 3.7 km and marked 53 times in one hour.

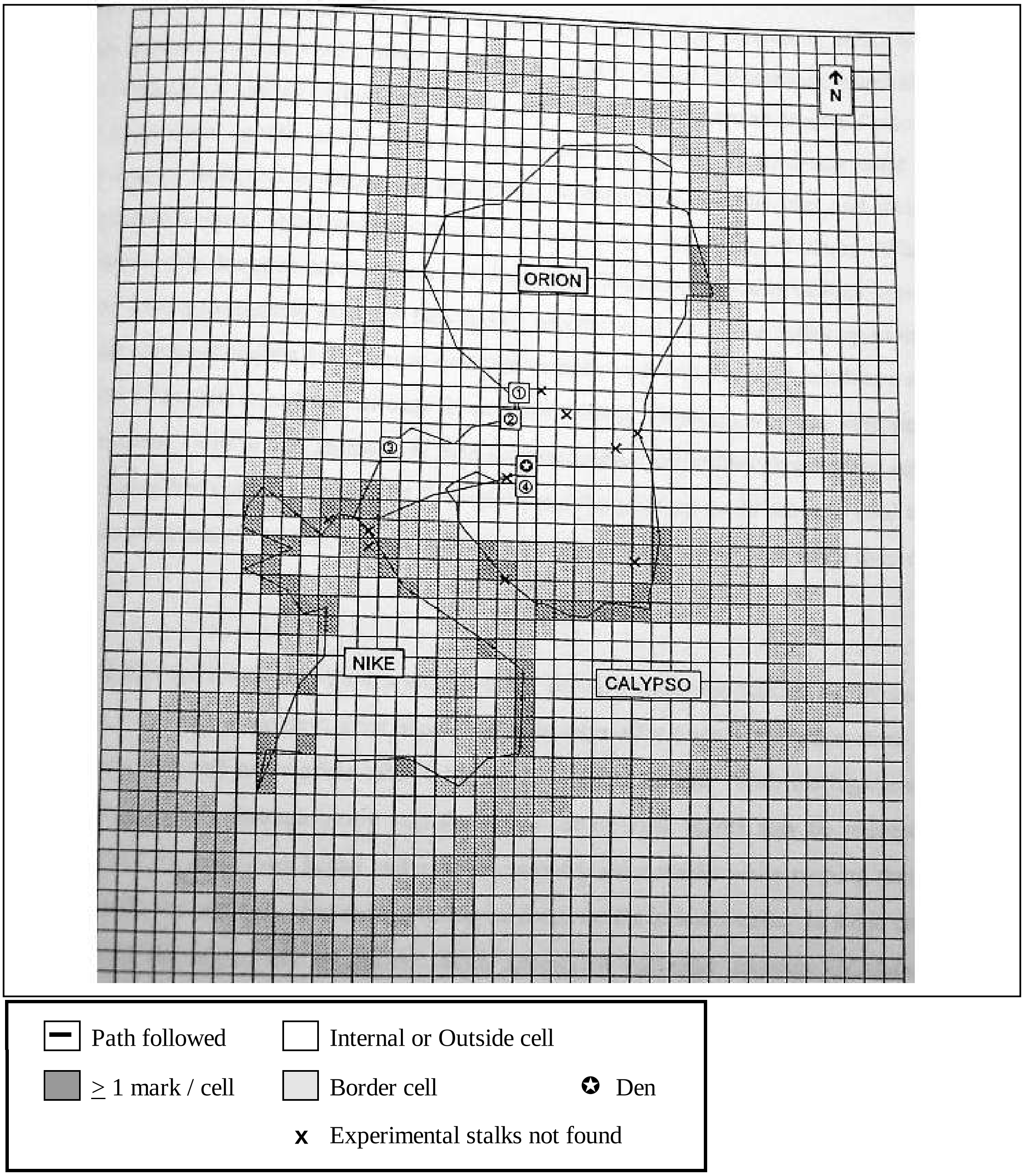


Figure 9.12 Map of path followed by Orion after he missed a stalk leaving his den during the mating season. He walked south and intruded briefly into Calypso's territory possibly to check if she was in oestrus. After patrolling the eastern and northern part of his territory he found ① from Nike in pro-oestrus and showed FL. After walking 100 m further, en route straight to Nike he found stalk ②. Another 700 m further stalk ③. He embarked on a 3.7 km long scouting trip into Nike's territory while particularly marking the dens of Nike's territory with 53 scent marks. He also intruded into Calypso's territory marking 12 times. He returned to his den to find ④, but went to sleep.

In five cases aardwolves failed to find translocated stalks on the midden where they defecated for the first time of the night, despite the wind blowing from a favourable position and the stalk being less than half a metre away. When the aardwolf passed middens later in the night chances of stalks being found were much higher (see Table 9.1), since middens were also visited for marking purposes without defecation (Chapters 5 and 6). Upon catching the scent of a stalk the tested aardwolf often lifted its head high up to draw up the scent and then tried to locate the stalk. In moderate wind conditions aardwolves had no difficulty to single out strange scents from the numerous own and their partners' marks on middens or dens. Wind seemed to played a crucial role in the finding of marks. When coming from an unfavourable direction aardwolves walked within half a metre of stalks without noticing them. When it came from a favourable direction they turned into the wind and found stalks up to 40 m away. In one case an aardwolf made a 120° turn of direction to walk back into the wind and find a stalk, after he had walked 10 m past it and was already 25 m away from it. With no wind the detection limit of stalks was at about 5 -10 m and aardwolves then seemed to have difficulties locating the stalk. They walked in a zigzag line over a breadth of 1-2 m while searching for up to 20 seconds until they found the stalk. The same search technique was used in very strong wind conditions, after they caught the scent.

In the cool and dry conditions of winter a neighbouring female's stalk was sniffed for 50 seconds and flehmen shown by a male three days after deposition. Six days after translocation that same stalk was sniffed for 24 seconds and overmarked afterwards by the resident female. With the high temperatures of summer and especially through heavy rain the signal life of scent marks may be reduced. In dry conditions aardwolves sometimes licked and exhaled onto dry scent marks while running their nose up and down the stalk, the moisture released appearing as drops on the animals nose. In some cases biotic factors influenced the signal life of stalks. Both species of harvester termites (*Hodotermes* and *Trinervitermes*), the main food of aardwolves, often harvested translocated stalks and so removed the signal.

DISCUSSION

Scent marks were hypothesised to be deposited by aardwolves in the non-mating season as a threat of physical attack to intruders (Richardson 1991, 1993; Chapter 5). Animals marking inside another territory may demonstrate their intent to take over this territory or at least to increase the size of their present territory and are expected to be prepared for physical escalation if the resident is encountered (Richardson 1993; Chapter 5). Therefore when an aardwolf would find scent marks in the interior of its territory it should be aware of the threat transmitted. In order to maintain its territory the resident should add its own mark as a counter threat (Richardson 1991).

The high incidence of overmarking (> 90 %) marks from the same sex may imply a territorial signalling function to the producer of the marks in case they would return. The tested animal may have attempted to nullify the original mark by overmarking it. In an experimental study on golden hamsters Johnston *et al.* (1994) proved that the distinctive information of the bottom scent was effectively masked by the top scent. However complete covering of the previous mark with the top scent in all overmarking attempts seems unlikely. These grass stalks could though still serve as a kind of bulletin board for animals, each one leaving its message to be read by other individuals (Johnston et al. 1995). As overmarking on stalks of aardwolves of the opposite sex was also strong, though less frequent than on stalks of the same sex, this is also suggesting a territorial reaction towards the opposite sex. Although not significant, males appeared to overmark female marks less during the mating season. Interesting was that the female overmarking response was always slightly higher towards any sex than that of males. An explanation for the observed responses could be that male aardwolf dispersion is determined by that of females', his paternal care keeping him close to the female during the non-mating season (Richardson 1985), but his main reward comes through mating during the mating season. By contrast females are defending feeding territories for themselves and their cubs, so they need to keep non-residents of both sexes out (Chapters 5 & 6). This system of female dispersion influenced by food and male dispersion influenced by female dispersion was experimentally demonstrated on grey-sided voles (Ims 1987, 1988).

Both sexes changed their dens marked by a same-sex 'intruder' during the non-mating season only. The aardwolf uses its den as a place to rest, as a refuge from predators (Smithers 1983) and presumably also from challenging intruders. Both sexes preferred to sleep in dens situated in the interior of their territories regardless of season (Chapter 5 and 6), where they would be more secure from intruders challenging them to fight. This afforded protection would be particularly advantageous when aardwolves had lowered their body temperature for several degrees (Anderson 1994) in order to reduce their metabolic rate. The concurrent lethargy would be a great handicap in an unsuspected fight. The lack of overmarking at the own den could have been a response of such a great perceived menace from a challenger finding the resident at its den that the owner may have reclined from giving away its position by overmarking. However aardwolves overmarked everywhere else while moving dens. In many carnivores competition is most intense from members of the same-sex due to added reproductive competition (Ewer 1973; Creel & Macdonald 1995). The menace from an opposite-sex intruder may therefore have be less strong and owners did not change their dens in response.

During the mating season dens were probably not changed since aardwolves may have been aware that neighbours were now intruding mainly to advertise their intentions of mating (Chapter 6). Scent marking still might function then as a threat to members of the same sex, but more in the context of competition for mating opportunities, rather than fighting the den owner at its own sleeping place for year-round feeding territory take-over. Thus there was less motivation to move dens.

The males' overmarking of female marks during the non-mating season was proportional to their familiarity. The message left by males overmarking a female mark could be addressed to two different parties - either to the returning original marker, or to a third party *e.g.* the neighbouring male. Males probably overmarked scent marks by intruding females during the non-mating season since any aardwolf was potentially stealing food from the territory. Female strangers' marks were overmarked less frequently by males than those of neighbours' possibly because they were less likely to form a permanent feeding threat in contrast to neighbouring females intruding frequently during the non-mating season (Chapter 5). Another reason for the reduced overmarking response towards strange females' stalks could be that males encouraged these females to return - giving them a mating option with another female. The question remains whether males were trying to lay claim to females marking in their territories or were they trying to chase them off? The tendency that males overmarked intruding females' marks less during the mating season when they would have encouraged female visitation (Chapter 6) indicated that overmarking seems to be intended as a threat to them. A males' aims towards intruding females during the non-mating season appear to be mutually exclusive. Maybe this is why they overmarked less than half of the females' stalks only. By overmarking all his partner's marks a male was possibly signalling to other males that this female already had a partner who was prepared to defend her (see Chapter 7 for mate guarding).

The flehmen response was rarely used toward the same sex, unless at the tested animal's own den. As the den owner would likely feel most threatened there it should spend time to accurately identify the marker. Males showed flehmen towards females' scent marks more frequently than females towards male marks. Males are the more active sex seeking EPCs (Richardson 1987b, Chapter 6 and 7) and presumably would need to have better knowledge of females' sexual status than vice versa in order to time their scouting excursions and copulations.

Flehmen seems to serve more of an identification function in the non-mating season, indicated by a higher frequency of flehmen shown towards strange females' scent marks by males. Males showed flehmen significantly more often during the mating season than outside of it, implying that it then may serve a sexual purpose. Flehmen seemed to be used when the aardwolf wanted to investigate an odour carefully. This compares favourably with functions flehmen has previously been associated with *i.e.* for detection of oestral state in herbivores (Schaller 1967; Stahlbaum & Houpt 1989; Houpt *et al.* 1989), and in felids in the general reading of odour signals and to enhance sniffing (Verberne 1970; Whittle 1981). In horses the flehmen response has been used to show their discrimination abilities between conspecifics (Marinier *et al.* 1988).

Similar to aardwolves sniffing translocated scent marks during this study, Columbian ground squirrels sniffed longest on acrylic cubes with oral gland scent of strangers, nearly half as long on that of neighbours and again half as long on their partners' scent than on neighbours' (Harris & Murie 1982). Sniff duration may simply reflect the time required by an aardwolf to identify the marker, as the exclusion of flehmened sniffs from the data set reduced the differences in sniff duration towards stalks of different familiarity. Once the first mark found had been sniffed and flehmened extensively for identification the finder seemed to show habituation to the following stalks.

Neighbour's marks were sniffed significantly longer by residents when found inside of their territories than in the borders, possibly reflecting a greater desire to identify the marker of these unexpected marks closer to the resident's den. Translocated stalks were more likely to be found when deposited in the border area, also reported from a small-scale scent mark translocation experiment with brown hyaenas (Mills *et al.* 1980). A territorial aardwolf habitually patrols its border area almost daily and marks proportionately more heavily there to ward off intruders (Richardson 1991; Chapter 5). This is probably because intruders would be expected to leave their marks at the point of their intrusion as a challenge to the resident.

The changes in number of marks deposited by tested aardwolves in response to experiments seemed to follow a similar pattern as shown in overmarking stalks. The reaction towards the same-sex was again stronger than to the opposite sex, suggesting the territorial threat. Residents also seemed to lose interest and thus decreased their mark number faster in the following days in response to a lower threat from the opposite sex. The stronger female than male response may have been elicited again due to her greater need to protect her food resources for herself and the cubs for the greater part of the year. Aardwolves deposited greater numbers of marks per distance moved after finding translocated stalks of the same-sex than opposite sex, suggesting once more a greater threat posed by same-sex members. An increase in density of fresh marks would serve as an indication of their eagerness to defend their territory (Chapter 5).

An aardwolf seemed to recognise its own scent marks in null experiments and did not refresh them by overmarking when they were one day old. One could therefore assume a resident seems to monitor its own scent marks to ensure their signalling ability. This compares well with other experimental studies (domestic dog, Dunbar & Carmichael 1981; Columbian ground squirrel, Harris & Murie 1982).

Many studies have claimed the demonstration of "individual odours" but precisely just showed the test species' ability to recognise heterogeneous subgroups instead of "true" individual recognition, defined as a "learned discrimination among conspecific individuals" (Barrows *et al.* 1975; Halpin 1986). In studies that have used a habituation-discrimination paradigm (*e.g.* Halpin 1974; Harrington 1976), or differential responses to own or conspecific odours (*e.g.* Müller-Schwarze 1971; Rasa 1973; Harris & Murie 1982; Johnston 1983; Clapperton *et al.* 1988) animals may simply be distinguishing between previously encountered odours from a new odour. In this study males were distinguishing between simultaneously presented stalks of their partners and those of non-resident females. However the present study presented evidence along several additional lines that aardwolves were capable of individual recognition. They showed different responses to partners', neighbours', and strangers' marks and also distinguished between males' and females' marks. In addition they went directly to the shared border area with the donor of translocated stalks therefore demonstrating true individual discrimination, while when finding a strangers' stalk reinforced the whole border areas. Only one study on humans (Porter & Moore 1981) has so far showed unequivocal ability to discriminate.

Individual recognition in the aardwolf could serve multiple and complex functions. The main function of scent marking during the eight month long non-mating season is to delimit the feeding territory and to deter intruders from entering the interior for prolonged visits as presented in the resurrected intimidation hypothesis (Richardson 1991, 1993, Chapter 5). Although considered to be of lesser importance for effective maintenance of territorial integrity (Richardson 1993) individual recognition abilities using scent alone enables aardwolves to react specifically to intruders of different familiarity, therefore enhancing the efficiency of their energetically expensive marking behaviour. A field study on male desert iguanas has demonstrated this (Glinski & Krekorian 1985). Even in the absence of the intruding challenger adequate measures can be taken by the territory owners. In the case of a scent marking familiar neighbour which would aim at a comparatively small extension of its territory a resident could conserve energy by specifically marking the shared border area most likely to be trespassed. It might also serve as an indication of strength of the marker which becomes important during the mating season (Richardson 1987b, 1990, 1993; Chapter 6). In the mating season individual recognition could give male aardwolves an indication of strength through the frequency a scouting male scent marks another territory and by remembering the results of fights with other males. In the case of a strong male trying to mate with a neighbouring female his previous marking of her territory could facilitate sexual behaviour when they physically meet. Daly (1977) first hypothesised for gerbils and later Coopersmith & Banks (1983) obtained strong evidence for the brown lemming that when a female is repeatedly exposed to a male's scent marks she will habituate to his odours and will be more likely to mate with him when she comes into oestrus. Scent marks that were deposited by females in oestrus along the borders of neighbouring males (Richardson 1987b) were used by the targeted males to time their scouting trips to that female (Chapter 6). Males were likely able to detect the oestral state of females by showing flehmen towards their scent marks, as was seen from several mating seasons. This may help in synchronising the sexes reproductive state through chemical communication since they normally lead a solitary life (Ewer 1973). Olfactorial differentiation between sexes was further supported through observations of natural encounters in aardwolves. Resident aardwolves chased intruders of the same sex much harder and vigorously than the other sex (Richardson 1985, Chapter 5), and therefore seem to be able to distinguish gender from olfactorial and possibly also visual cues.

The results of this chapter can be used to support or contradict debated hypotheses of territorial scent marking. The “intimidation hypothesis” (Hediger 1949; Geist 1965; Richardson 1991, 1993) states in contrast to the “scent matching” hypothesis (Gosling 1982, 1990) that scent marks serve as territorial threats in the absence of the signaller. Translocated scent marks were effective in eliciting differentially strong response, in the territory owners in the absence of the donor, dependant on their placement, sex of donor, and season. This contradicts the assumption of the ‘scent matching’ hypothesis (Gosling 1982, 1990) where a territory owner has to make himself available to be smelt by the intruder, matching his scent to that of his territory, and so be identified as a territorial resident. Another assumption of the intimidation hypothesis that scent marks function as a threat of physical attack was expressed in the changing of dens by the tested animal when its own den was “scent marked” by an intruder of the same sex. The changing of den could be seen as a retreat through intimidation, since the threat of the intruder finding the owner at its own den was so great.

The observed deposition of a higher density of marks in the relevant border area after finding a simulated intruder’s scent mark gives support to the assumption that scent mark density indirectly communicates to intruders the potential of being encountered by the owners (Gorman & Mills 1984; Richardson 1993). The threat of being detected with resulting fighting should keep intruders to the border region, when not deterring them completely from intrusion. The observed change in strength of response to simulated intrusions between non-mating to mating season was likely caused by the change of defended resource. In the non-mating season both sexes defend their food resource (Richardson 1991, 1993), while during the mating season males challenge each other for access to receptive females and not for complete or partial territorial take-over (Chapter 6). During the mating season both sexes would be expected to lower the transmitted territorial threat via scent marking in order to encourage individuals of the other sex to revisit them for extra-pair copulations (Richardson 1987b, 1993; Chapter 6 and 7).

This chapter has demonstrated the capacity of known translocated scent marks to be interpreted by other aardwolves with varying response in the absence of their producer. An increase of scent marking activity at relevant borders and the demonstration that intimidation can be transmitted without physical presence of the marker thus provides further support for the intimidation hypothesis. Scent marks are used to transmit complex messages dependant on the sex of the producer, or where the stalk is deposited, as well as individual identity of the donor. Seasonally there seems to be a change in the message transmitted coinciding with a switch in the principally defended resource. Since all the data is more consistent with the notions that scent marks act as a threat to intruders one is able to exclude most of the assumptions that the aardwolf practices scent matching (Gosling 1982).

CHAPTER 10

CONCLUSIONS

Many mammals scent mark their territories in order to advertise both their presence and ownership of a territory (Gosling 1982; Gorman & Mills 1984). It is however still a subject of debate how scent marks help in maintaining a territory. It is disputed whether scent marks actually intimidate and therefore deter intruders from entering the territory, or from confronting the territory owner (Hediger 1949; Geist 1965; Gosling 1982; Richardson 1991). Another function scent marks may serve is in the attraction of mating partners (Richardson 1987b) if a female solicits males to visit her and if so what role scent marks play. In order to answer these questions both male and female aardwolves were followed extensively during both non-mating and mating seasons and their scent marking behaviour was recorded. In addition to interpret the observed patterns I conducted 43 experiments translocating scent marks of known aardwolves into territories of aardwolves to be tested. The response of the tested aardwolves was monitored and gave the opportunity to determine how aardwolves reacted to 'simulated' intrusion of a scent marking intruder.

For a more comprehensive account of the aardwolf's olfactory communication system I looked at the histology of the anal pouch and the ontogeny of scent marking. The histology of the anal pouch showed large aggregations of sebaceous glands producing the long-lasting fatty secretion and interspersed apocrine scent glands arranged in the wall of the anal pouch. The mixing of the two gland products creates the pasting secretion. Differing proportions of the two products are likely to mix to an individually distinctive signature for each aardwolf individual and sex. This signature would be expected to show seasonal variations in its chemistry dependant on the reproductive condition of the individual. Odour profiles of 50 scent marks, analysed with gas-chromatography, from different sexes, and seasons, using the dynamic-solvent effect (Apps 1988) were produced in this study. These profiles from each individual aardwolf's scent marks analysed were highly complex and variable in the peaks for different fatty acids and esters present (Apps *et. al* 1989). They varied such that statistical analysis for patterns was not conclusive for the available sample size. This part of the thesis was therefore left out. However the behaviour of observed aardwolves towards paste marks deposited by different individuals during simulated intrusions were highly distinctive. The aardwolf male's penile pad's function, especially its seasonally irregular secretory activity, still remains unsolved. However its histology closely resembles that of the anal pouch.

Other scent marking agents, like urine and faeces, perform a minor but complementary role during times when their odour may not interfere e.g. with aardwolves finding their termite food. Acoustic communication used by the aardwolf was not considered in this thesis. Recordings of vocalisations from a hand-raised female cub and various vocalisations heard around the breeding den and between adults particularly during the mating season however suggest that sound was important for fast acting short to medium range communication. When aardwolves are within short range body postures and pilo-erection serve in visual communication.

Aardwolf cubs were practising pasting from the time they first emerged from their breeding den although then still without secretion. With increasing age they were producing scent marking secretion, which was not yet perceived as threatening by the parents. The full capabilities of producing scent marking secretion and to perform pasting movements, or even overmarking existing paste marks on grass stalks, were attained only with sexual maturity at about ten months of age. Aggression from parents occurring at this phase implied that scent mark secretion of subadults had the properties of adults and were then perceived as coming from competitors for the territory. With increasing parental aggression subadults either emigrated or ceased to scent mark completely while staying in their parents' territory. This behaviour supported the assumption of the intimidation function of scent marks that an animal should scent mark only if it is prepared to fight for the ownership of a resource (Richardson 1991, 1993). The strategy of non-marking subadult males staying in the natal territory may have been to gain strength by making use of the territory resources while not advertising their presence. They started scent marking again only when they seemed prepared to fight for territorial ownership. Floaters or aardwolves that lost their territories could be expected to behave in a similar way while waiting to establish a territory. Differences in the frequencies the sexes scent marked were already noticeable at five months and probably continue into later life.

Scent marks were found to be placed in order to maximise their advertising power (Gosling 1982; Richardson 1991, 1993). The change in the primary resource being defended and acquired through scent marking throughout the year by a high quality male aardwolf could be summarised as in Fig. 10.1. During the non-mating season residents seemed to be defending their food resources in their territories by scent marking inside and along the borders of their territories, but never outside of them, and by attacking intruders when they were encountered. Two types of intruders were distinguished. Most were neighbours apparently with the sole purpose of feeding. They did not scent mark while intruding and fled immediately when becoming aware of the residents. The second type of intruder seemed to challenge territorial residents by scent marking inside their territories. This form of challenging was experimentally simulated during this study and probably increasing the perceived intruder pressure into two aardwolf territories. The resident aardwolves increased their mark rate up to 2 - 3 fold in response to these experiments and overall their scent marking activity increased from the 1991 to the 1992 non-mating season - when most of the experiments were conducted. Further evidence came from the response of the male Orion to one 'natural' challenge by a scent marking intruder during the non-mating season. He increased his marking effort specifically in the part of his border where the challenger intruded. One could hypothesise that as long as territory owners were not challenged and did not perceive high intruder pressure they should have showed a uniform scent marking effort throughout the non-mating season. Aardwolves would be expected to mark at a rate which is proportional to the perceived intruder pressure and which would be sufficient to advertise their commitment to defend their territories (Richardson 1991). A scent mark is signalling towards all conspecifics a threat with immediate physical attack, though to a lesser degree to members of the opposite sex. That scent marks were able to induce intimidation was demonstrated by aardwolves changing their sleeping dens in the non-mating season when they were scent marked by a same-sex challenger - simulated by translocating scent marks there.

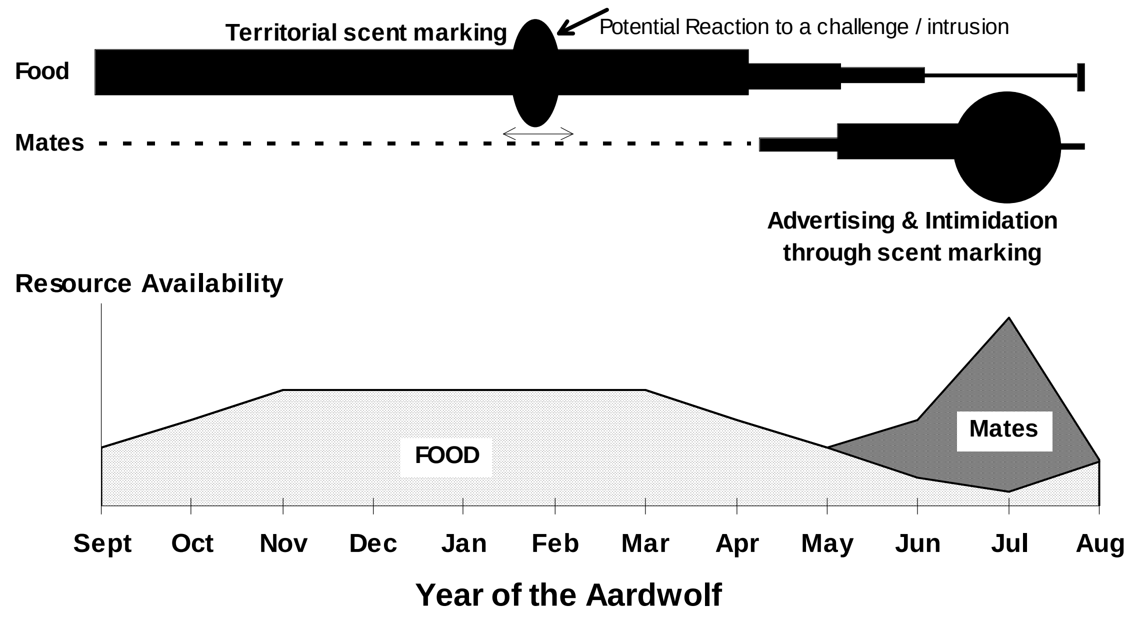


Figure 10.1 Diagrammatic representation of scent marking intensity over the year by a high-quality male relative to the two most important resources, food and mates. Increasing width of bars indicate intensity of scent marking.

During winter with low food availability and the approaching oestrus of females a switch in decisive resource took place in the short mating season, though males started to scent mark at higher rates several weeks before actual mating took place. High scent marking rates identify high quality males able to afford the cost of such energetically costly advertisement (Zahavi 1975, 1977). The high cost of scent marking is not through the number of marks deposited but amount from the extra activity, that is the time required and distance covered, to deposit scent marks at a time with no food. This would serve as an advertisement to females of the male's quality and for her to accept him later. Thus during a short time period the potential gains for an intruding male, namely mating access to a female, are greatly increased and therefore reduce the asymmetry of payoff to the neighbouring contestants (Maynard Smith & Parker 1976). On the other hand the potential losses through cuckoldry to the resident male are also immense, having defended his territory with his female partner for a whole year. This resulted in more and higher intensity fights between males, that would have otherwise not taken place during the non-mating season. During the mating period scent marking by an intruder in a neighbour's territory was possibly not directed towards the specific territory holder for spatial ownership but to advertise his strength and preparedness to fight with the resident male over mating rights with his female. Scent marks may serve then to intimidate the resident male and advertise that he is prepared to fight for access to the female. The failure to change sleeping dens by males during this period in response to them having been 'scent marked' with an intruders' translocated stalks supports this hypothesis.

Shifts in the same decisive resources being defended from food to mates has been recorded in stoats (Erlinge & Sandell 1986) and American badgers (Minta 1993). Like the aardwolf, a shift from a strictly territorial to a mixed reproductive as well as territorial pattern was evident for male stoats with territorial behaviour and a promiscuous mating system (Erlinge 1977). After the mating season in August (Fig. 10.1) scent marking decreased to the lowest level of the year. This corresponds to the time when both resources are at a low. Aardwolves are still suffering from the effects of cold temperatures in winter, with little termite food available. In order to save energy they reduce their activity and hence their scent marking. As the weather warms up termites become increasingly available (Richardson 1985) and aardwolves can afford to be active and to scent mark again.

A similar change in decisive resource takes place for females, though to a lesser degree than in males. Aardwolf females retained their territories in the mating season as observed in stoats (Erlinge & Sandell 1986), but invested less energy in the maintenance of territorial integrity than in the non-mating season. Females generally marked less than males during both non-mating and mating season and did not engage in the prolonged scouting period during the mating season or even guarding their mate from other females. They scent marked just during a brief, crucial period in the week around oestrus soliciting males to visit them for IPCs and EPCs. By conserving their energy females would both survive the winter better and retain more energy for nurturing their offspring. Female scent marks served as an attractant for mating partners. The translocated marks collected from a neighbouring female in pro-oestrus were able to elicit a scouting response in a male. The same experiment type failed to elicit a similar response two weeks earlier when the female was not in pro-oestrus. This provides strong evidence both for the presence of sex attractants in the female's scent mark during pro-oestrus, and that aardwolves are capable of olfactory recognition of sex, widespread throughout the vertebrates (Stoddard 1980).

Interestingly females reacted strongly to other females' translocated scent marks by overmarking them during the mating season. This may have been both to prevent for territory takeover and to prevent her male from defecting and guarding the intruder's cubs. Female competition for male assistance in feeding nestlings has been well documented in the facultatively polygynous European starling (Pinxten & Eens 1990, 1994; Eens & Pinxten 1995). An aardwolf male's commitment to guard his resident female's cubs from jackal predation could be weakened depending on his certainty of paternity. In an unusual case a male defected from guarding his partner's offspring to guard the offspring of a female where he had a higher certainty of paternity (Richardson & Coetzee 1988). Joseph engaged in many EPCs during this study did not guard his female Calypso's cubs at all after detecting her engaging in EPCs. Before the start of this study Joseph was observed to guard his females' offspring for about 30 % of his time (P.R.K. Richardson, pers.comm.). He was never an ideal parent but at least did some guarding. Similarly male European starlings adjusted their chick feeding dependent on their certainty of paternity (Wright & Cotton 1994).

The motivation for territoriality in aardwolves seems to differ for the sexes. For males it is not access to females in the mating season alone but also the importance of his paternal care to the survival of the cubs keeps him resident throughout the year. His reproductive success would be wasted if the cubs don't survive. For females the motivation would be to defend feeding territories for themselves and their cubs. This may explain the difference in scent marking between males and females. The function of flehmen as determined from the responses to experimentally translocated scent marks was to identify an intruder while overmarking by the resident may serve to hide the intruder's mark and to reassert itself. In translocation experiments the female's overmarking response was always stronger than the male's - both for same sex-intruders and opposite-sex intruders. Males appeared to overmark female marks less in translocation experiments during the mating season when they would not have wanted to scare intruding females away.

In a brief digression from scent marking the polygamous mating system of the aardwolf is worth describing. Extra-pair copulations were frequently observed (> 60 %), though without extensive DNA fingerprinting we will not be able to prove whether there is mixed paternity in aardwolves, as reported from other carnivores (Creel & Macdonald 1995), or whether EPCs are at all successful during a sub-optimal time for fertilisation. Since cuckolding males took a considerable risk of being detected and receiving injuries through fighting with the resident males it seems probable that there should be a reasonable chance for siring offspring. The results of this study suggest that an EPC male's chances for siring offspring are probably highest when he aggressively displaces the resident male during the most favourable time for fertilisation. Mating with a female for maximum duration while ejaculating frequently should further increase his siring success (Hanken & Sherman 1981; Huck *et al.* 1985). The argument for a critical period for fertilisation was supported by the frequent sniffing and flehmen of female scent marks by male partners, as well as males withholding from copulation for extended time periods while the female was ready to accept copulation. This was especially evident in the mating pair runs observed. Males also seemed to abandon their mate-guarding to seek further mating opportunities when neighbouring females came into oestrus.

Despite the females' danger of loosing their partners' commitment to cub-guarding, all were seen to seek EPCs. Increased genetic variability of their cubs (Maynard Smith 1978) could have been the motivation of females paired with high-quality males to seek EPCs. Females seemed interested in letting EP males copulate for shorter periods only, while keeping their partner's committent to guarding cubs by letting them copulate for longer. This likely depended on the quality of the resident male. A female partner of a low quality resident male engaging in EPC with a high quality male neighbour may gain additionally by obtaining 'sexy sons' with the cuckolding tendencies of their father (Weatherhead & Robertson 1979). The Females' influence on the course of the copulation was prominent - by becoming available by leaving their den; by not following the male far away from their den; and by terminating copulations by pushing the male off at the den entrance. So despite males being the more obvious sex to bring about copulations in this mating system, females appeared able to exert considerable choice and to stimulate competition when male interest was low, by signalling to other males by means of extra-territorial scent marking.

In conclusion the evidence that resident aardwolves rarely marked outside of their territories, that subadult aardwolves stopped to scent mark inside their parents' territories as they matured, that intruders always ran away on seeing or being detected by residents of the same sex, and that a resident changed its den in response to it being scent marked by a same-sex intruder provided strong support that scent marks function in intimidation. They act as a threat with immediate physical attack if the intruder is encountered. During the mating season the primary function of scent marks changes. In females they may continue to act as a threat to intruding females, but during her pro-oestrus and oestrus they act as a sex attractant to males and may be used to solicit EPCs from neighbouring males. In males they may also convey different messages to the different sexes. To females they may advertsise the males quality given the handicap he must experience in order to scent mark at this time of year, while to the males they may indicate that the male is prepared to fight for access to the female when she becomes receptive. Thus because access to a receptive female is probably of similar value to both the resident male and an intruding male, the asymmetry of contest that normally exists between residents and intruders during the non-mating season and maintains territorial integrity, largely disappears. Therefore high quality males start intruding and scent marking in the territories of lower quality males. Thus during the mating season an intruding male's scent marks are generally not a threat of territory take-over, but just for access to receptive females.

SUMMARY

A functional analysis of scent-marking in the aardwolf *Proteles cristatus* was conducted over a two and a half year field study near Kimberley, Northern Cape Province, South Africa. A total of 42 000 paste marks were recorded while following 14 adult aardwolves and 13 cubs for 2 300 hours over a distance of 3 100 km in a vehicle.

The anatomy of the anal pouch revealed an efficient apparatus for applying scent-marking secretion onto grass stalks. Histology showed large numbers of secreting sebaceous glands and interspersed apocrine scent glands in the wall of the pouch, and additional lateral sacs for production and storage of lipid-rich sebaceous secretion only. The mixing of the two gland products in the anal pouch yielded copious amounts of long-lasting pasting secretion of different colour. The histology of the penile pad of aardwolf males was similarly geared to production and application of secretion, though its exact function is still not clear. As it occurs only in males it might play a role during mating, though it was also seen active during the non-mating season.

Aardwolves started practising scent-marking motor patterns soon after emerging from their breeding den at about four weeks of age but then produced translucent secretion only. Scent-marking secretion resembling that of adults was however used only at complete physical maturity at ten months of age and independence from their parents. Cubs practised paste marking by overmarking scent marks of their parents, adjusting their mark-rate to that of the adult followed. The case of a hand-raised female offered insight into the importance of practising the scent marking motor pattern and learning from their parents through imitation. Male cubs marked more intensively than female cubs. Individual variation in frequency of marking was also detected in male cubs. Early differences could precede later individual differences in adult marking effort. Just after cubs showed adult mark-rates and were able to deposit a secretion similar to that of adults they stopped marking completely, coinciding with parental aggression, and some remained in their parents' territories for another year. They started to paste again only when attempting to establish their own territory.

Uncovered faeces away from established middens and urine on middens, deposited predominately by male aardwolves, were likely to act as additional scent-marking agents during the mating season.

During the eight month non-mating season there was a great deal of variation in marking activity due to differing territory size, individual effort, and territory establishment. Aardwolves marked rarely outside

of their territories. They seemed to respond to greater perceived intruder pressure in the non-mating season of 1992 by increasing their marking activity in their borders and intruded less frequently themselves into neighbouring territories for feeding. They also scent marked border middens more and both marked and slept more at dens in the interior of their territories in the second season. Mark-rates in the borders were not significantly different between the sexes since no consistent pattern was discernible for all territories. Aardwolves usually marked at higher rates in the border than in the internal areas. Borders where intrusions were most likely to occur were marked selectively more than others. Aggressive interactions between territory owners and non-residents were rarely observed. During the present study the rate of aggressive interactions was less than half of that recorded by Richardson (1991) which seemed to agree with the pattern that aardwolves defended territories about twice the size of those during Richardson's study, making encounters less likely. During the non-mating season scent-marking patterns suggested that scent marks functioned as a representation of an aardwolf's claim to a territory area and its readiness to resort to physical attack. Despite this, both male and female neighbours frequently crossed over well-marked borders to feed. The intimidation message represented by territorial scent marks seemed to be directed more at members of the same-sex than at members of the opposite sex, since they were chased less vigorously, although they were also stealing food resources. Neighbours were just intruding to feed and did not scent mark. Challenges for territorial take-over were perceived by territory owners through scent-marking by non-residents, and when a challenger was caught it led to a fight. Males and females differed in marking the border and interior of territories at different rates and densities, possibly reflecting divergent motivations for territorial marking. Males may chiefly defend their access to females and to a lesser extent food resources to feed themselves and the cubs they fathered, whereas females are defending feeding territories only.

Scent-marking activity varied strongly over the course of the mating season. Both sexes started marking outside their territories presumably to advertise to neighbouring mating partners before and when females were in oestrus. Females increased their mark-rates only when not attended by males. By marking at a high rate males scouting in territories of females in pro-oestrus were possibly demonstrating their determination to achieve extra-pair copulation (EPC) to both their neighbouring males and females. Prolonged scouting and scent marking during this time of low food resources are presumed energetically costly (Richardson 1991). At least 62% of observed copulations were extra-pair copulations and therefore a prominent strategy in the aardwolf's mating system. The analysis of behaviours shown by males and females before and after copulation suggests that there may be a critical period within the oestrus where fertilisation of females is most likely. Male residents seemed to try and mate at the critical point in time for female fertilisation while EP males either fought the resident aggressively or they were able to copulate without being detected by the resident male. This was usually after the female had already mated with the resident male. Females seemed to encouraged extra-pair copulations by scent marking outside or along their borders, attempting to attract neighbouring males, but still copulated longer with their partners. Their ability of exerting choice was strong by becoming available to specific males when leaving their den, by not following the male too far away from the den, and by terminating copulations by pushing the male off at the den entrance. Females also seemed to encourage male-male aggression by laying a scent-mark trail for other males to follow. All males guarded their females for varying periods, and for especially long periods when they interrupted an EPC of their female. The exceptional case of one male defending two females, and possibly the close temporal spacing of these females' oestrus, may have weakened this male's ability to guard both female partners efficiently. In one case an EPC may have been successful when a male resident defected completely from guarding his female's cubs. After the mating season when resources, mating partners and termite food were scarce, scent-marking activity was low, to increase again when re-establishing territorial borders at the start of summer.

In 43 experimental nights 617 scent marks that had been collected from known aardwolves were put out at specific points throughout other aardwolves' territories. The response of these tested aardwolves was monitored when they found 164 of the translocated scent marks. Both males and females responded more strongly towards scent marks of individuals of the same sex than to those of the opposite sex, except during the mating season. Responses varied depending on where the scent mark was deposited within the territory. Along territory borders and at middens, most marks were sniffed for short periods and overmarked. However, marks at dens in use were seldom overmarked but sniffed for much longer, often while showing flehmen. Flehmen and prolonged sniffing seemed to indicate investigatory behaviours as they were most prevalent towards the first mark of a non-resident found that evening and particularly towards stranger's marks or those of a female in pro-oestrus found by a male. Overmarking seemed to be a behaviour asserting territorial ownership. After locating a neighbour's scent mark the resident also immediately increased the number of scent marks deposited by an average of 91 % while depositing marks in greater densities per distance walked, and went directly to scent mark the respective border. This demonstrated individual recognition of scent marks in aardwolves. When at the same time males were presented with scent marks of their resident female and those of other females they responded differently towards these marks suggesting an ability to distinguish between them. The fact that aardwolves changed their dens after it was scent marked by a same-sex intruder demonstrated that intimidation could be transmitted without physical presence of the marker and thus provided support for the intimidation hypothesis. The message transmitted by a scent mark changed seasonally coinciding with a shift in the principally defended resource, food or mating opportunity. During the non-mating season a scent mark deposited inside the territory was likely perceived as a challenge for territory take-over, whilst during the mating season it would serve primarily to signal the marker’s intention to mate with the resident’s partner. The reactions to translocated marks changed accordingly and marks were perceived as less of a threat towards the residents.

OPSOMMING

‘n Funksionele analise van reukafbakening in die aardwolf *Proteles cristatus* was oor ‘n twee en ‘n half jaar veldstudie naby Kimberley, Noordelike Kaap Provinsie, Suid Africa, behartig. ‘n Totaal van 42 000 smeerselafbakenings was aangeteken terwyl 14 volwasse aardwolve en 13 welpies vir 2 300 ure oor ‘n afstand van 3 100 km per voertuig gevolg was.

Die anatomie van die anusbuidel het ‘n doeltreffende apparaat vir die toepassing van reukafbakeningafskeidings aan grasstingels onthul. Histologie het groot aantalle vetafskeidingskliere en deurspekte apokrienafskeidingskliere in die wand van die buidel en bykomende laterale sakke vir die produksie en berging van lipiedrykvetafskeiding alleenlik, getoon. Die menging van die twee klierprodukte binne die anusbuidel het oorvloedige hoeveelhede van langdurige smeerselafskeiding van ‘n ander kleur getoon. Die histologie van die peesterkussinkie van die aardwolfmannetjie was ook vir die produksie en aanwending van afskeidings gerat, hoewel die presiese funksie daarvan nog nie duidelik is nie. Aangesien dit slegs in mannetjies voorkom, mag dit ‘n rol tydens paring speel, hoewel dit ook as aktief tydens nie-paartyd gemerk was.

Aardwolve ouer as sesweke het vir omtrent vierweke reukafbakening motoriese patrone kort nadat hulle hul gat verlaat het begin oeffen. Behoorlike reukafbakening was egter slegs teen fisiese volwassenheid teen agt maande ouderdom en onafhanklikheid van hulle ouers gebruik. Welpies het smeerselafbakening geoeffen deur die reukafbakeningsmerke van hulle ouers oor te merk deur hulle reukafbakeningstempo aan dié van die ouer wat gespoor was, aan te pas. Die geval van ‘n hansgrootgemaakte wyfie het insig tot die belangrikheid van die reukafbakening motoriese patroon oeffening en die leer van hulle ouers deur na-aping, gelewer. Welpiemannetjies het meer deeglik as welpiewyfies reukafbakening uitgevoer. Individuele wisselings in die frekwensie van reukafbakening was ook in welpiemannetjies opgemerk. Vroeër verskille kon latere individuele verskille in volwasse reukafbakeningpogings voorafgaan. Kort nadat welpies volwasereukafbakeningtempos getoon het en kon ‘n afskeiding gelyksoortig aan dié van volwassenes neerlê, het hulle heeltemal met reukafbakening opgehou, ooreenstemmende met ouerlike agressie en van hulle het binne die gebied van hulle ouer vir nog ‘n jaar gebly. Hulle het slegs weer met smeerselafbakening begin sodra hulle hulle eie gebied probeer vestig het.

Blootgestelde faeces, weg van bestaande mishope en uriendeponering op mishope, hoofsaaklik deur manlike aardwolwe tydens paartyd, het as bykomende reukafbakeningagente tot smeerselafbakening met hulle anusbuidel geskik opgetree.

Tydens die agtmaand nie-paartyd het ‘n goort hoeveelheid variasie in reukafbakeningsaktiwiteit weens verskillende gebiedsgrootte, individuele poging en gebiedsvestiging plaasgevind het. Aardwolwe het slegs selde buite hulle gebiede reukafbakening gedoen. Hulle het oënskynlik op aansienlike waargenome indringerdruk tydens nie-paartyd van 1992 gereageer deur hulle reukafbakeningsaktiwiteit op hulle grense te verhoog en het minder self in aangrensende gebiede om voeding betree. Hulle het ook in die tweede seisoen op grensmishope meer reukafbakening gedoen en beide meer reukafbakening gedoen en meer geslaap by gatte in die binneland van hulle gebiede. Die vermoë om ‘n gebied te verdedig mag ook in die lig van die groot verskille in reukafbakeningpoging en gebiedsgroottes op indringerdruk afhang. Reukafbakeningtempos op grensgebiede was nie onder geslagte betekenisvol verskillend nie, aangesien geen vaste patroon was vir alle gebiede waarneembaar nie. Aardwolwe het gewoonlik hoër reukafbakeningtempos op grensgebiede as op die binnelandse gebiede getoon. Reukafbakening op grense waar indringing meer moontlik kon plaasgevind het, was meer selektief as elders. Agressiewe interaksies tussen gebiedseienaars en buitelanders was min waarneembaar. Tydens die huidige studie was die tempo van agressiewe interaksies minder as die helfde van dié wat deur Richardson (1991) vermeld was, wat oënskynlik gepaard gaan met die patroon dat die aardwolwe gebiede van tweemal die grootte as dié wat deur Richardson vermeld was, verdedig het. Tydens nie-paartyd, het reukafbakeningpatrone aangedui dat reukafbakening soos ‘n voorstelling van ‘n aardwolf se eis tot ‘n gebied en sy bereidwilligheid om na fisiese aanval te resorteer gefunksioneer. Ondanks het beide manlike- en vroulikebure dikwels goed reukafgebakende grense oorgevaar om te voed. Die intimidasieboodskap wat deur gebiedsreukafbakening voorgestel word, was oënskynlik meer streng tot lede van dieselfde geslag as lede van die teenoorgestelde geslag gerig, aangesien hulle minder flink nagejaag was, alhoewel hulle voedingsbronne gesteel het. Bure het slegs ingedring om te voed en het nie reukafbakening gedoen nie. Uitdagings om gebiedsoorname was deur gebeidseienaars deur reukafbakening deur buitelanders waargeneem. Mannetjies en wyfies het verskil t.o.v. reukafbakening van grense en binnelandse gebiede, teen verskillende tempos en digthede, wat moontlik uiteenlopende motivering vir gebiedsreukafbakening weerspieël. Mannetjies mag hoofsaaklik hulle toegang tot wyfies en in ‘n mindere mate voedingsbronne om hul self en hulle welpies te voed, verdedig, terwyl wyfies voedingsgebiede alleenlik verdedig het.

Reukafbakeningsaktiwiteit het sterk tydens die verloop van paartyd gevarieër. Beide geslagte het die aantal reukafbakenings wat hulle buite hulle gebiede neergelê het verhoog, vermoedelik om vir paringsvennote voor- en wanneer wyfies in-bronstyd verkeer het, te adverteer. Wyfies het hulle reukafbakeningtempos slegs wanneer hulle nie deur mannetjies opgepas was nie verhoog. Mannetjies met hoë reukafbakeningtempos het gebiede van wyfies, wat in pro-bronstyd verkeer, verken, dalk om hulle vasberadenheid te demonstreer om ekstra-afparing paring (EPC) vir beide hulle naburige mannetjies en wyfies te behaal. Landurige verkenning en reukafbakening tydens hierdie tye van lae voedselbronne is vermoedelik energieduur (Richardson 1991). Ten minste 62% van die waarneembare parings was ekstra-afparing parings en dus ‘n prominente stratagie in die paringstelsel van die aardwolf is. Die analise van gedragte wat mannetjies en wyfies voor- en na-paring vertoon het, het daarop gedui dat ‘n kritiese tydperk tydens bronstyd waar bevrugting van wyfies mees moontlik is, bestaan het. Dit het enigsins gelyk dat mannetjies gepoog het om paring teen kritiese tye van wyfie bevrugting te bewerkstellig deur aggressief hulle mannetjievernoot te veg, of deur skelms parings te steel gewoonlik nadat sy met haar venoot gepaar het, terwyl hulle ‘n toename in fisiese kontak vermy het. Dit het enigsins gelyk dat wyfies ekstra-afparing parings aangemoedig het deur reukafbakening buite of op hulle grense te doen, om naburige mannetjies aan te lok, maar het steeds met hulle vennote langer gepaar. Hulle vermoë om voorkeur uit te oeffen was sterk om toegangklik aan spesifieke mannetjies, sodra hulle hull gat verlaat het, te word, deur die mannetjies nie ver van hulle gat te volg nie, en deur paring te termineer deur die mannetjie by die gat ingang weg te stoot. Wyfies het tussen-manlike agressie aangemoedig deur reukafbakening wat ander mannetjies kon opspoor, neer te lê. Alle mannetjies het hulle wyfies vir uiteenlopende tydperke beskerm veral vir lang tye wanneer hulle ekstra-afparing paring van hulle wyfie onderbreek het. Die uitsonderlike geval van een mannetjie wat twee wyfies beskerm het, en dalk die saamvallende bronstye van dié wyfies, mag die vermoë van hierdie mannetjie om beide wyfie vennote doeltreffend te beskerm, verswak het. In een geval, mag horingdragtigheid deur ekstra-afparing paring suksesvol gebeur het, aangesien die manlike vennoot naderhand van sy wyfie se welpies afgeval het. Na paartyd wanneer bronne, paringsvennote en termietkos skaars was, was reukafbakeningsaktiwiteit laag, slegs om weer toe te neem sodra met hervestiging van gebiedsgrense teen die aanvang van somer begin was.

Tydens 43 nagte van eksperimentering, 617 oorgestelde reukafbakenings wat van bekende aardwolwe versamel was, was by spesifieke plekke in ander aardwolwe se gebiede geplaas. Die gedrag van die aardwolwe wat getoets was, was gekontroleer toe hulle 164 van die oorgeplaasde reukafbakenings ontdek het. Beide mannetjies en wyfies het sterk gedrag tot reukafbakenings van enkelinge van dieselfde geslag as dié van die teenoorgestelde geslag, behalwe tydens paartyd, getoon. Gedrag het afhanklik van waar die reukafbakening binne die gebied gedeponeer was, gewissel. Langs gebiedsgrense en by mishope was die meeste reukafbakenings vir kort tye gesnuffel en oorgemerk. Alhoewel, reukafbakenings by gatte wat in gebruik was, selde oorgemerk was, maar was vir langer tye terwyl *“flehmen”* getoon was, gesnuffel. *“Flehmen”* en langdurige snuffeling het oënskynlik ondersoekende gedragte getoon, aangesien hulle mees oorweegend was teenoor die eerste reukafbakening van ‘n buitelander wat daardie aand ontdek was en veral teenoor ‘n vreemdeling se reukafbakening, of dié van ‘n wyfie in pro-bronstyd, wat deur ‘n mannetjie ontdek was. Oormerking was oënskynlik ‘n gedrag wat gebiedseienaarskap bevestig het. Nadat ‘n buur se reukafbakening opgespoor was, het die inwoner ook onmiddelik die aantal reukafbakenings wat gedeponeer was, teen ‘n gemiddeld van 91% verhoog, terwyl reukafbakening teen hoë digthede per afstand wat geloop was, gedeponeer was, en het direk op die onderskeie grens reukafbakenings gedoen. Dié het individuele erkenning in aardwolwe getoon. Wanneer mannetjies tegelykertyd met reukafbakeningmengsels van hulle inwoner wyfie en reukafbakenings van ander wyfies aangebied was, het hulle verskillende gedrag aan hierdie reukafbakeningmengsels getoon wat ‘n vermoë om tussen hulle te ondeskei, opper. Die feit dat aardwolwe hulle gatte verander het, nadat dié deur ‘n gelyksoortige geslag indringer reukafgebaken was, het getoon dat intmidasie kon sonder die fisiese teenwoordigheid van die merker gesein word en het dus ondersteuning vir die intimidasie hipothesis verleen. Die boodskap wat seisoenaal deur ‘n reukafbakening oorgedra was, het ooreenstemmend met ‘n skuiwing van hoofsaaklike verdedigde bron, voedsel of paring geleentheid gepaardgegaan. ‘n Reukafbakening wat binne die gebied tydens nie-paartyd gedeponeer was, was oënskynlik as ‘n uitdaging vir gebiedsoorname waargeneem, terwyl tydens paartyd sou dit primêr as ‘n sein deur die aardwolf om sy voorneme om met die inwoner se vennoot te paar, gedien. Die gedrag tot oorgeplaasde reukafbakenings het dienooreenkomstig verander.

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APPENDIX I

COMMON AND SCIENTIFIC NAMES OF ANIMALS CITED IN THE TEXT

Mammals

Order Carnivora

Hyaenidae

aardwolf	*Proteles cristatus*
brown hyaena	*Hyaena brunnea*
spotted hyaena	*Crocuta crocuta*
striped hyaena	*Hyaena hyaena*

Viverridae

African civet	*Civettictis civetta*
African dwarf mongoose	*Helogale undulata rufula*
binturong	*Arctictis binturong*
small-spotted genet	*Genetta genetta*

Felidae

African wild cat	*Felis lybica*
black-footed cat	*Felis nigripes*
caracal	*Felis caracal*
lion	*Panthera leo*
tiger	*Panthera tigris*

Mustelidae

American badger	*Taxidea taxus*
European badger	*Meles meles*
ferret	*Mustela furo*
otter	*Lutra lutra*
pine marten	*Martes martes*
stoat	*Mustela herminea*
striped polecat	*Ictonyx striatus*

Canidae

African wild dog	*Lycaon pictus*
bat-eared fox	*Otocyon megalotis*
black-backed jackal	*Canis mesomelas*
Cape fox	*Vulpes chama*
coyote	*Canis latrans*
domestic dog	*Canis familiaris*
Ethiopian wolf	*Canis simensis*
red fox	*Vulpes vulpes*
wolf	*Canis lupus*

Phocidae

Northern elephant seal	*Mirounga angustirostris*

Order Primata

man	*Homo sapiens*

Order Rodentia

brown lemming	*Lemmus trimucronatus*
Columbian ground squirrel	*Spermophilus columbianus*
capybara	*Hydrochaeris hydrochaeris*
coypu	*Myocastor coypu*
grey-sided vole	*Clethrionomys rufocanus*
hoary marmot	*Marmota caligata*
Mongolian gerbil	*Meriones unguiculatus*
porcupine	*Hystrix africaeaustralis*
red squirrel	*Sciurus vulgaris*
springhare	*Pedetes capensis*
Syrian golden hamster	*Mesocricetus auratus*

Order Lagomorpha

rabbit	*Oryctolagus cuniculus*

Order Tubulidentata

aardvark	O*rycteropus afer*

Order Perissodactyla

horse	*Equus caballus*

Order Artiodactyla

African buffalo	*Syncerus caffer*
black wildebeest	*Connochaetes gnou*
blesbok	*Damaliscus dorcas phillipsi*
Coke’s hartebeest	*Alcelaphus buselaphus cokei*
dik-dik	*Madoqua kirkii*
eland	*Taurotragus oryx*
gerenuk	*Litocranius walleri*
greater kudu	*Tragelaphus strepsiceros*
grey duiker	*Sylvicapra grimmia*
impala	*Aepyceros melampus*
pronghorn antelope	*Antilocapra americana*
springbok	*Antidorcas marsupialis*
steenbok	*Raphicerus campestris*
suni	*Neotragus moschatus*
Thomson’s Gazelle	*Gazella thomsoni*
warthog	*Phacochoerus aethiopicus*

Birds

Order Strigiformes

giant eagle owl	*Bubo lacteus*

Order Falconiformes

martial eagle	*Polemaetus bellicosus*

Order Columbiformes

ring dove	*Streptopelia risoria*

Order Passeriformes

bank swallow	*Riparia riparia*
collared flycatcher	*Ficedula albicollis*
dunnock	*Prunella modularis*
European starling	*Sturnus vulgaris*
golden-winged sunbird	*Nectarinia reichenowi*
mountain bluebird	*Sialia currucoides*
pied flycatcher	*Ficedula hypoleuca*

Reptiles

desert iguana	*Dipsosaurus dorsalis*
Jamaican anole lizard	*Anolis garmani*

Amphibians

American bullfrog	*Rana catesbeiana*
green tree frog	*Hyla cinerea*
natterjack toad	*Bufo calamita*

Crustaceans

Order Eucarida

Neotropical fiddler crab	*Uca deichmanni*

Insects

Order Isoptera

snouted harvester termite	*Trinervitermes trinervoides*
harvester termite	*Hodotermes mossambicus*