CHAPTER SEVEN

SOCIAL BEHAVIOUR AND ORGANISATION

Introduction

A social system has been defined as the manner in which individuals position themselves in space and time in relation to other conspecifics and some features of the environment (Ferreras, Beltran, Aldama & Delibes, 1997). Social organisation refers to the number of individuals in a social group, their behavioural and genetic relationships, and the way in which reproduction is partitioned among them. Social organisation comprises the most fundamental defining features of animal societies, forged by ecological and social selection acting over the history of a population, and creating social and genetic environments that govern the course of subsequent social evolution (Creel & Macdonald, 1995; Ross & Keller, 1995). Some of these powerful evolutionary forces acting on animals are those imposed by group living, the interaction between, and competition among members of the same species. The study of social behaviour, called behavioural ecology or socio-biology seeks to understand how relationships between individuals shape the social systems and mould the evolution of individual form and behaviour (Mills, 1978; Ross & Keller, 1995; Frank & Glickman, 1996). For example, a species' social system can act as a natural regulatory mechanism, limiting the proportion of the population reproducing and, consequently, the rate at which the population can increase (Ferreras *et al.*, 1997). Therefore understanding the social organisation of predator species and the factors that influence their social behaviour is of fundamental importance for their management and conservation.

Most anatomical, physiological, and behavioural adaptations have evolved through the interaction between heredity and the environment, having been fixed genetically, and are passed from parent to offspring. The key to evolutionary success is very simple: leave more offspring than other members of your species. Genetic changes that increase the number of one's descendants (or the descendants of one's close relatives) will spread through the species (Hamilton, 1964; Dawkins, 1989). The fitness of each individual organism in a biological community may be affected by the adaptations of all other individuals. That creates the essential elements of a 'game' among the individuals (Vincent, Van, & Goh, 1996). It is an evolutionary game where the individual organisms (players) inherit their phenotypic characteristics from continuous play of the game from generation to generation. Any dynamic process where the 'fitness' of a given individual in a population is determined by the adaptations used by all individuals has the potential to evolve with time.

Biologists measure an organism's relative genetic potential with a theoretical construct termed fitness. An individual with greater fitness is more likely to leave descendants than one with less. All aspects of an organism's biology - for instance, longevity, tolerance of environmental extremes, and the abilities to feed itself, escape predators, find mates, and raise offspring - contribute to its fitness. One of the most important components of fitness is reproductive success, which can also be measured in various ways: number of mates, number of offspring born, number of offspring that survive infancy, or number of offspring that survive to reproduce. Each of the four aforementioned measurements gives a better tally of descendants than the preceding one, but each is successively more difficult to measure in practical terms. Only through long-term studies of known individuals (e.g. Schaller, 1972; Kruuk, 1972; Moehlman, 1978, 1979, 1980) can one gain good measures of reproductive success and understand the behavioural characteristics that contribute to it and, hence, to fitness.

Since a great many aspects of a species' social behaviour ultimately affect individual survival and reproductive success, social forces have profound implications for the evolution of most animals, including humans. Selection has favoured the capacity for social animals to adjust group size in response to a suite of ecological factors, primarily those affecting temporal and spatial patterns of resource availability (Caraco & Wolf, 1975; Emlen 1982a, b). These patterns influence foraging efficiencies, mating probabilities, and reproductive success (Moehlman, 1983). Predation pressure also often constitutes another important factor determining social tendencies. Group size may then be optimised in response to the most important environmental characteristics, in an attempt to maximise the total benefit-to-cost ratio for individual group members. Among social animals, stable groups are almost always characterised by dominance hierarchies such that certain individuals have priority of access to food, mates, or other limited resources. In the absence of stable relations among individuals, life would be an endless squabble over resources. Dominance relations impose order and stability, albeit often to the detriment of low-ranking individuals (Mech, 1970, in Meia & Weber, 1996; Macdonald, 1980) and sometimes even to dominant individuals themselves (Creel & Creel, 1996; Morell, 1996)!

An individual's social behaviour can be represented by analogy as the solution to a cost-benefit analysis of the interacting consequences of its actions (Macdonald & Moehlman, 1983). The choice between different rules for action is dynamic in the sense that the magnitude of the costs and benefits of a given behaviour vary continually with each individual's circumstances. So, as animals can adapt their social behaviour to prevailing circumstances, we should expect not only that different individuals will behave differently, but also that each individual's behaviour will vary as the social and ecological circumstances change (Kruuk & Macdonald, 1985). However, real costs and benefits are so notoriously hard to measure that one too easily ends up in speculation (Macdonald & Moehlman, 1983).

Social organisms exhibit conspicuous intraspecific variation in all facets of their social organisation. It has become evident that social organisation varies not only among species but also within species or even populations. Striking variation in group composition and in the partitioning of reproduction among group members is proving to be the rule rather than the exception in a wide array of vertebrate and insect species. Variation in social organisation is the product of diverse extrinsic selection pressures generated by the local ecology that interact with intrinsic selection pressures related to competitive and cooperative interaction among group members. Thus studies of variation in social organisation may shed light on how ecological and social factors jointly influence the course of social behaviour (Ross & Keller, 1995). Within the Carnivora, there is much variation in social organisation between species, with some participating in cohesive, intricately structured groups whereas others live alone (Kruuk & Macdonald, 1985). Moreover within several species, different populations show marked variation in social organisation, for example with respect to group size and range size (Macdonald, 1983). The question arises as to what environmental factors underlie this variation. Understanding intraspecific variation is fundamental to understanding the evolution of carnivore communities and, furthermore, it is important for predicting the consequences of management of these species and their habitats (Kruuk & Macdonald, 1985; Creel & Macdonald, 1995).

In Africa, few animals are as unfairly maligned and as intrinsically fascinating as black-backed jackals. Commonly reviled as lowly scavengers, they are, in fact, highly successful predators and the most abundant of the larger carnivores in Africa. It has been shown that jackal diets vary markedly within and between habitats (Wyman, 1967; Lamprecht, 1978a,b; Du Bothma, 1971; Rowe-Rowe, 1976, 1983; Hiscocks & Perrin, 1987). A conspicuous feature of this variation, in addition to the diversity of the diet, which is made up of different-sized prey (see Chapter on Foraging Ecology), is the proportions in which the different-sized prey are taken. In addition to variation in diet, there is evidence that jackal social organisation varies from one area to another (Ferguson, 1978; Moehlman, 1978; Fuller, Bikneviscius, Kat, Van Valkenburgh, & Wayne, 1989). Given this variation in diet, it seems likely that the social organisation of jackals could also vary in relation to other factors such as hunting pressure and habitat type.

Territoriality and the nature of the mating system (e.g. monogamy, kleptogamy, etc.) are arguably some of the most important behavioural traits affecting the spatial organisation of animal populations and, therefore, population dynamics. The existence of territories, under one definition or another, is integral to many models relating the availability of resources such as food, mates, and shelter, to social behaviour and density dependent regulation (Brown & Orians, 1970; Macdonald, 1983; Carr & Macdonald, 1986; Doncaster & Macdonald, 1991; 1992). In practice, the acts recognised as defence of an area include two categories (Brown & Orians, 1970), namely: 1) actual defence, such as attacking, chasing, and threatening rival intruders, and 2) identifying acts that designate the defender and that make his presence conspicuous to his rivals; these include certain vocalisations, displays, and scent-markings. When such acts typically fail to keep out rivals, the area should not be designated a territory.

Thus the essential characteristics of a territory (Brown & Orians, 1970) are: 1) a fixed area, which may change slightly over a period of time (otherwise known as 'drifting territoriality', Doncaster & Macdonald, 1991), 2) acts of territorial defence by the possessor which evoke escape and avoidance in rivals, so that, 3) the area becomes an exclusive area with respect to rivals. These conditions must be satisfied for an area to be recognised as a territory. However, although in many species the entire home range is defended, in others defence may be limited to a mating spot, a nest, a feeding area, or a roost. It should also be noted that territoriality is intraspecific.

Monogamy, as defined by Kleiman (1977) is a rare mating system which is common only among birds (roughly 90%) (Moehlman, 1986), but is among the more highly evolved forms of social organisation in mammals. Among canids, the basic mating system is long-term monogamy, a system that is taxonomically scattered among mammals (< 3%, Kleiman, 1977; 3-5%, Mock & Fujioka, 1990). However, an examination of the social organisation in the continuum of small to large canids reveals major trends in adult sex ratio, dispersal, mating systems, and neonate rearing systems (Moehlman, 1986; 1989). Small canids (< 6.0 kg) tend to have an adult sex ratio skewed towards females, dispersal biased towards males, female helpers, and they exhibit a tendency toward polygyny. Medium-sized canids (6.0-13.0 kg) have equal sex ratios, equivalent sexual emigration, both sexes as helpers, and observations at present indicate that they are strictly monogamous. Large sized canids, with the exception of the maned wolf (*Chrysocyon brachyurus*), have sex-ratios skewed towards males, primarily female emigration, male helpers, and indications of polyandry (Moehlman, 1986). Medium-sized canids may have the most flexibility in terms of altering their social behaviour and organisation (Moehlman, 1986).

Black-backed jackals are one of the species that do maintain enduring pair bonds in animal societies (Moehlman, 1986, 1989; Rowe-Rowe, 1986), some of which may remain intact for up to six or eight years, which effectively means that the animals can pair for life. Moehlman (1979, 1983,) asserted that some jackal offspring (called 'helpers') of both sexes remain in their natal territory where, although not breeding themselves, they help provision and guard subsequent litters and also feed the nursing mother. All offspring that remained in their natal range past age 12 months did so for only one year. Since jackals can be reproductively mature at 11 months old, those that stayed with parents were perhaps delaying their own reproduction (Moehlman, 1983; Macdonald & Moehlman, 1983; Rowe-Rowe, 1986; Creel & Macdonald, 1995). Mated pairs hunted cooperatively but helpers were rarely involved in collaborative hunting. In some respects, the social organisation of black-backed jackals is similar to that of baboons and other terrestrial primates that have long served as models for understanding human social behaviour. In any event, jackals present a rare opportunity to observe and perhaps to understand how and why family bonds develop among hunting-and-gathering mammals. They give us ideas about the evolution of monogamy and helping behaviour (Moehlman, 1980). As social carnivores who share their food and care for dependent young, they contend with conditions similar to those experienced by early man, and provide insight into our own behaviour.

Methods

General Observations

Quantitative data were collected through systematic counts, incidental observations, and through radio tracking of known individuals. Some individual jackals could be identified from natural markings such as ear notches, scars, and colour differences. Observations were made by following individuals as they foraged and also at dens. Every sighting of jackals during the study period was registered and behavioural attributes as stipulated in Chapter Four recorded, with further notes on date, time, position, group size and composition according to age and sex, where possible. During the day, the area was searched for tracks and signs, such as faeces, regular paths and resting sites.

In addition to the three radio-collared jackals, eleven jackal corpses were incidentally collected (run over by vehicles or shot during problem animal control operations). Approximate ages of all jackals were determined from tooth eruption sequences or wear on the incisors (Lombard, 1971). According to size and behaviour, the sighted jackals could be classified according to three broad age categories: adults, juveniles (sub-adults), and young (see Chapter Three). The difference in size between sub-adults and adults was usually discernible when the two classes were together; seen alone, subadults might have been mistaken for adults. But in spite of the difficulty differentiation facilitated the recognition of family units.

During incidental observations, determination of sex and identification of individuals could not be carried out since sexual organs were often difficult to see, as long hair and the bushy tail obscured them. Additional sexual characteristics used were the teats of lactating females and the positions adopted during urination, which is typical of most canids (Kleiman, 1967).

Categories of Social Interactions

Social interactions among black-backed jackals were divided into three categories (Kleiman, 1967; Ferguson, 1978):

(a) Aggressive interactions, in which the confident animal physically attacks the subordinate jackal, and the apparent aim of the confident jackal is to harm its subordinate counterpart physically.

(b) Agonistic interactions, in which the confident animal asserts its superior social status over the subordinate jackal. Actions are mostly exaggerated or ritualised. Although physical contact may occur as in aggressive interactions, it is not with the apparent intention of inflicting any bodily harm on the subordinate.

(c) Amicable interactions, in which confident or subordinate jackals cannot be clearly recognised and no clear elements of aggression or agonism can be seen.

Agonistic and aggressive interactions are characterised by distinct elements of threat and submission, and amicable interactions by the lack of these elements. During aggressive interactions, threat and submission are intense, and a fight/flight type of interaction is the result. In agonistic encounters, there are no signs of attack or flight by either of the interacting jackals, although threat and submission still characterise these interactions (Ferguson, 1978). Functionally, amicable interactions serve to strengthen social ties, i.e. the equality of social status among animals, whereas agonistic and aggressive interactions reinforce the difference in social status among animals (Fox, 1971; in Ferguson, 1978), and thus effectively separate them socially.

Vocalisation

Data collection involved opportunistically recording the incidence of jackal calls in the study area. Records were made of whether the calls were made by an individual or group (two or more animals). It was not possible to be more specific about the number of jackals calling in a group because more than two animals could not be distinguished with confidence.

Two types of vocalisations were noted; single and group. During a bout of howling, a single jackal usually called about once every 30 sec. Thus a single session was considered terminated if more than one minute of silence followed a single howl. Group sessions were generally started by one or two single calls, with other animals joining immediately.

Denning

The study area was searched for dens occupied by jackal litters. Footprints of jackal pups, prey remnants and smell of jackal scent and putrefying prey remnants at the den openings were signs of jackal litters. In addition, at weaning the pups begin to play around the den and this flattens the vegetation around the den. These signs together made it possible to determine whether a jackal litter occupied a den or not.

Results

Group Size and Composition

During the present study, 226 sightings of black-backed jackals were recorded representing 377 animals. Most sightings (48.2%) were of single animals, 39.3% were of two, 9.7% were of three, and six groups of four animals were seen (Table 18). Mean group size was 1.7. Mean group sizes were smallest during autumn (1.4) and greatest from winter (1.7) through spring (1.8) and summer (1.8). The greatest number of jackals that I observed at any one time was 5, but this probably represented under half of the total number living within the reserve. These jackals indulge, several times a night, in howling and in so doing provided me with a means of estimating their numbers. While it was extremely difficult to distinguish individual voices from the chorus, I estimated the vocal population of the area to be in excess of five individuals (at least two pairs with some transient, solitary, or satellite individuals) (also see Chapter Four).

Only one case of group hunting (> two individuals) was observed in this study (Chapter Six). I found little evidence of jackal groups in MNR (28 out of 226 sightings) and as such they could be classified as transients, solitary residents, and members of pairs or packs (adult pair with offspring). Resident pairs defended well-defined territories (with sizes lesser than home ranges) which were maintained by scent marking, vocalizations and dyadic interactions. Superimposed on this territorial mosaic were the nomadic movements of transient or dispersing individuals.

Seasonal variation was also observed in the number of single animals, two's, and groups of 3 to 4 individuals (Figure 6). Seasonal differences were pronounced for single animals and groups of two, and followed a pattern that was related to reproduction and social behaviour (Chapter Four). Family groups usually consisted of two parents and from 1 to 3 young - an average of 1.2 (n = 7) young. This effectively means that jackal pairs in MNR were able to successfully raise only a single offspring on average, and observed offspring were obviously those that had survived neonatal mortality.

Table 18. Seasonal occurrence of black-backed jackal group sizes in Mokolodi Nature Reserve from November 1995 to February 1997

	SEASONS							
GROUP SIZE	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All Seasons**	**Relative percentage**	**Total no. of jackals sighted**
1	19 (48.7)	31 (64.6)	25 (37.3)	16 (47.1)	18 (47.4)	109	48.2	109
2	10 (25.6)	16 (33.3)	37 (55.2)	11 (32.4)	15 (39.5)	89	39.3	178
3	8 (20.5)	1 (3.2)	4 (6.0)	6 (17.6)	3 (7.9)	22	9.7	66
4	2 (5.1)	0 (0.0)	1 (1.5)	1 (2.9)	2 (5.3)	6	2.7	24
Total	**39**	**48**	**67**	**34**	**38**	**226**		**377**
Mean group size	1.8	1.4	1.7	1.8	1.7	1.7		

Note: Figures in parentheses represent the seasonal frequency of occurrence (%) of each group size

Although no clear seasonal pattern was evident in the relative frequency of solitary animals ($\chi^2 = 6.45$, $d.f. = 4$, $p > 0.05$) most sightings (31) of single animals were recorded during autumn. Pairs were most numerous in winter ($\chi^2 = 17.5$, $d.f. = 4$, $p < 0.05$; Fig. 6) and this was probably the pairing-mating season, as the first cubs were seen during August to September. However, it is likely that seasonal differences in visibility levels could also have influenced the number of sightings. Groups of more than two were most numerous around summer (December and January) but no significant differences between seasons were revealed. ($\chi^2 = 3.5$, $d.f. = 4$, $p > 0.05$). As no sub-adults were seen after March, the animals are presumably fully grown at 5-6 months, and groups of three to four animals are predominantly families with grown-up offspring. These groupings seemed to split up when the next breeding season approached

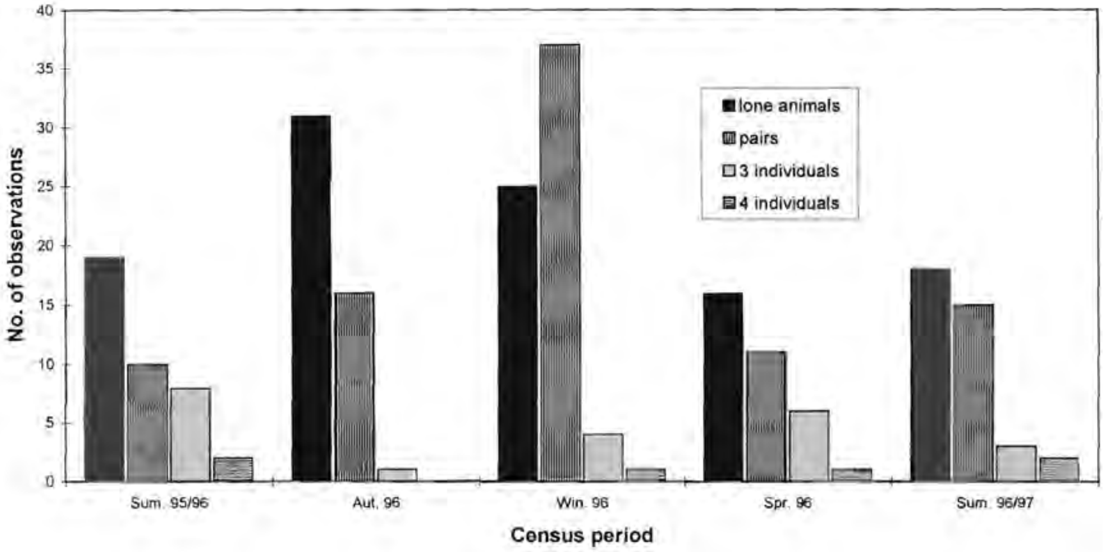

Fig. 6. Seasonal occurrence of black-backed jackal group sizes in Mokolodi Nature Reserve from November 1995 to February 1997

Sex Ratio and Age-group Structure

Direct counts of jackal pups could not be conducted in the present study due to the wary nature of the jackals within predominantly stock-farming areas (such as the area around MNR) and as such, cannot be readily observed in most free-ranging situations. Wherever age and sex could be determined, pairs were found to consist of an adult male and female. Adults could be identified within groups of all sizes, usually in pairs, and larger groups often together with young (Fig. 6). In 117 recorded groups (i.e. pairs included), pairs with young were only seen on seven occasions, usually at the den accompanied by non-breeding yearlings.

The live-trapped and radio collared animals consisted of two males and a single female, while the eleven incidentally collected jackals comprised five males and six females, yielding an overall sex-ratio of unity, despite the small sample sizes. Morphometric measurements and relative age-groups of all 14 jackals are presented in Table 1. Adult male mass averaged 7.8 kg (range, 6.9-9.2 kg, n= 6), while the average adult female mass was 7.0 kg (range, 5.8-8.7, n=4). Juvenile jackals comprised two males and two females of the sample population available for analysis. No young were available for morphometric measurements.

Rowe-Rowe (1978) reported that jackal males are significantly larger than females and possibly kill larger prey than do females, as has been found in some predators exhibiting sexual dimorphism. Moehlman (1983) reported that an adult jackal hunts and kills for his mate who remains with her pups in the den for the first few weeks after whelping. In some cases, samples may consequently be biased in favour of males who may be encountered too often during their foraging excursions.

Categories of Social Interactions

In all social interactions between pair members in which food was not involved, the behaviour of both animals towards each other was classed as amicable or friendly (n. Grooming between and behind the ears, and on the back was recorded. Allogrooming was usually accompanied by self-grooming as reported by Ferguson (1978) and Moehlman (1983). When members of a pair had been separated for some time, a short greeting ceremony took place. No sign of dominance was observed in pairs, except when with subordinate offspring.

Agonistic postures and signals are well-developed in black-backed jackals (Ferguson, 1978). Of the 182 observed social interactions, 44 (38%) belonged to this type. During aggressive interactions, there was a definite dominant animal and an extremely submissive jackal, but the dominant animal either physically attacked the intruder, or otherwise tried to attack an intruder if one came near. Aggressive interactions occurred on 38 occasions (19.8%) and were not observed between members of a pair. Most of the aggressive interactions occurred around food (23 out of 38 occasions) and on known territorial boundaries (on 9 occasions).

Of the 13 recorded group contacts, 10 occurred during March-July 1996, the time of year when family groups seemed to break up, and the animals were typically seen in pairs. Of these 10 contacts, seven included biting and chasing, and in only one case, two jackals merely watched one animal, which trotted past some 100 m away. Six more group encounters were noted in August at a time when gravid females and families with pups had been recorded. The rest of the encounters could be described as indifferent. In four of these encounters the animals were resident neighbours. The increase in territorial activity coincided with the breeding season and an increase in mobility of the resident and non-resident jackals. This suggests that mating activities and increased territoriality of jackals initiated a late summer/early autumn dispersal peak by non-resident jackals (Chapter Four).

Social encounters within pairs or family groups (n= 86) included social grooming (24%), play fighting (45%), and running play (31%). Intra-group aggression was in connection with incidents involving ano-genital sniffing of females by males, and sometimes some attempts at mounting. Occasionally, the female jackal responded by snapping, whereupon the male withdrew. On one occasion the female held still and allowed the male to sniff, without defending herself. Nevertheless, no copulation was observed. Seventy-eight percent (78%, n = 15) of ano-genital sniffing was recorded from May to July. Encounters between heterosexual individuals of different groups never ended in biting and/or chasing, whereas this seemed to be the rule in encounters between two strange females (n=3), and between two strange males (n=5). Encounters between neighbours (n= 11) were less aggressive than between apparently strange groups (n=13).

Sexual behaviour was not observed among helpers, and male helpers had small testes when visually compared with their sires. The social status of helpers was always submissive with respect to the parents (n=19). Black-backed jackal parents rarely regurgitated to helpers (n=2) but did share food with the older offspring and engage in such affiliative behaviour as allogrooming (n=8). Subordinates or helpers did assist their same-sex parents in territorial defence against same-sex conspecific intruders (n=8). However, these subordinates did not engage in scent marking. Unlike their parents, helpers trespassed on adjoining territories and foraged for rodents and fruit (n= 17), sometimes until they encountered a resident and were driven back to their natal area. This type of trespassing may provide important information to young jackals on the availability of unoccupied or suitable habitats. Mated pairs only left their territories to drink water and scavenge from carcasses (22%, n= 191). When leaving their respective territories for water, residents trotted steadily in fairly direct routes (following paths to waterholes) and did not scent-mark.

Little to no overlap existed between territories of adjacent pairs, and boundaries between adjacent pairs were often distinct, although it is likely that over long periods they may shift somewhat. In several areas in which resident groups or pairs were encountered, only one pair of these jackals was found a year later. However, only once was another pair observed for a considerable amount of time, but these were certainly not any of the animals seen the previous year. It therefore appears safe to assume that black-backed jackals at MNR did not use the same territory or breeding range year after year, although in relatively undisturbed environments, territories may tend to remain stable in size and location over some period of time.

Territorial Marking

Boundaries and the internal area of the territory were actively defended. All observed territorial conflicts involved aggression between animals of the same sex. Territories were maintained indirectly by scent marking and vocalisation.

Adult males usually raised and extended a hind-leg side-ways when urinating, while the back was held straight, and the tail held straight out behind in the typical adult male dog (*C. familiaris*) urination posture. The urine was ejected side ways, aimed at a grass tuft or small shrub (height usually <30 cm) while balancing on three legs. However, there were a few instances when male jackals urinated with both hind-feet on the ground and stretched backwards, while the urine was ejected downwards just behind the forefeet (n=3). Individuals that assumed this posture were taken to be immature or subordinate males that had not yet perfected the typical raised leg urination posture.

Female jackals urinated while flexing forward a lifted hind leg, but also in some intermediary positions between squatting and leg-lifting while the urine was jetted backwards onto the ground. After urinating, both sexes executed some mild scratching movements with all four legs next to the site of micturition. The most frequent sequence was sniffing, micturition, and scraping/scratching for both sexes.

A total of 112 urinations of adult paired males and 72 of females were recorded. Males directed urine 67 times onto sites where the female had first urinated, mostly within 30 seconds of each other. In all instances the male first sniffed at the female's urine or faeces before depositing his onto it, and sometimes repeated this behaviour. The remaining 45 urination events of males were often directed at small tufts of vegetation, and on the base of tree trunks, typical of male *C. familiaris* urination. In 17 of 28 cases where notes were made, the male first sniffed at the site. Sniffing preceded urination in males 88.2% of the time. This indicates a frequent deposition of sites by males, which is typical of territorial marking behaviour. In 13 of the 72 urinations of female jackals, urine was directed onto the spot where the male had urinated, each after preliminary sniffing. In the remaining 59 episodes, urine was directed onto flat ground, six times with preliminary sniffing and 42 times without. This suggests that females too were also involved in territorial marking, albeit to a lesser extent.

During defecation both males and females assumed similar postures, closely resembling the 'squatting' of the females during urinations. The only difference was that defecation took longer than urination. Of the 17 observed and documented defecations, 11 were on or closer to older black-backed jackal faeces. Two pairs defecated in succession 5 - 10 m apart. Lone faecal depositions on sites other than on older scat deposits were observed on nine occasions. Black-backed jackals at MNR used 'latrines' and these were probably visited by the same pair as indicated by radio tracking. In most cases, faeces were lodged on small tufts of vegetation (grass and shrubs of height <30 cm) shorter than the hindquarters of the animals. No faecal material was found deposited on flat ground. The animals were never observed sniffing at faecal deposits before or after defecating. Adults were not documented defecating in the vicinity of denning sites, while only one instance of a juvenile was observed defecating next to the den within a radius of approximately 10 m. However, direct observations and the presence of small-sized faecal pellets around dens suggested that pups utilised the den vicinity for defecation.

Studies of hyaenas (Kruuk, 1972), golden jackals *Canis aureus* (Macdonald, 1979), and others suggest that the positioning and distribution of faeces can have an important intraspecific communicative function for carnivores. While collecting jackal faeces for scat analysis some were found singly, while others were found in piles or middens. Faeces constituting a pile were defined as those within a circle of 1m diameter (Macdonald, 1979). At each of the 132 defecation sites, I estimated the minimum number of separate faeces, judged on the basis of similarities of colour, age, and shape; the biggest pile contained an estimated 14 separate faeces. The positions of all these sites were recorded using GPS and are plotted in Fig.7. In the field, it was apparent that some piles were linearly arranged, usually following an obvious jackal path, road or some topographic discontinuity. Most of the latter cases were on rocky outcrops and so it remains probable that they too followed a well-trodden jackal route even if the hard ground obscured the tracks. In contrast the single faeces were scattered more randomly across the study area. Following the lines of piles gave the impression that they bordered an area, which was otherwise devoid of middens, but through which were scattered many singles as reported by Macdonald (1979) for golden jackals in Israel.

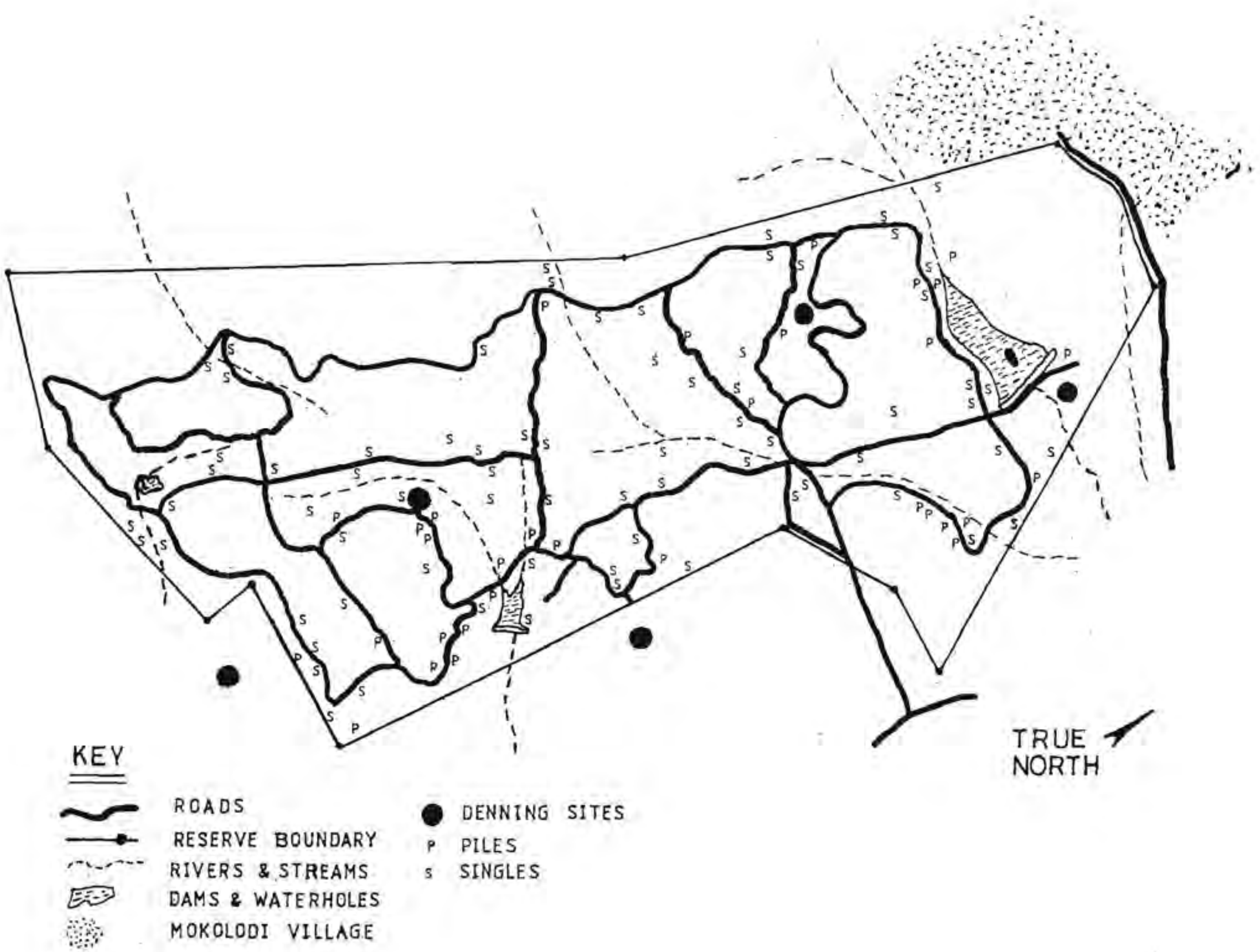

Fig. 7. Map showing the distribution of faeces in the study area as revealed by combing the area on foot. Locations of solitary faeces are distinguished from those where piles of faeces (middens) were found.

While recording the position of jackal droppings, I also noted whether they were on what could be judged as visually conspicuous objects, such as stones and tufts of vegetation. Single droppings were prominent (31 out of 52) compared to those in middens (25 out of 71). Possibly single deposits are positioned wherever prominent sites are found, whereas piles are put in specific locations, irrespective of the features of the terrain but according to social requirements, i.e. those of demarcating a boundary between group territories. The correspondence between the courses followed by piles, where the two jackal families were seen, and the locations of disputes between them suggested that the line of piles constituted a territorial border between the ranges of the two jackal families. At each pile only two scats were collected per monthly session for diet analysis to avoid altering the attractiveness or intrinsic utility of the pile.

Not much foraging was done during territorial marking; the jackals traversed the paths while trotting, and only stopped to urine-mark for a few seconds and immediately proceeded trotting. Prey encountered during these activities were however pursued with varying success (see Chapter Five). Rolling was also observed on five occasions when jackals wallowed in dust or in sandy and slightly gritty areas, and thereafter shaking their bodies from side to side vigorously. Sites where jackals had rolled in dust were frequently found associated with their tracks. Usually, such sites suggested that the activity involved more than a single animal, indicating that pairs or groups engaged in the activity in tandem.

Vocalisation

A total of 265 calls were recorded during the study period (Table 19). The incidence of vocalisation was highest during winter (34.3%, n = 265), followed by autumn (24.2%), whereas the frequency of calling during spring and the two summer periods were in similar proportions. Calling was thus relatively more frequent during the pairing-mating season (winter) than during the denning season (spring) ($\chi^2 = 5.78$, $d.f. = 1$, $p<0.05$). Calls during the pairing-mating season were most frequent by groups (presumably the dominant territorial pairs) ($\chi^2 = 4.3$, $d.f. = 1$, $p<0.05$) during the late afternoon (16h00-22h00) and in the early morning (04h00-06h00). Usually when one jackal called, others within hearing distance responded or joined in successively.

Denning

Dens were used by black-backed jackals for two different activities: 1) as resting sites during the non-active period (non-breeding dens), and 2) as sites for birth and rearing of pups (breeding dens). Dens were found by combing through the study site, following radio-tagged animals, and also by following jackal spoor, usually in well-drained sandy soils under the cover of shrubs and trees. Occupation of a den by a jackal was confirmed by direct observation. Jackals were also opportunistic with respect to den occupancy. They did not dig their own dens when other possibilities availed themselves. Denning sites were old excavations of warthog (*Phacochoerus aethiopicus*), springhaas (*Pedetes capensis*), aardvarks (*Orycteropus afer*) etc., to which the jackals may have added a couple of entrances. These were usually dug at the bases of inactive termite mounds. The number of den entrances varied from one to seven. The need for a variable number of entrances to dens is probably related to breeding status whereby breeding dens would have a higher number of entrances than non-breeding ones, and this may be related to the need to escape quickly into shelter when disturbed. However, this could not be conclusively ascertained due to small sample sizes, and the high turnover of den occupancy. Although jackals were observed excavating at times, the superficial nature of this undertaking suggested that this was probably for caching food or some other territorial function, rather than for den construction. The soils in MNR were generally shallow, and the difficulty for jackals to find or excavate suitable dens for breeding could explain their scarcity and random distribution. I consider that the distribution of dens was limited by the availability of suitable sites, moreso because in the adjacent commercial farms where soils were more well-developed, dens were plentiful even though access to such areas by the investigator was somewhat limited.

Table 19. Incidence of calling by black-backed jackals at Mokolodi Nature Reserve, Botswana

Time Period	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All Seasons**	**Relative % of calls**
16h00-18h00	4	16	27	10	9	**66**	24.9
18h00-20h00	6	21	18	10	2	**57**	21.5
20h00-22h00	3	7	9	2	4	**25**	9.4
22h00-00h00	2	3	1	1	0	**7**	2.6
00h00-02h00	0	0	0	0	0	**0**	0.0
02h00-04h00	5	2	4	2	3	**16**	6.0
04h00-06h00	6	6	12	10	8	**42**	15.8
06h00-08h00	3	5	7	7	7	**29**	10.9
08h00-10h00	1	2	5	0	2	**10**	3.8
10h00-12h00	0	0	0	0	0	**0**	0.0
12h00-14h00	0	0	0	0	0	**0**	0.0
14h00-16h00	2	2	8	0	1	**13**	4.9
Total	**32**	**64**	**91**	**42**	**36**	**265**	

Radio tracking of jackals resulted in avoidance behaviour to the extent that dens were sometimes vacated within days after I had located them. On the first occasion a den was vacated two days after locating it. This was probably caused by the detection of human activity around the den after I had collected some faecal material from around the den. As for the second occasion the jackal den was vacated because of heavy rainfall which inundated the area, filling up the den. The female initiated all changes in the location of the den but was assisted by the mate. No more jackals with young were thereafter located within MNR. Once abandoned, no holes were re-occupied for the duration of my field study.

The female of one collared pair showed signs of lactation but attempts to locate the denning sites were futile. Dens could have been relocated to areas of limited human interference (especially from tourists) such as within inaccessible Acacia thickets, and outside MNR in farms that were relatively undisturbed. This is quite plausible since radio tagged animals (and presumably the ones I frequented most) ended up being relocated outside MNR on the south-western part. These areas had limited through-routes and were consequently less disturbed relative to the much-traversed interior of MNR with its extensive network of roads. Some landowners in the surrounding farms were however loathe to allow people within their property at the 'awkward times' which typified peaks of jackal activity periods at MNR. This greatly hindered the collection of vital information on jackal behaviour on these farms. But whenever opportunities to enter such farms availed themselves, they were duly exploited although such activities were limited to daylight hours only. This effort resulted in the location of two more active dens in one of the farms (Lion Park).

Helping

My sample sizes were too small to detect any helper effects upon breeder survival, juvenile growth rates or inter-birth intervals, but these factors are important for cooperatively breeding mammals and birds. In the present study population, there was little sexual dimorphism, either physically or behaviourally. Although females are responsible for gestation and lactation, their mates provisioned them during the nursing period. The jackal family of the radio-collared female AFJ1 revealed some aspects of helping behaviour

(Moehlman, 1986) since its two surviving subadult young born in September 1995 were sighted with their parents on several occasions within the natal territory, even after reaching potentially reproductive age after 10 months of age. During November 1996 surveillance of dens revealed that these sub-adult young also took part in tending to the 1996 parental litter by bringing food back to the den, and also regurgitating food to pups on four occasions. Most interactions between yearling jackals and pups involved play behaviour that presumably had a social function. Several sightings of jackal groups consisting of the adult pair and one or two grown-up subordinates suggested that the incidence of helping behaviour could have been more prevalent in MNR than revealed by direct observations. In order to reveal helper effects in an exploited jackal population such as the one in MNR would require more detailed and rigorous assessments.

Discussion

Monogamy

Among black-backed jackals, the form of monogamy is strongly obligatory (Kleiman, 1977; Mock & Fujioka, 1990) with little sexual dimorphism, an equal sex ratio, mating exclusivity, predominantly intra-sexual aggression, similar behavioural roles and a high degree of behavioural synchrony including cooperative hunting and tandem marking. Jackals have affiliative behaviours such as grooming each other, sharing food, and feeding and protecting sick and injured partners (Moehlman, 1983, 1986). They tend to rest together and when individuals have been resting or hunting apart, they locate each other with contact calls before starting to forage. The presence of both members of the pair may be necessary to maintaining territory. Moehlman (1986) observed that when a male of a pair disappeared during the whelping season, the female and its pups all died. A high degree of affiliative behaviour, food sharing, synchrony of activity, year-round maintenance of the feeding territory, cooperative hunting, and intrasexual aggression maintained the monogamous bond and exclusive mating. The fitness of a female tolerating bigamy would potentially be lower than the reproductive success of monogamous females because of the division (or even the absence) of the male's parental investment.

Although the female parent bears heavy reproduction costs in terms of gestation, lactation, and regurgitation to pups, she is assisted by her mate and older offspring (helpers) when they are present. Moehlman (1983, 1986) found that when a pair without helpers raised a litter they had to divide their activity between staying at the den guarding the pups and foraging for food. Typically, adults do all their resting near the den such that when they are not guarding they are foraging. The presence of a single adult at the den constitutes protection for the pups. Adults both vocally warn pups (who run into the den) and threaten potential predators. Moehlman (1986) reported that the presence of one helper in black-backed jackal families led to a significant decline in the amount of time the parental pair spent at the den, allowing more time for foraging. Thus the presence of helpers may indirectly improve the provisioning of pups by allowing the parents to hunt as a pair and hence increase their hunting success rate on larger prey (Wyman, 1967; Lamprecht, 1978a,b). It may also allow the parental pair to defend, retain, and exploit carcasses killed or scavenged more successfully.

Selection for monogamy and long-term pair bonding may reflect both physiological and ecological constraints in black-backed jackals. Monogamy, especially in canids, is also closely associated with the occurrence of social groups (Moehlman, 1986). Black-backed jackals, like most canids, have a relatively large litter size and there is a long period of infant dependency (Kleiman & Eisenberg, 1973; Kleiman, 1977). Black-backed jackals at MNR are omnivorous and utilise small-sized abundant food resources that are energetically costly to collect. Paternal investment is critical to pup survival and if a male were to partition his care between several litters, then possibly no pups would survive and both male and female reproductive success would suffer (Moehlman, 1986). Domestic dogs (*C. familiaris*) can produce litters with multiple sires (Beach & Gilmore, 1949, in Moehlman, 1983). Thus maintenance of mating exclusivity may be important in all *Canis* species so that the monogamous male does not invest in offspring that he did not sire. Long-term pair bonds are also critical for territorial maintenance. I have already alluded to the fact that Moehlman (1983, 1986) reported that when one member of a pair dies or disappears during the whelping season, the remaining adult cannot sustain the pups and control the territory. The mate could potentially form another bond, but this was not observed in the present study, and single animals may not be able to retain a territory for very long. Several other potential benefits of monogamy accrue from retaining one's former partner (Mock & Fujioka, 1990): the former partner is known to be seasoned as a parent, may possess a suitable breeding site (or useful knowledge of the one used before), and is relatively familiar as an individual (which may help coordinate reproductive activities). Furthermore, because his/her qualities as a mate have been sampled personally, the partnership's past record may come into consideration.

When monogamy does occur it tends to be correlated with 1) minimal sexual dimorphism, 2) a long period of dependency in offspring, 3) high paternal investment, 4) delayed sexual maturation of juveniles in the family group, and 5) parental investment by juveniles in younger siblings (Eisenberg, 1966, in Kleiman, 1977). In species exhibiting long-term pair bonding such as black-backed jackals, there is often a reduction in the degree of sexual dimorphism, both behavioural and morphological (Kleiman, 1977). Black-backed jackals exhibit sequential urine marking of the same sites by bonded pairs, either initiated by the male or female. Along with a trend towards monomorphism in the frequency of scent marking, there is a tendency for dimorphism to be reduced in the behaviour patterns of scent marking, the development of scent glands, or both. Adult females in black-backed jackals use the modified leg lift when they urine mark. Thus the urine-marking movement is somewhat convergent with the typical leg lift of the male.

Group Size

Mated adult jackals often hunt in pairs and most young jackals are born during the winter and one of the parents (often the female during the suckling period) would be caring for the young. Hence fewer adult pairs and more single animals can be expected to be seen from July onwards (Rowe-Rowe, 1984). Furthermore, when an adult female jackal has a litter, immature animals from the previous litter may remain as 'helpers' (Moehlman, 1979, 1986), or become independent lone sub-adults, thereby increasing the number of single animals. Even those jackals that remain as helpers would be single animals, as sub-adults and unmated subordinate adults rarely hunt in pairs or larger groups. Since young jackals begin to forage with the adult female, or both parents, at the age of 14 weeks (Moehlman, 1980), therefore most groups of three or more can be expected from November onwards.

Seasonal differences in jackal group sizes have rarely been related to social organisation and reproduction (Rowe-Rowe, 1984). In black-backed jackals large group size is important during summer when pups must be fed and protected, but when pack members hunt alone. In a study on coyotes *Canis latrans*, which have similar social structure to black-backed jackals, Bekoff & Wells (1980) recorded group-size means of 1.3 in summer and 1.8 during winter. These authors attributed the differences to available food; during summer the coyotes lived chiefly on rodents, but mainly carrion was taken in winter, and the clumped food resource appeared to result in larger groups. Rowe-Rowe (1983) did not reach these findings in his study on jackals because in his study area carrion was usually consumed by vultures and so did not lie long enough to attract large numbers of jackals over a longer period.

It seems reasonable to propose that the social organisation of jackals may be an adaptation to the abundance and distribution of food, factors already held as determinants of many intra-specific differences in social organisation for various species of carnivores (Macdonald, 1979; Macdonald & Moehlman, 1983; Moehlman, 1986). But cooperative hunting does not seem to be an appropriate explanation for the groups of jackals observed in MNR. An alternative suggestion is that the highly clumped dispersion of the food supply presented an economically defensible resource. Furthermore, in black-backed jackals, benefits of living in a group can arise while members operate alone (e.g. provisioning pups with food by helpers).

Lamprecht (1979) indicated that one benefit of communal foraging becomes apparent when we consider patches of termites (Order: Isoptera), from which several individuals together can extract more food than one, because the resource is exhausted with time and not with consumption. Active harvester termites (*Hodotermes mossambicus*), an item in the diet of black-backed jackals in the present study, are commonly found teeming around their foraging holes wherein they take refuge when disturbed. Upon locating such a resource patch, an individual jackal can feed on the fleeing insects only for a limited time. A few other related animals cooperated in the defence of concentrated food against kleptoparasites. Kleiman & Brady (in Bowen, 1981) suggested that in species with a strong pair-bond such as black-backed jackals, variation in group size and social structure results from differences in the age of dispersal of young. Hence, delayed dispersal may result in a pack structure similar to other social canids.

Although there is evidence that prey size and seasonal variation in prey size in the diet may determine social organisation in canids (Bowen, 1981), other factors may also play a role in determining group size. However, when explaining inter- and intra-specific differences in ecology, causes are often difficult to distinguish from effects. Group living in carnivores appears to be widespread and occurs in a variety of environments (Macdonald, 1979). It is therefore unlikely that a single selective pressure has led to the evolution of sociality in all these of species, even though it is clear that pride size and cohesiveness in lions (*P. leo*) is very dependent on the absolute abundance of food (Schaller, 1972). In addition, a high population density resulting from abundant food and perhaps the inability to disperse may also influence group sizes in jackals independent of prey. Our inability to clearly characterise the social structure of canids may be due in part to heavy human persecution of these populations. Thus it may not be so surprising that where jackal populations are heavily hunted, group living is seldom reported as was the case in MNR.

The evolution of group life in the canids has probably been most strongly favoured by improved food acquisition (Kleiman & Eisenberg, 1973), for it has been shown for several species that hunts involving two or more individuals are more successful than a solitary hunting pattern. Bygott, Bertram, & Hanby (1979) showed that compared with singletons and pairs, male lions in groups of three or more can reliably gain tenure of female prides, retain tenure for longer, mate with more different females, and produce more surviving offspring; thus each individual has higher fitness through cooperation. Thus for lions, there is a marked increase in the inclusive fitness of a male the more related companions he has, such that inclusive fitness of a male in a large group is 5.7 times that of one male or of one of a pair.

Indeed, pair hunting in jackals may be an adaptation to overcome hunting problems because young antelopes such as impala lambs are often defended by their mothers (Schenkel, 1966; Jarman, 1976), and a pair of jackals can more easily cope with the double task of catching the lamb and distracting its mother. In the Serengeti, black-backed jackals lost almost 30%, golden jackals about 11%, of their self-caught hares and lambs to the much stronger spotted hyaenas (Lamprecht, 1978b). Several behavioural peculiarities are possibly adaptations to overcome this considerable competitive pressure: after a kill jackals were much more apprehensive than before. Large preys were hectically devoured while beetles or mice, too small to be snatched from them were chewed a long time before being swallowed. Hares and gazelle were torn in two, and the mates ate their portions some metres apart presumably that should one get robbed by kleptoparasites, they would share the other's piece (Lamprecht, 1978a, 1981).

The pair or family can share food from an unexpected localised food source when it has been discovered by only one individual in the group, even while foraging and feeding behaviour is typically individualistic. Pair hunting may also offset the considerable competitive pressure, as two jackals can eat a lamb much faster than one, thus lessening the risk of being robbed. This consequence may be the function of pair hunting in black-backed jackals, as pair hunting was no higher than for individuals, thus offering no support for the hunting hypothesis. There is however no correlation between hunting group size and prey type in jackals which could not also be explained by seasonal changes in social organisation (Lamprecht, 1981). When pups must be guarded, the parents must alternate at this, and hunt singly. But when the pair is not tied to a breeding den, the mere need to keep the mate available while on the move could lead to pair hunting, even though hunting, and consuming the kill would not require more than one jackal.

However, in as much as I appreciate the importance of diet in shaping the social structure of canids, I contend that social organisation (especially group size) in MNR is moulded to a greater extent by heavy man-induced mortality (i.e. 'predation' or hunting pressure) and intra-specific competition - and not even by intra-guild predation or interspecific kleptoparasitism, primarily due to the absence of the large social carnivores within MNR.

Home-range size appears not to be affected by hunting pressure at MNR. It is only in the absence of such persecution that the relationship between the jackal population and food abundance may apply. Thus, it is most likely that black-backed jackals at my study site reduced group size under an increased risk of 'predation' from humans, although in contrast, social groups of other species become more compact in the presence of predators (e.g. mongooses, *Mungos mungo*, pers. obs.). During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realise no reproductive success, but in the long-term, the day's shortcomings may have minimal influence on the lifetime fitness (Lima & Dill, 1990). Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness. Predation may thus be a strong selective force over evolutionary time, and it has long been recognised as important in the evolution of adaptations, such as cryptic and aposematic coloration, protective armour, chemical defences, and asynchrony in activity periods. Predation has also been implicated in the evolution of sociality in both the breeding and non-breeding season (Bertram, 1978; Pulliam & Caraco, 1984). While predation pressure may vary little over evolutionary time, during ecological time (i.e. an animal's lifetime) the risk of being preyed upon may vary greatly on a seasonal, daily, or even minute by minute basis (Lima & Dill, 1990). Since an animal must accomplish more during its lifetime than simply avoiding predation, its antipredator adaptations should somehow be sensitive to the current level of predation risk (the 'risk of predation' - hereby intuitively defined as the probability of being killed during some time period). Such antipredator flexibility may be achieved by integrating gross morphological adaptations with the behavioural decision-making process.

A morphological or behavioural characteristic can be useful in various procedures, but it is not normally adapted to all of them. Large hunting groups, for instance, may be more advantageous than small ones in many ways, yet it is usually only one particular problem that actually requires groups of the observed size. Not even for a single species (e.g. lions, spotted hyaenas) is there only one particular consistent function of social hunting; it can differ with the ecological or social setting.

Territoriality

Territories were maintained directly by aggressive and agonistic interactions, and indirectly by scent marking (olfactory) and vocalisations (acoustic). Black-backed jackals at MNR exhibited territorial behaviour according to the following criteria: 1) stability of home ranges throughout the study period; 2) no overlap between pairs; 3) frequent inter-group boundary chases and clashes; 4) scent marking behaviour; and, 5) vocalisations.

Scent-marking

Resident pairs or groups appeared to be territorial, or at least intolerant of others, but as Lamprecht (1979) indicated, it was unclear whether they marked their territories as a signal to strangers or to familiarise themselves with the terrain. Jackal territorial boundaries were demarcated by piles of faeces as was found by Macdonald (1979) for golden jackals, although other workers have not mentioned finding black-backed jackal middens (e.g. Rowe-Rowe, 1976). Jackal territory is sometimes partly independent of feeding range and presumably has other functions such as breeding sites (Macdonald, 1979). The dense nature of the vegetation at MNR during the present study, coupled with the site's rugged topography provided few access routes for intruders; however, most of the main paths were well endowed with middens. The situation is confusing because the dry season climate favours the preservation of faeces for months, so part of the present day pattern may be an artefact of history. Several other species are known to use similar piles of faeces (Macdonald, 1979). The black-backed jackal is apparently territorial in some parts of southern Africa (Ferguson, Nel, & De Wet, 1983; Skinner & Smithers, 1990.) and East Africa (Moehlman, 1978,1979), but shows no sign of midden use and thus, when contrasted with the black-backed jackal population in the present study, constitutes another example of a canid species known to use middens in one territorial situation but which does not do so in a different, but still territorial, situation. Golden jackals in Israel (Macdonald, 1979) were found to use middens while in East Africa, midden use was not reported for the same species

When foraging with their mates, territorial individuals mark at almost twice the rate as when they are foraging alone (n =22). When travelling together they mark the same spot in tandem (n=80). The presence of scent from both members of the pair may advertise to potential intruders that they are both actively in residence (Moehlman, 1986). In wolves, boundaries of territories of neighbouring packs where contests take place have been referred to as buffer zones, and therefore 'regions of intraspecific strife' (Mech, 1994). Wolves were reported to run a greater risk of fatal encounters from adjacent conspecifics along the edges of their territories than in their centres. Like the jackals in MNR, wolves patrol the borders of their territories and scent mark the edges much more than the centres (Mech, 1994).

Among canids, scent-marking may serve as (Gese & Ruff, 1997 and references therein): a mechanism for territory maintenance or sex recognition; a signal of empty food caches; an indicator of sexual condition, maturity or synchrony, or internal information to orient members of the resident pack and to dispersing animals entering occupied territories. Individual recognition from urine marks has not been demonstrated for canids, but it has been shown that domestic dogs (*C. familiaris*) can detect a female's reproductive status (Beach & Gilmore, 1949, in Moehlman, 1983) and that chemical compounds found in male red fox (*V. vulpes*) urine are absent in female red fox urine (Macdonald, 1979). Scent marking is probably an alternative to agonistic interactions used by black-backed jackals for territorial defence. Findings from the present study are consistent with studies of mammalian scent marking in which the dominant pair marks the most and are the territorial owners (Randall, 1989).

Social Interactions

Boundaries and the internal area of the territory were actively defended against intruding conspecifics. All observed territorial conflicts involved aggression between individuals of the same sex (n=9) . The resident females threatened, attacked, and drove off intruding females while resident males looked on. The resident males threatened and drove off other intruding males (n=5). However, the presence of a clumped food resource such as a carcass or refuse dumping site attracted individuals from adjacent territories in such numbers that it was impossible to drive them all away (n=5). Nonetheless, aggregations of trespassers were usually short-term. Residents left their own territories to drink water and to scavenge elsewhere. They occasionally went on exploratory forays but were seldom off their territories for more than a few hours. It appears that in the time between the dissolution of the families and the pairing-mating season, pairs rove about more than usual, in search of suitable breeding grounds, so that they are more likely to meet, and there is an increased risk of altercation over favourable sites (Lamprecht, 1979). Encounters during the breeding season however, will probably be mainly with resident neighbours, known to each other, to whom less aggression will be directed as competition for living space is no longer acute.

Neighbours play a diverse role in territorial systems. They can be intruders, neutral, or even beneficial (Randall, 1989). At the least, neighbours can be friendly rivals, 'dear enemies' and tolerate each other. An established neighbour offers little threat, compared to an unsettled transient searching for a territory, so the gain from an agonistic encounter with a neighbour would be small (Maynard-Smith & Parker, 1976). Mutual avoidance rather than aggression probably contributes most to spacing in mammalian territorial systems. Social intolerance or aggression commonly increases after reproduction when population densities increase and juveniles disperse. High population densities should promote an increase in agonistic interactions, because individuals at high densities are less familiar with each other than at low densities (Bekoff, 1981, in Randall, 1989) and there is increased competition for territories.

Jackals were much more aggressive towards each other when there was competition for food (n=5). In these situations, the interactions between pair members were much friendlier than between other jackals. This suggests that the pair bond in black-backed jackals is strong (Ferguson, 1978). Lone animals live nomadically in large areas usually encompassing several family territories and rarely interact except during the breeding season or when loosely associating around a kill. The behavioural patterns of black-backed jackals during social interactions observed in the present study were consistent with those reported by Ferguson (1978) in the Kalahari Gemsbok National Park, save for the timid nature of the former at MNR. Direct aggression sometimes serves as a backup system when indirect territory maintenance such as scent marking and vocalisation fails. The distribution of scent-marks throughout the jackal's territory, their frequency of application, and the information that they contain help maintain the territory structure. Although scent-marks advertise an animal's location long after it has passed, they require direct and close scrutiny, and they fail to inform interested parties of their marker's current location.

Some overlap of group home ranges, especially at crucial spots such as watering holes or garbage sites, was observed for *C. mesomelas* in which the groups are normally mutually exclusive. In such instances, agonistic behaviour within the group is important in the development of social organisation, and the position of each group member in respect to others of the same group is relatively stable. In contrast, dominance relationships of an individual from one group with any member of another group cannot be expected to have been established. In some species, an individual or a pair may be dominant in the core area of its home range but not in the periphery. This tends to produce a regular dispersion by effectively excluding other individuals from breeding in the core without necessarily excluding their presence there as subordinates engaged in other activities (Brown & Orians, 1970).

Areas that were abandoned from one group range subsequently became part of a neighbour's range. High rates of range drift from February to April are likely to reflect (i) a reshuffling of the social hierarchy as yearling jackals disperse in autumn and early winter, followed by (ii) intense activity during pairing-mating in May to July (the relatively low rate of drift in May perhaps reflecting a staking out of territories by pairs, preparatory to mating), and (iii) subsequent changes to the range structure of denning females (Doncaster & Macdonald, 1991). The environment surrounding MNR, as well as within, to some extent is inherently disturbed by human activities such as road traffic, problem animal control operations, etc. These factors may act in concert, reducing the average life-span so that pairs have barely sufficient time to produce the first litter, but also causing rapid and unpredictable perturbations in the pattern of food availability (Doncaster & Macdonald, 1991). I suggest that drifting territoriality in MNR is largely a consequence of the social instability entailed by such abrupt changes to population structure and food availability brought about by intense disturbance and accelerated harvest. High population turnover may de-stabilise the dominance hierarchy and reduce the age difference of survivors (Doncaster & Macdonald, 1991). A likely outcome would be disruption of social mechanisms that under undisturbed populations prevent subordinate individuals from achieving breeding status (J.D. Skinner, pers comm.).

Within the jackal family, helpers have a subordinate status to the parents, and the former may experience suppression of endocrine function and reproductive behaviour (Moehlman, 1983, 1986; Creel & Macdonald, 1995). The reason for intrasexual aggression may be linked with reproduction. If a female permits another female on her territory, she may have to share the male. The male might then have two litters of pups to defend and feed. Since the male has finite paternal investment, fewer pups would survive if this investment were to be partitioned. Conversely, male intrasexual aggression ensures that the male alone will mate with the female, eliminating the possibility that he will care for pups that are not his own progeny.

Vocalisation

Vocalisation ('calling' or 'howling') by canids is believed to function primarily as a passive means of territory maintenance whereby neighbouring groups mutually advertise their locations over sufficiently long distances so as to warn each other and non-territorial transients where to avoid (Jaeger, Pandit, & Haque, 1996). Peaks in calling occur during the annual reproductive cycle when pairing and mating takes place, and following abandonment of dens when family groups become more mobile and use rendezvous sites within their territories. Calling diminishes at the end of the reproductive cycle when young are fully mobile. Calling is also low at the time of denning when it might endanger immobile young by signalling the location of their den site to rivals or other predators. A dynamic state of conflict therefore seems to occur among neighbouring territorial groups, which is probably mediated by changing needs to compete for resources.

There are three responses that dominant animals can conceivably use to defend their territories when intruders are known to be present (Jaeger *et al.*, 1996): vocalise and warn-off con-specifics; approach and confront; or howl followed by approach. Jackals, coyotes, and wolves all approach a source of broadcasted calling (Joslin, 1967; Skead, 1973). Available evidence suggests that it is territorial, dominant animals or groups that approach (Harrington & Mech, 1979). If calling functions to reduce confrontations and if elicited calling is higher during pairing-mating than during denning, we would expect approach and confrontation to be higher during denning than during pairing-mating. If calling conversely promotes confrontation, approaches would occur more frequently during mating; and if calling and confrontation were not directly associated, approaches would occur with equal frequency during both pairing and mating. This hypothesis was not tested in the present study but merits further investigation.

The difference in the frequency of calling between spring and winter may be because of the shorter nights in spring, but it also probably reflects seasonal differences in human activity. During winter, farmers retire earlier to their dwellings, whereas in spring and summer it was hot and humid and people tended to remain outdoors relatively late (pers. obs.). Because jackals were very wary of humans and avoided them at all costs, they restricted their activities (including calling) to those periods when humans were relatively less active (see Chapter Four). This is of adaptive value because broadcast calling in an environment where there is wholesale persecution would obviously attract humans to the position of the howling animal, which may subsequently be zeroed in and end up being killed. In addition, it was also evident in the field that howling jackals did not maintain the same position but also moved considerable distances during subsequent outbursts of calls.

The seasonal pattern of jackal calls, and of pair-wise or group calls in particular, is consistent with the hypothesis of a territorial function during the pairing-mating and denning seasons. These patterns showed the same annual trends reported for other canids, being relatively more frequent during pairing-mating when territories are being established and relatively low during denning when vulnerable young are present. This pattern is consistent with the explanation that it is territorial animals that call, and that calling functions primarily as a mechanism to advertise territorial occupancy and the location of dominant animals, so that confrontations with neighbouring pairs and transients can be reduced (Harrington &

Mech, 1979). The annual occurrence of territoriality is coincident with the reproductive season and probably an adaptation to rearing young. If transients call at the same level as territorial, breeding animals, we would expect no difference in the frequency of calls between separate stages of the breeding season, unless transients were relatively few in numbers.

Group or pair-wise calls further support a territorial function for calling because non-territorial, transient canids do not typically associate in groups (Harrington & Mech, 1979; Jaeger, *et al.*, 1996) other than when feeding on carcasses, refuse dumping sites, or other clumped food resources. Group or pair-wise calls (like tandem scent marking) may carry more authority, in terms of territory ownership, than howls by individuals (Harrington & Mech, 1979). In addition, mates are probably together more during pairing-mating than during denning when females are suckling young and males are out foraging. Dusk and dawn peaks in howling during pairing-mating are consistent with the findings of Skead (1973), who reported that spontaneous calling in the same species in the Transvaal during the mating season peaked during 19h00-23h00 and 04h00-07h00. Howling in wolves also peaks bimodally during 20h00-00h00 and 04h00-07h00 (Harrington & Mech, 1978), and in golden jackals (*C. aureus*) during 20h00-00h00 and 04h00-06h00 (Jaeger *et al.*, 1996).

Another explanation for the preponderance of calling in one of the seasons may be that, calling is high when territories are being established and that the need for territory advertisement diminishes during denning when neighbouring pairs (or groups) have learned one another's territory (Jaeger *et al.*, 1996). Furthermore, the effect of calling may even extend beyond pairing-mating and reduces trespassing by conspecifics during the subsequent denning period. It is possible that the inhibition of calling by adults during early development of pups has survival value for the pups, for by keeping silent the adults do not reveal the den site to potential intraguild predators.

Apart from intergroup communication, calling is also likely to function for intra-group communication (Harrington & Mech, 1978, 1979), which is supported by evidence from wolves for individually distinct vocalisations (Tooze, Harrington, & Fentress, 1990). The need to regroup probably is greater for large social carnivores such as clans of spotted hyaenas, lion prides, and wolf packs that cover large areas than it is for jackals at MNR. An intra-group function also offers an explanation why calling is low during denning (i.e. because a fixed and predictable den site precludes the need for howling) but one that is not mutually exclusive of territorial maintenance (Jaeger *et al.*, 1996).

Vocalisations, unlike scent-marks, provide instant information concerning the elicitor's current location, and in many species, vocalisations are important in territorial maintenance (Harrington, 1978; Harrington & Mech, 1979). Joslin (1967) felt that howling could serve this role in wolves, and thus keep packs aware of each other's locations so that near-fatal encounters could be avoided by modifying their movements. The same could be said for black-backed jackal vocalisation although this was not intensively investigated in the present study. In wolves, howling has been reported to play a role in intra-pack communication, especially in expediting and coordinating events such as departures, reunions, or movements (Joslin, 1967; Harrington, 1978). The progressive increase in howling in summer may reflect an increasing need for long-range, intra-pack communication as pups become more mobile, and packs begin the gradual abandonment of their predictable home site locations.

Territory holding by animals is seen as an adaptation to defend a limiting resource, often, although not always, a food resource (Davies & Houston, 1984; Carr & Macdonald, 1986). Since territoriality involves costs (e.g. defence against conspecifics) as well as benefits, territories are expected to be of the minimum size necessary to satisfy the requirements of the occupants. Enlargements would bring extra costs without net benefits. The defence of territories requires a not insignificant investment in terms of time and energy. In addition, by behaving in conspicuous ways, often involving vocalisations, the individual is probably subject to increased predation. For such behaviour to evolve there must be compensatory advantages so that the overall fitness of the individual is increased.

It is possible to find at least one common denominator for all of the diverse types of territorial behaviour. They can all be viewed as behavioural adaptations which are selected for in the course of evolution because they aid individuals in competing for the requisites for reproduction or survival (Dawkins, 1989). Territorial behaviour does not evolve because it has a function. Rather, it is favoured if individuals acting in that manner are more successful in surviving and reproducing than individuals behaving in other ways (Brown & Orians, 1970; Dawkins, 1989). Such a view is useful in generating testable hypotheses because it focuses attention on those aspects of the problem that must be studied, i.e. the ecological factors that determine fitness differentials among individuals who behave in different ways.

Denning

The number of breeding dens has been related to the number of canid breeding groups elsewhere (Hewson, 1986; Meia & Weber, 1992) and, in a similar vein, may thus be an indication of the number of resident jackal breeding pairs within MNR, especially given that jackals at MNR maintained exclusive home ranges. However, the estimation of jackal density is difficult because the number of jackals in an area also depends on the social organisation of the population: Jackals usually live in pairs or in groups according to habitat, prey availability, level of hunting pressure and the availability of immigrants. Hunting pressure may have an important influence on the number of breeding dens the following year. Jackals probably avoid breeding at sites with a history of high levels of human disturbance. However, although MNR provided a safe haven for breeding relative to surrounding farms, the unavailability of well-developed soil profiles and termitaria (termite mounds) militated against the establishment of dens in the predominantly rocky terrain that characterises a large proportion of the study area.

Burrowing or denning is an important behavioural adaptation for many organisms, for which this underground network provides a convenient refuge from the rigours of life on the surface (e.g. risk of predation). Soil is an excellent insulator against temperature extremes, and an animal resting just a few centimetres below the surface may comfortably survive the hottest day and coldest night. In a burrow, the humidity is relatively high and this helps animals reduce moisture loss. The humidity in an animal's breath - trapped in the burrows - also plays a part in keeping the tunnels humid and preventing moisture loss from the animal's body. Jackals whelp in dens and young typically spend most of their time in dens until they are weaned. Thus predation pressure is reduced and may allow jackals to produce more young in a more altricial state with a longer period of development. Since jackals also regurgitate food to their young, such behaviour enables them to efficiently and safely bring larger amounts of food to the den.

Helping

The young of several species of carnivores are often cared for by individuals that are not their parents. Tending to infants other than one's own is termed alloparental behaviour and may involve either 'helpers' with no young of their own, or adults with their own offspring who also tend to those of other parents. The presence of the parents' genes in future generations depends on the differential survival of their own progeny in comparison to those of other parents. Activities defined as 'helping' in mammals include feeding, grooming, baby-sitting, helping infants in distress, assistance in thermoregulation and allosuckling (Jennions & Macdonald, 1994 and refs. therein). In practice, 'helping' has been used to describe any activity directed towards infants or their parents which is likely to benefit the recipients and increase breeding success (e.g. alarm calling or provisioning a lactating female).

In the present study, it was difficult to document direct evidence of helping behaviour due to the highly secretive nature of the jackal population at MNR. In addition, it must be noted that the presence of helpers is partly dependent on the age of the parents because a pair with its first litter would not have any helpers anyway, unless the 'helpers' are not their own offspring. Besides, such facets of jackal behavioural ecology under human persecution pressures require a not insignificant allocation of time and resources to unearth. Thus direct evidence for helping behaviour would best be studied for at least two years, given that jackals breed once a year, and that the current progeny would most likely be helpers in the next breeding season. Although this was beyond the scope of the present study given its necessary brevity, the subject can hardly be ignored because of its theoretical interest and importance.

The incidence of 'helping' is partly related to the onset of dispersal in jackals. First, juveniles disperse in some cases because they have to: They are forced to disperse by their parents or other resident adults, when they are perceived by these as becoming a threat in the competition for resources (e.g. food, shelter, and mates). Those that are not strong or fit enough to resist eviction are forced to leave. On the other hand, juveniles disperse because they can: By leaving their natal range they may increase their chances of breeding successfully and perhaps avoid inbreeding. They do this if suitable areas are available to disperse into, and if they are fit enough to compete for a new home range. In other words, the fitter individuals disperse. These two categories correspond to the 'Resident Fitness Hypothesis' and the 'Emigrant Fitness Hypothesis' respectively, defined by Anderson (1989) with respect to rodents. According to the former hypothesis, juveniles are fundamentally philopatric, settling on their natal sites if permitted to do so. Dispersal is driven by the aggressive behaviour of adults and intragroup aggression increases under food stress (Kruuk & Parish, 1982; Anderson, 1989).

Four factors may be considered by an offspring who chooses between dispersing and attempting to breed independently, or postponing departure and remaining as a non-breeder with the parental group (Emlen, 1982a): the cost (risk) of dispersal itself; the probability of successful establishment on a suitable territory or area following dispersal; the probability of obtaining a mate; and the likelihood of successful reproduction once 'established'. The paradox of why animals have similar social organisations in seemingly opposite ecological situations was extensively treated by Emlen (1982a, b). In addition, dominance interactions among littermates may determine who remains on the home territory (Moehlman, 1986). Dominant pups tend to be more independent and better foragers; they might have a higher rate of reproductive success when they emigrated, if one or more of their siblings stayed and helped. However, if successful emigration was difficult (e.g. if the jackal population was at high density) then a pup might improve its fitness by remaining with its family for an additional year. Thus if emigration was not feasible, dominant pups could remain on the home territory and possibly force siblings out (Moehlman, 1986).

It is also likely that there is a reproductive advantage of delayed dispersal and increased group size. Moehlman (1979) showed that 'helpers' assisting the parents increase the survival of black-backed jackal pups. In her study, Moehlman (1979) found that helpers contributed food directly to the pups and also regurgitated food to the mother during the period of lactation. Helpers also contributed by guarding the pups while the parents were absent. Families with more adults (i.e. those with helpers) had an attendant adult at the den most of the time, thus providing greater protection to the pups against potential intraguild predators. Hence Moehlman (1979) found that the number of helpers positively correlated with pup survivorship (r=.967). On average each helper added 1.5 surviving pups to the litter. The presence of helpers was found to be independent of food density, and the critical factor in pup survival was deemed to be the number of provisioning adults that can capture prey and make it available to the pups.

An animal's 'inclusive fitness' (Hamilton, 1964; Dawkins, 1989) is the sum of its direct fitness, derived from its own offspring, and indirect fitness, derived from the offspring of its relatives, with which it shares genes. Inclusive fitness examines the lifetime effect of an individual's behaviour on the next generation's gene pool, not only in terms of her own reproduction but that of related individuals. Jackal helpers are as closely related to their full siblings as they would be to their own offspring. As their contributions as helpers increase pup survivorship, their own inclusive fitness is enhanced by kin selection until such a time that breeding is attempted. In fact, an adult helper gains more (yield one pup per adult) by being a helper of its parents than by finding a mate (yield 1/2 pup per adult). Helpers have also been reported in red foxes (Macdonald, 1979; Von Schantz, 1984a), wolves (Mech, 1970, in Bowen 1981), golden jackals and wild dogs (Van Lawick & Van Lawick-Goodall, 1970), and coyotes (Bekoff & Wells, 1980). Thus, helpers may derive benefits through inclusive fitness. Although helpers may have a low probability of obtaining breeding positions on their own, but by taking care of related individuals, they increase their inclusive fitness.

The fact that an individual is closely related to its full siblings as it is to its offspring prompts the question of when to breed. The answer to the question of whether an individual should begin to breed or persist in alloparenthood may lie in the calibration of costs and benefits by environmental factors. For example, if a young jackal has the option of remaining at home as a helper or leaving to attempt to become a breeder, the pros and cons of the alternatives are largely determined by ecological circumstances. If conditions are such that the chances of becoming established as a breeder elsewhere are very low, then the long-term prospects of inheriting the natal territory and the immediate advantages of hunting prey and avoiding danger in a familiar terrain may be added to the possibility of helping rear siblings whilst gaining in both experience and inclusive fitness. These may all combine to favour staying at home. In the case of black-backed jackals studied by Moehlman (ignoring the costs of helping), helpers delayed reproduction for one year and potentially increased their inclusive fitness on average by 0.87 pups. Gittleman (1982, in Macdonald & Moehlman, 1983) also found that across the Carnivora, the relative birth weight and litter sizes are greater among species showing paternal and /or alloparental behaviour, but neither increase with group size alone. This may indicate that alloparental behaviour does in general represent an increased investment in the young.

If the cost of helping is high (i.e. food shortage), then it is unlikely to occur, and so is 'an epiphenomenon of delayed reproduction, occurring under ecological conditions making the cost of helping low' (Harrington & Mech, 1980; in Macdonald & Moehlman, 1983). However, the age-status of helpers (i.e. whether they are yearlings or adults) may have an important impact on the provisioning of pups. Wild dog adults allow yearlings to eat first at a kill. During periods of scarce resources, yearlings will not only have first access to carcasses but also steal regurgitations from pups. Hence their provisioning is favoured over pups, to the extent that in four wild dog packs with yearlings, no pups were successfully raised (Macdonald & Moehlman, 1983). More importantly, we could expect the opportunities for, and consequences of, alloparental behaviour in any species to be tempered by prevailing ecological circumstances. Consequently, there is no necessary incompatibility between studies, even to the same species, which find conflicting indications of the consequences of alloparental behaviour.

Several potential benefits have been hypothesised to explain the behaviour of helpers in all species where helpers have been found (Von Schantz; 1984a,b; Jennions & Macdonald, 1994; Creel & Macdonald, 1995). These include:

1. Increased chances of survival by remaining as a subordinate in a group rather than by dispersing. Remaining in a natal group leads to benefits of increased foraging

efficiency and predator detection while avoiding the high mortality associated with dispersal in relatively unfamiliar and potentially hostile terrain.

2. Increased chance of filling a reproductive niche in the future. If suitable breeding sites or territories are extremely limited, an individual can wait until a breeding vacancy occurs in the natal group, or may be able to bud a territory from the natal territory.

3. Increased reproductive success when helpers can reproduce. Helpers may acquire skills in infant care-taking, foraging ability, predator detection, and defence that leads to greater reproductive success as a result of deferring reproduction instead of reproducing immediately.

Parents in turn benefit from the presence of helpers through increased reproductive success as parents accrue more reproductive benefits by helpers investing in their pups (degree of relatedness, $r = 1/2$) than by helpers investing in their own pups (grandpups, $r = 1/4$). Thus it is in the parent's best interest to accommodate helpers. However, the available food resources potentially mediate retention of helpers. The food requirements of secondary animals may be lower than those of primaries since additional group members, perhaps through lower status, might not reproduce and, if the alternative were emigration (and increased risks of starvation and death), might accept a lower than optimal nutrition rate (Carr & Macdonald, 1986). The phenomenon of reciprocal altruism involves one individual aiding another, who subsequently is helpful in return, when the need arises. Although such a symbiotic arrangement would benefit members of trustworthy coalitions, it seems susceptible to cheating (Maynard-Smith, 1976; Dawkins, 1989). However, Axelrod & Hamilton (1981) have shown that reciprocity could evolve as a stable stratagem if an individual's reaction mirrored its partner's action (i.e. tit for tat).

Theoretical Considerations

The proximate mechanism underlying the regulation of group size is complex and imperfectly understood (Zimen , 1976; Messier, 1985). An increase in prey abundance seems to produce a direct increment in the within-group recruitment and survival rates (Keith, 1983, in Messier, 1985). Moreover, group size may be related to the dispersal strategy of group members. As prey abundance increases, the territory mosaic becomes progressively saturated (lower territory vacancy) which could provoke delayed dispersal (Messier, 1985). Thus given the rarity of vacant areas, a maturing jackal may benefit more by trying to obtain reproductive status within its natal area than by dispersing; i.e. a non-disperser could take advantage of the ability of the whole pack to defend space in which it may eventually breed. This advantage can be crucial under highly saturated conditions. Variation in black-backed jackal social structure has led to a maximisation of its resource base. Sociality is surely a strategy allowing access to large prey without sacrificing the advantage that smaller body size gave it in the efficient use of small prey (Bowen, 1981). This, in part, may explain the singular success of black-backed jackals in most parts of Africa in the face of human persecution, unlike its larger carnivorous counterparts.

Caraco & Wolf (1975) also contended that selection has favoured the capacity for social animals to adjust group size in response to a hierarchy of ecological factors, primarily temporal and spatial patterns of resource availability. These patterns influence foraging efficiencies, mating probabilities, and reproductive success. But predation pressure also often constitutes another important factor determining social tendencies, as is the suggested scenario for the social organisation of jackals in the present study. Group size will be optimised in response to the most important environmental characteristics, in an attempt to maximise the total benefit-to-cost ratio for individual group members. Even within broadly similar habitats there is room for considerable intraspecific variation in the basic parameters of carnivore social organisation, i.e. group size and home range size.

Creel & Macdonald (1995) summarised studies on a variety of social carnivores, noting that tolerance of other animals provides benefits by allowing cooperative hunting and defence, and promoting a reduced vulnerability to predation. Large groups meet the costs of reproduction by providing alloparental care that leads to a greater number of litters, larger litters, and increased survival of offspring. Litter mass and litter growth is higher in species with communal or biparental care. Because there is high within-group relatedness in social carnivores, non-reproductive or minimally reproductive helpers are able to benefit from increased inclusive fitness.

It has already been noted that two main selective pressures that have been invoked to explain why some of the Carnivora live in groups are the need for assistance in hunting and killing large prey, and the need for defence against attacks by other predators (Lamprecht, 1981). However, neither of the above selective pressures explains why some species live in groups but travel and hunt alone (Macdonald, 1983). Benefits, which vary according to the species or population, do not only come from cooperative hunting, defence of territory and prey, and defence against predators. They also derive from the opportunity to learn from other group members' experiences, division of labour, care of the young and sick, and other advantages associated with alloparental behaviour. However, all the many benefits of group living must operate within a framework of constraints determined largely by the dispersion and abundance of available resources (Lamprecht, 1981; Macdonald, 1983; Kruuk & Macdonald, 1985). Considering the great diversity of social systems in the Carnivora, both inter- and intra-specific variations in the ecological costs of sociality are as relevant as is variation in the behavioural benefits. Hence resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate.

Another theoretical paradigm that explores the influence of an animal's foraging ecology on its social life is the Resource Dispersion Hypothesis (RDH, Macdonald, 1983; Doncaster & Macdonald, 1992). According to this hypothesis the smallest home range with an economically defendable configuration which will reliably support a basic social unit (a pair of animals) may sometimes support additional individuals. These are tolerated in numbers and at times when any costs to the basic pair due to their presence are outweighed by the overall benefits. This may happen when resources are spatially and temporally heterogeneous. Such additions are governed by the patterns of resource dispersion, and presumably where resources may be prey, mates, breeding sites, etc. In this case RDH suggests that territory size is constrained by the dispersion of patches of available (food) resources, whereas group size is independently limited by the richness of these patches (e.g. Kruuk & Parish, 1982). The RDH thus provides an ecological explanation of how, at minimum costs to themselves members of a pair could incorporate additional group members into even the smallest economically defendable territory that will sustain them. Kruuk & Macdonald (1985) indicated that while some animals, termed 'contractors' might defend such minimum territories, others, termed 'expansionists', might benefit from forming larger groups and thereby defending larger territories in excess of minimal requirements for breeding. The distinction between contractors and expansionists is important in so far as it may help in understanding the processes underlying the adjustment of population density, group sizes and range sizes to the availability of resources [see Kruuk & Macdonald (1995) for an in-depth analysis]. Knowledge of the processes involved allows prediction of the outcome of the management of carnivore populations. In cases where jackals are persecuted in an attempt to forestall predation on small livestock and game as in the agricultural areas around MNR, it is important to know how jackals living adjacent to eradication areas will behave, e.g. what will happen to the territories (and sizes thereof) of those groups adjoining an eradicated group. Since it appears that jackals at MNR are contractionists, Kruuk & Macdonald (1985)'s predictions would be that the neighbours of evacuated territories will continue to cover the same range, as before. However, the situation is further compounded by the fact that by creating vacua in otherwise 'saturated' habitats, satellite, transient or dispersing individuals may immigrate into vacated territories (see Chapter Four and Chapter Eight).

Macdonald (1983) concluded that once group-living in carnivores has evolved as an adaptation to resource dispersion then other benefits accruing from sociality *per se* (e.g. cooperative hunting and defence of kills) further moulds the social organisation in each population or species and that 'the balance of these contemporary benefits is not necessarily the same as that which originally selected for group living'. Predictions from the RDH about spatial organisation require information about three features of a territory (Doncaster & Macdonald, 1992): (i) its food security, (ii) its defensibility, and (iii) the social behaviour of its components. Food security and defence costs are both affected by the spatial and temporal pattern in which food is available, and further consequences of members of a social group arise from the benefits of cooperation and the costs of dispersal.

Von Schantz (1984) proposed an alternative but still compatible model, the Constant Territory Size Hypothesis (CTSH). This hypothesis also requires environmental heterogeneity, but in this case habitat quality is hypothesised to fluctuate in the long term. Territories have fixed boundaries over long periods of time and encompass areas sufficient to support an individual or breeding pair through the worst periods. The model predicts that as food abundance increases, the territory owners, for example the breeding pair, take advantage of this resource surplus by allowing their offspring to remain at home, thereby increasing the group size. When food abundance decreases the subordinate group members will be evicted from the territory by the breeding pair. Hence in any given territory of say, jackals or foxes, group size will be positively correlated with the annual food abundance whereas territory size will be constant from year to year. Von Schantz (1984) argued that if territory quality fluctuated over periods which were long, but less than the lifetime of the animal concerned (and considering the disadvantages of repeated symmetrical border disputes), territories would have to be large enough to accommodate the primary pair in the worst circumstances. In a study of pied wagtails (*Motacilla alba*), Davies & Houston (1981) found that territory owning wagtails varied their tolerance of satellites so as to maximise their own daily feeding rate. When food was very abundant the owners gave up defending their territories altogether and ignored intruding wagtails, but if the food supply decreased again, normal territorial behaviour was quickly resumed. Under the conditions that an owner tolerates a satellite, the owner enjoys an increased feeding rate because the benefits gained through help with defence outweigh the costs incurred through having to share the food supply with another bird.

Von Schantz (1984c) argued that RDH is severely limited because he believed that it depends on the existence of 'bottleneck' periods when only one patch is available in a territory and is therefore not applicable to groups whose members regularly forage in different patches simultaneously. However, Macdonald (1984) asserted that RDH could apply to territories within which several patches were fruitful simultaneously and that whether or not group members forage together simultaneously, will depend on the selective pressures moulding their sociality. He saw the scenario of inter-annual variation in resource availability as being compatible with RDH, rather than as an alternative to it.

In conclusion, many variations exist on the general theme of black-backed jackal social behaviour. As similar intra-specific variation is emerging for other carnivores, it seems unhelpful to wax mystical about *the* social organisation of the black-backed jackal or any other species. Rather we should stress the dynamic nature of the species' *social systems* (Macdonald, 1979) and examine intraspecific variations in terms of the selective pressures acting on different classes of individuals within each society. With sufficient information about the intra-specific variations in social behaviour for different species, the limits of flexibility for social systems of each could be defined and thereafter compared. Such comparisons could shed some light on the evolutionary significance of puzzling differences between social systems (Macdonald, 1979). It should be emphasised that many factors influence the social organisation of a species and that, under different ecological conditions, a population may stray from what is considered to be the species' modal social system in an optimum habitat (Kleiman, 1977).

CHAPTER EIGHT

CONSERVATION AND MANAGEMENT

Introduction

Since earliest times canids, especially the black-backed jackal *C. mesomelas*, the red fox *Vulpes vulpes*, the coyote *C. latrans*, and the wolf *C. lupus* and its domesticated descendants, have had a significant impact on human populations. The success of black-backed jackals, and their close association with humans, has meant that all feature prominently in the mythology of indigenous Africans. It is interesting to note that those canids that have had the greatest impact on human culture in the past are also the very species that still pose some of the most complex wildlife management problems today. In particular, in many areas, extensive canid population control operations are undertaken, yet few of these programmes seem to have achieved their desired goals.

There is one indisputable fact about the problem of jackals in game ranches and small livestock farming areas. Killing the jackals alone is incapable of containing the problem. Despite impressive records in the number of problem animals killed by farmers, the problem is on the increase. In some areas small livestock losses have been so severe that farmers have abandoned the enterprise (e.g. Fair, 1994). Small livestock farmers who are experiencing heavy losses to predators should consider applying several control measures. Electric fencing may be very effective in keeping marauders out of selected areas or farms, but it is important to realise that there is no single simple solution to the problem and that each control method has its strong and weak points. Understanding these is vital for success.

Game and livestock farmers hit by stock losses through depredations on stock by black-backed jackals might feel justified in trying to kill the suspected culprits. But farmers and the human society at large are party to the predator problem. The supplanting of a wide spectrum of wildlife species and their natural habitats with farmland and domestic animals has set the scene for the predator 'problem'. Farmers in particular must accept that their farmland was once the home of a variety of species on which the black-backed jackals preyed (as carrion or as live animals). I suggest that society comes to terms with the black-backed jackal. This animal is often the only survivor of the medium-to-large carnivores in vast areas of sub-Saharan Africa.

Jackal control has been practised for many decades in many parts of Botswana and southern Africa (particularly in South Africa) in general. Although it might have had good short-term results, no study of its long-term effects on ecosystems seems to have been made. The importance of selective elimination that deals with culprits cannot be overemphasised for cost-effective control of problem animals. This chapter examines some methods of jackal population control, and the possible impacts of management actions on their ecology. In particular, the discussion focuses on the effects of jackal population reductions, since this is the most common of jackal control methods currently being used. Although emphasis will be on black-backed jackals, the ideas equally apply to other canids or mammalian carnivores in general.

Population Reductions

Canid population reduction is attempted for a variety of reasons (Van Heerden, 1988; Harris & Saunders, 1993; Reynolds & Tapper, 1996):

1. To prevent disease spread from canids to (a) man, e.g. rabies; and (b) livestock and/or companion animals, e.g. sarcoptic mange.

2. To prevent predation on (a) human populations; (b) livestock; (c) endangered indigenous species; and (d) vulnerable populations of nesting birds.

3. To prevent competition with, or predation on, rare species of canid.

4. To reduce crossbreeding with endangered species of canid.

5. To prevent competition with human populations by hunting game species.

In addition, canid populations are hunted for a variety of reasons not directly related to population reduction or problem animal control:

1. Commercial harvest, usually for furs

2. Recreational hunting of (a) indigenous species; and (b) non-indigenous species introduced for hunting purposes.

3. Traditional harvesting/hunting by indigenous people for medicinal purposes and other societal obligations.

Management Strategies for Jackal Populations

Society is demanding that administrative and decision-making processes involve the public and, where possible, satisfy a variety of public interests. Conservation plans should therefore seek to; (1) maintain sufficient wildlife use and value to compete more effectively with alternative land uses destructive of ungulate-predator systems, e.g. domestic animal production, or agriculture; (2) assure the long-term security of predators in most managed areas; and (3) provide sufficient wildlife to satisfy many non-consumptive and consumptive uses of predators and their ungulate prey. It is envisioned that management following this plan will help fulfil wildlife desires for people living in areas adjacent to parks.

When predation limits the growth of ungulate populations, wildlife managers have three options: (1) wait for a more-or-less natural change of events, (2) reduce or eliminate harvest by man during critical periods for prey populations, or (3) hasten the increase in prey by reducing predators (Gasaway *et al.*, 1983). Considering the lengthy period (may be decades) that may be required for natural events to produce a major increase in numbers of ungulates, Option I is not viable due to impatience on the part of wildlife users. Option II, decreasing or eliminating harvest does not specifically apply to the situation in MNR since there has been insignificant impala harvest ever since the park was established. If harvest had been practised, its elimination could forestall jackals limiting impala but it is unlikely to prevent it. Reducing or eliminating harvest will have little effect once predators exert sufficient control to cause a prey decline or to maintain prey at low densities; therefore control of harvest is best used in conjunction with other options rather than alone.

Artificial predator reduction in conjunction with reduction in harvest of prey is the most viable management option to increase impala populations over short time intervals. In general, as the ungulate population grows, predator removal can be reduced and harvest of prey by man increased. Increased predation and harvest will reduce the growth rate of the ungulate population, and eventually predation will again become a major limiting factor. Therefore, when exploitation and moderate densities of the prey population are to be maintained, predators must be managed (Gasaway *et al.*, 1983). Predator management, which includes the periodic reduction of predator numbers, can ensure a sustained long-term sharing of the ungulate resource between man and predators, while avoiding low prey densities that support few predators, exploiters, or wildlife tourists. The contention that wildlife should pay its way to ensure its conservation has much relevance to predator management. In most rural settings in Africa, society is finding it difficult to accept that predators should be conserved for the simple reason that predators are viewed as competitors utilising a potential resource that could have been utilised by people instead.

Hence there is need to search for a socially acceptable predator management system. Cooperation between wildlife users can produce conservation plans that will reduce the divisiveness of predator-prey management. Area-specific plans can address wildlife values and use ranging from natural densities with little or no harvest to increased abundance and higher harvests of wildlife. Conservation plans can define what is acceptable management in specific areas. Maximum lamb-rearing success is attained when mature mothers predominate in the breeding population (see Chapter Six). Management of harvest to produce such an age structure may be an important strategy where predation on neonates markedly reduces impala recruitment, particularly in areas where other options (e.g. predator control) are limited and predators and hunters compete significantly.

In principle, one can seek to reduce the losses to predators by reducing the number of predators (lethal control) or by reducing their access to, or availability of, the prey (non-lethal control). In practice, predator reduction is much the most common approach and, on first principles, much the least promising. Jackals can be killed in a number of ways, each with its advantages and disadvantages. From the point of view of conservation, lethal methods that are not species specific (e.g. trapping and poisoning) frequently result in the inadvertent killing of 'non-target' animals. In areas where common predators coexist with rarer animals, non-specific lethal control results in what can only be called the reckless endangerment of the rare and vulnerable species.

Several means of jackal population control are currently used or under consideration:

1. Poisoning: This includes the use of poisoned baits, gin traps, toxic collars, etc.

The killing of non-target species by these methods has disastrous effects with possibly wide-ranging ecological effects. The killing of bat-eared foxes *Otocyon megalotis* and aardvarks *Orycteropus afer*, for example, has resulted in the loss of other important allies in the farmer's battle against harvester termites (Van Heerden, 1988). The use of poison collars (livestock protection collars - LPC) although not 'humanely acceptable' to animal rights activists offer some promises. Jackals usually go for the throat of their prey. The collar protects the sheep, but in puncturing the collar the predator is given a lethal dose of poison, killing it instantly. The collars contain a quick acting poison under pressure that kills the jackal almost instantaneously on puncturing it. Once a collar has been punctured it is removed from the sheep and sent back for repair. The collars come from Livestock Protection Company in Mariental, Namibia and cost about ZAR100 each. Where various predators such as caracal (*Caracal caral*) and jackals are sympatric, lambs as well as adult stock should be collared because of differential selectivity of predators particularly with respect to prey size. For example, jackals commonly go for the small sheep or lambs while caracal prefer larger lambs or adult sheep (Byford-Jones, 1994).

2. Trapping - cage traps, leg-hold traps, snares, etc.

First, jackals should be caught before they get moonstruck, mate and produce offspring from May up to July. If this has failed, location of dens with pups should be embarked upon mainly during July, August and September. Finally, if nothing has worked thus far, emphasis should be directed to catching the inexperienced youngsters who should start running around from September onwards because they are relatively easy to catch. Preventive control during the dispersal period (February to April) would mostly remove many non-resident transient jackals that would normally be absent in the control area during the jackal breeding period. Preventive control during May to July would be more efficient because resident territorial jackals (i.e. the local breeding population) would most likely be removed. The reproductive period and its associated activities imposes an energetic constraint on breeding jackals such that there is a tendency for such individuals to kill more prey during this period so as to meet their own energetic requirements, in addition to that of the current progeny.

However, it must be borne in mind that studies with some radio-collared canids (e.g. coyotes) have revealed that individuals are relatively invulnerable to capture within their territories or home ranges (Windberg, 1996, and references therein) and, by extension, this implies that capture success for jackal territory owners or holders would be minimal in most cases. Lures used with capture devices generally rely on the food seeking, curiosity, or social behaviours of jackals to elicit attraction. The behavioural responses of animals to novel stimuli involve the combined effect of attraction or aversion, which appears to be influenced by the familiarity with the site where the stimuli are encountered (Harris, 1983; in Windberg, 1996). In experiments with captive coyotes (*C. latrans*), Harris (1983) demonstrated that coyotes exhibit neophobic behaviour toward novel stimuli, and showed that neophobic responses occur most frequently in familiar environments (i.e. territories and home ranges). My experiences while trapping jackals in the field in MNR further suggest that it may even be possible that some individuals may have learned to avoid (human) odours associated with trap-sets. Often, after a lapse of about one week during trapping in MNR, baits were found to undergo a gradual decline in luring ability. If the composition of the bait was slightly modified, however, trap visits (but not subsequent catches) would increase again. Thus, the use of techniques for surveying, capturing, or otherwise manipulating jackals should include a consideration of their potential for generating neophobia toward novel visual stimuli. Acting on these biological aspects of predator control may pay dividends in the final analysis.

3. Hunting with dogs - digging out dens with terriers, pursuit with hounds, etc.

Hunting using packs of foxhounds, greyhounds, and foxterriers, has been successful in combating the black-backed jackal on the Transvaal Highveld during summer, while hunt clubs usually employ a variety of farm dogs (Van Rensburg, 1965). The use of foxhounds is however limited as they rely on their sense of smell and the dispersion of animal scent, which in turn is dependent on the amount of moisture present. Foxhounds may thus find it difficult to trace an animal on its scent in dry weather such as prevails during the greater part of the year in southern Botswana. Feral or vagrant dogs which cannot be controlled by means of foxhounds are also suspected of being responsible for a considerable percentage of small livestock lost through predation such that effective control may eventually, depend upon destroying these animals in addition to the black-backed jackals.

Organised jackal hunts sometimes involving horses and packs of dogs, often result in the indiscriminate killing of anything on four legs that may be intercepted in the veld. The use of hunting dogs is however recommended for removing residual populations of medium-sized problem animals after other forms of control have ceased to be effective. In theory, hunting dogs could catch or corner jackals that have become bait- or trap-shy, or those that avoid being seen using other methods, e.g. from a helicopter. Hunting with dogs is ineffective for the large-scale reduction of jackal density, compared with poisoning. Therefore hunting dogs are highly successful in capturing and cornering solitary jackals encountered and provides an alternative technique for removing residual jackals from an area after large-scale reduction by another method.

4. Shooting - night-shooting, aerial shooting, etc.

5. Use of calls to attract canids to guns or waiting hounds: The use of calling (mostly scrubhare/rabbit distress calls and lamb bleats) is one of the oldest hunting methods, and is well-developed in Europe and the USA. Black-backed jackals are usually called in to sites where they can be shot. The best calling times are the early morning or late afternoon when activity is high. Effectiveness can be increased by conducting nighttime calling, using

powerful infra-red search lights. Farmers who cannot master the art of calling can use tapes which are played over loudspeakers (Schneekluth, 1995).

6. Gassing of dens and using smoke to bolt animals from dens.

7. Chemically, surgically, immunologically, or hormonally reducing birth rates in predators can reduce growth rates in predator populations.

8. Habitat destruction - removal of harbourage, destruction of dens, removal of garbage, etc.

9. Habitat manipulation - giving a competitive edge to canids less inimical to local needs.

Alternative strategies that may be used in an attempt to reduce jackal impact are:

1. Exclusion fencing, such as electric fences.

Relocation coupled with physical exclusion of predators just before lambing can improve impala survival in small and enclosed areas such as in MNR. Jackal-proof fences help restrict the movements of black-backed jackals and, if used in conjunction with foxhounds, can be a fairly effective control method. Apart from the fact that jackal-proof fences are expensive and difficult to erect and maintain in rugged terrain as in MNR, they are frequently undermined by burrowing mammals such as porcupines *Histrix africaeaustralis*, aardvarks *Orycteropus afer*, bushpigs *Potamochoerus porcus*, warthogs, *Phacochoerus africanus*, as well as black-backed jackals, and springhaas *Pedetes capensis*. When holes are dug under these fences they become ineffective for jackal control and maintenance costs are increased. In South Africa, government standards specify that at least 150 mm of the fence netting must be laid flat on the ground and covered with stones or pinned to the ground with wire staples, or 100 mm of the netting wire should be buried vertically and packed with stones on both sides. Notwithstanding these efforts, in certain localities, chacma baboons (*Papio hamadryas*) remove these stones from the bottom of the fences during their foraging activities.

As a result of jackal-proof fences being undermined, the game or livestock farmer not in many cases effectively reduces black-backed jackal depredation on small stock, despite a costly outlay on fencing. This in turn leads to unselective gin trapping by farmers, as it is most common for these traps to be placed in holes under the fences. Individual farmers will even launch an extensive extermination campaign against burrowing animals. The aardvark *O. afer* is often the culprit and so has been a target of farmers. But killing aardvarks has lost the farmer an important ally in the fight against termites. Another animal that may also suffer severely because of its tendency to ram fences is the ostrich. For example, on many northern Cape farms in South Africa, where once large flocks occurred, ostrich numbers have dwindled (Van Heerden, 1988). In addition, jackal-proof fencing may create isolated populations of animals such as the grey duiker and steenbok, and may aid potential predators, including domestic dogs, in preying on such enclosed animals (Heard & Stephenson, 1987). Where there is evidence of animals digging under nature reserve fences as in MNR, entering neighbouring farmlands and raiding crops or stock, it frequently happens that the neighbouring farming community develops negative attitudes towards nature conservation and the reserve in particular.

2. Aversive conditioning, such as the use of lithium chloride to reduce predation on sheep. Conditioned taste aversion is a natural phenomenon of feeding behaviour, but here individuals learn rapidly at the subconscious level to avoid by taste foods associated with illness: following consumption of a poisonous food and its unpleasant effects, all food with the same taste will evoke strong avoidance behaviour. Learning is rapid, and a single experience can suffice to create a lasting avoidance. Research on this is however in its exploratory phase.

3. Increasing alternate prey may reduce predation on the resident impala population in MNR. Interestingly, jackal foraging ecology espoused in the present study reflects the availability of a wide variety of food items and the differential vulnerability of prey. The dramatic seasonal shift by jackals to feeding on indigenous fruits, when they were abundant, and consumption of insects in significant amounts, when other foods were available, suggests that fruits and insects may substantially buffer predation on other species. Hence, it may be possible to predict the intensity of jackal predation on vertebrate prey through routine monitoring of fruit and insect abundance (Andelt & Kie, 1987). The high consumption of fruits also suggests the

potential, in some areas, for strategic plantings of appropriate fruiting species to buffer predation on desirable species, or possibly to lure jackals to areas where they might be easily captured.

4. Diversionary feeding of predators on or near impala lambing grounds for 4-5 weeks may reduce predation on neonates.

5. Habitat enhancement (e.g. through fire management) may increase impala numbers through improved impala physical condition and reproductive rate.

6. Vaccination against diseases such as rabies, or fumigation of burrows to kill parasitic mites in order to reduce the prevalence of sarcoptic mange in areas where canids are prized for their pelts.

7. Compensation for stock losses or the adoption of alternative enterprises less susceptible to canid predation.

8. Timing livestock production in adjacent agricultural and wildlife properties to minimise predation.

9. Using guard dogs to protect livestock.

10. Using light or sound stimuli, or other scarers, to reduce predation.

11. Removal of carrion (and human refuse), so that canids are not attracted to these areas.

In many parts of semi-arid Botswana, black-backed jackals are undoubtedly the most problematic predators. But not all jackals kill small livestock and game. It is no longer necessary to wage a war against the jackal in an attempt to eliminate them from farming properties. The truth is that such wars are rarely successful; more often than not they are costly and futile campaigns, and non-problem jackals are seen as allies in the management of problem animals (Fair, 1994). Jackals serve an important function in controlling caracal

(*Caracal caracal*), dassies (*Procavia capensis*), and rodents, all of which can cause heavy losses to farmers. In most cases in Southern Africa, killing jackals has resulted in the increase of caracal numbers in particular, primarily because jackal predation on caracal helps maintain caracal populations at low levels (J.D. Skinner, pers. comm.). Jackal eradication is therefore not only senseless but also foolish. Eradication is also senseless because jackals are incredibly resistant to it. They counter when put under a downward population pressure, by increasing not only the number of litters they produce per year, but also the number of pups per litter (Van Heerden, 1988). The answer lies in dealing on a selective basis, with individual killer animals (Fair, 1992). A strategic problem animal control plan is one that focuses on eliminating only the culprits (J.A.J. Nel, pers. comm). Such a plan allows the existence of a non-sheep-killer-predator-population, because they keep potential killers out of their territory (see Chapter Seven). The use of the livestock protection collar (LPC) on farms has proved that not all jackals kill small livestock and game - it is only a relatively small number that do the killing.

Goats and sheep are particularly vulnerable to predation by jackals, while cattle for the most part, are relatively immune. The choice of the type of livestock to be raised in a particular area may be influenced by various factors: market demand, the type of forage available, cultural traditions, or historical accident. However, in areas where a particular species of predator is causing problems with a particular species of livestock, one option is to remove the predator. But where it is culturally, ecologically, and economically possible, a simpler solution might be to raise a different type of animal. This is all very well from the perspective of the conservationist. But the peasant farmer who loses part of his meagre small stock to jackals would be in a far different position had a similar number of livestock been lost to a commercial farmer (for example) since sheep and goats are the poor man's cattle in most parts of rural Botswana.

The lucid reality of all this is that, no matter what the method of lethal control is employed, reducing predator numbers is an expensive process that requires a long-term commitment on the part of government or private producers. When deciding to manage an abundant canid population, three major factors need to be considered before embarking on a management programme:

1. The cost-effectiveness and/or cost:benefit ratios of predator control and/or management

2. The effects of control operations on canid populations

3. The non-target effects of control programmes in (a) increasing the number of prey species, which in turn may be pests; and (b) the ecological/environmental impact of population reduction techniques. For this presentation, emphasis will be on item (2) and (3) above, since these are essentially of biological interest.

Predation

Traditionally, biologists have attributed a major decline in ungulate numbers to starvation, whereas in reality this represents the tip of the iceberg. Failure to detect and gauge natal mortality could pose grave bio-sociological problems especially where the need for such information led to the wrong management strategy.

Some of the factors which may predispose livestock property and small game to jackal predation include; an abundance of suitable habitats to provide harbourage, autumn/winter lambings during the main jackal dispersal period, low availability of alternative food types, and individual livestock properties lambing out of sequence. It is true that a high proportion if not all, of the prey taken by jackals possess some trait that predisposes them to predation. Many factors that predispose prey to predation by jackals are obvious, such as senility due to poor nutrition, injuries, parasites, diseases, and merely being relatively small in size, or simply being newborn. However, many traits predisposing prey to predation are far subtler and not easily measured by biologists. For instance, the 'grandmother effect', in which the nutritional state of an individual's grandmother becomes a factor in its survival, is a good example (Mech *et al.*, 1991; Paquet, Nelson, & McRoberts, 1991).

The very contest between carnivore and prey seems to imply that far more prey will escape than get caught and that usually the least fit individuals will succumb easily to predation. However, beneficial effects of this culling by carnivores are not immediately obvious. Philosophically one can argue that an ecosystem that includes its full complement of carnivores is more natural and therefore better. Certainly, the nature of the energy flow and biogeochemical cycling in a carnivore-free ecosystem would be different from that in an ecosystem with its natural carnivore complement. The problem is the time scale. Carnivores like other orders of mammals have exerted their influence in ecosystems in minuscule increments over millennia.

Keith (1974) provided the following guidelines for evaluating the relative importance of a factor that may affect populations;

a) Identify its immediate demographic effects and compare its impact with other factors

b) Describe its interaction with other factors in terms of additive (the effects of two factors sum up), compensatory (a change in the magnitude of one factor produces the opposite change in magnitude of another so that their combined effect on the population is unchanged), or modifying effects; and

c) Characterise its action in relation to population density.

However it is difficult to detect interactive effects in the absence of experimental manipulation. We also need to know how predation rates vary with prey densities (Boutin, 1992), and whether predation rates are limiting or regulatory as described by Sinclair (1989). One can assess the degree of limitation imposed by a factor by studying a population at a single density using Keith's criteria, or by removing the factor of interest experimentally and observing subsequent changes in population density relative to control areas. However populations of varying densities are required to determine if a factor is regulatory.

Experimental studies potentially reveal so much more about dynamic relationships than descriptive studies. Predator removal/restocking experiments are the classic example of such manipulations. Unfortunately, simple predator removal experiments must be followed for a long time to try to separate experimental effects on equilibria and stability - which is a difficult separation to make (Taylor, 1984). Instead, one could also investigate the influence of predation by altering *prey* densities - which is precisely the design advocated by Nicholson (1957) and Murdoch (1970) as the most direct way of detecting population regulation. In this case it is important to acknowledge that both predation and dispersal, motivated by intra-specific aggression, must play critical roles (Slade & Balph, 1974). These two factors may also interact to form a complex that is too interrelated to be treated as merely the additive or multiplicative effects of predation and dispersal considered alone (Mitchell *et al.*, 1992). Notwithstanding time and budgetary constraints, the manipulative experiment that would adequately investigate predator-prey relationships would conceivably consist of a factorial arrangement of enhanced, diminished and control prey populations compounded with enhanced, diminished and control predator populations (Taylor, 1984).

The Carnivora, as the name implies, are generally predatory, and to a greater and lesser extent, all canids live by killing prey. This ecological/evolutionary truism raises three related questions in the context of conserving and managing wild canids (Ginsberg & Macdonald, 1990):

(1) To what extent does their prey limit the populations of canids, and to what extent do they limit the numbers of their prey?

(2) With respect to valuable prey, is the impact of predation by canids in general disadvantageous to people?

(3) Where predation by canids throws them into conflict with people, how might such conflict be resolved?

As previously indicated, problems are likely to arise with predation on three categories of prey: domestic stock, wild game, and endangered species, although in reality the delineation is less distinct. Nearly every species of canid has been implicated in livestock damage. Ginsberg & Macdonald (1990) reported that of the 34 canid species, 21 have been implicated to kill livestock or poultry at least occasionally. By virtue of their numerical ascendancy, black-backed jackals find themselves in circumstances under which their predation is economically significant, especially to the low-income sectors of society who depend on small livestock for their livelihood. Goats and sheep are the poor man' s cattle in many parts of Africa, especially in the moisture limited Kalahari ecosystem where other forms of agriculture are difficult to embark upon. In Botswana, whose rural populace inhabits most parts of the dry Kalahari, it is black-backed jackals that are usually blamed for excessive predation on small domestic stock.

When a farmer encounters a dead lamb being eaten by a jackal, or when a game hunter sees a pack of wild dogs devouring an ungulate carcass, they commonly feel a wrath born of competition: both farmer and hunter had wanted the prey for themselves (albeit for different purposes). But underlying such anger, is the assumption rather than proof of competition. Had the lamb or ungulate carcass been eaten as carrion, then it would already have been valueless. Livestock seen being consumed by a predator may have died of natural causes and, subsequently, been scavenged by the predator. Equally, if the predators had singled out sickly individuals that were nevertheless destined to die, then the measure of competition with man would be unimportant (Ginsberg & Macdonald, 1990; Boutin 1992; Gasaway *et al.*, 1983). If preys are destined to die from starvation, and a predator's feasting is confined to the proportion destined to perish, then the predator only acts as the hangman! Only if predation affects the breeding stock that could have otherwise survived could predation be said to be limiting a natural population. For example, during my study on jackals at Mokolodi Nature Reserve, Botswana, I documented pairs of jackals moving among the female ungulates presumably inspecting them for signs of lambing during the calving/lambing season. These jackals fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In fact, what happened in certain cases is that jackals occasionally attacked ungulates when the latter were recumbent during parturition. In such instances the partly born calf or lamb would be eaten, while the vulva of the female may also be eaten, with the result that the dam or cow may subsequently be destroyed. It is in such cases when jackal predation could potentially limit population growth and be a source of conflict.

Evidence that predators eat a given prey is not evidence that by doing so they are a pest. To evaluate pest status, much must be known of the circumstances, including both biological and economic information (Ginsberg & Macdonald, 1990; Harris & Saunders, 1993). After ascertaining the magnitude of the problem, then the costs and benefits of proposed solutions require careful assessment, and such assessment should be instituted in the perspective of local economies. If the concern is over live prey, then the evaluation of damage must exclude those that were eaten as carrion. In a similar vein, if predators take sickly individuals, the cost of their predation must be devalued by what it would have cost to care for the ailing prey.

How then, do we measure the magnitude of livestock losses that are caused by canids? Most field studies of canid feeding ecology are made from the perspective of the predator, not the prey. They give some indication of the proportion of livestock in an animal's diet. From this, if one knows the population density of the carnivore being studied, an estimate can be made of the numbers of sheep, goats, or chicken that might be lost to that particular population of canid. However, Ginsberg & Macdonald (1990) argue that when measuring the impact of canids on livestock production, "the question we need to answer is not 'what percent of the diet is composed of livestock?' or even 'how many sheep are eaten by canids?' but 'what effect does canid predation have on total livestock production?'

Basically, calves are eaten at higher rates than cattle, lambs more frequently than sheep, and predation on lambs is more common than on adult ungulates. This suggests that canid predation will be the greatest problem at times when livestock are bearing and raising young. Of course, at other times of the year, jackals are surviving on other types of food. Hence if young animals can be protected, jackals may well stop eating livestock, and switch to more easily acquired foods. Clearly the influence of jackals on domestic livestock will depend on the interactions between jackals and their wild prey. The extent of predation on livestock may be related to the quantity or quality of other prey species, from a jackal's point of view.

It is often assumed that canid predation on wildlife reduces the amount of wildlife available for human consumption and sport. Before such an assumption can be made, data must be collected on the following questions (Ginsberg & Macdonald, 1990):

(1) Is the consumptive utilisation of the prey species by humans on a scale with that of jackals or canids in general? If, for the most part, humans are the major

predators in a system, removing other causes of predation may result in only a marginal increase in human harvests.

(2) If jackals and other canids are removed from an ecosystem, or reduced in number, does the prey they eat become available to man or do these animals die from other causes? For example, black-backed jackals often specialise on young prey animals. If removal of jackals results in a greater rate of predation by other predators (e.g. caracal, birds of prey, feral dogs, etc.) or increased natal mortality from starvation and disease, canid reduction alone is unlikely to result in greater human harvests of adult animals.

The above analysis assumes that the important question to ask is how to mitigate the cost of depredation of livestock by canids. However, in many circumstances, the costs of predation may be irrelevant. Most of the time when wild predators kill domestic animals, people react instinctively, rather than logically. Despite some infinitesimal losses that may be incurred, it is those few incidents that may provoke dispirited public controversy. Such an outcry would not have occurred had domestic dogs been responsible for the losses, or had a few sheep died of starvation or disease. Predation by wild carnivores in such cases is seen as a loss that can and should be controlled; not an act of God, but the result of negligence on the part of the wildlife or game managers.

Effects of Control Operations

Predator control by humans is as old as livestock husbandry. The deliberate, often organised destruction of many mammalian predator species has been a feature of human development in Europe - and later in countries to which Europeans spread - for centuries (Reynolds & Tapper, 1996). Destruction to the point of extinction was basically practised for purposes of protection of life and commodities (livestock, game, fur, etc.). Reduction of predator numbers specifically to allow an increased harvest of some game species was mainly a nineteenth century development, while the adoption of predator control to benefit endangered species for their own sake belongs to recent decades.

Wildlife scientists and managers are fond of calling Aldo Leopold (1949) the father of wildlife management. However, many professionals overlook or ignore one of his central messages, as embodied in one of his most famous quotations: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong if it tends to do otherwise." Leopold saw a distinction between the true sustained-yield management, in which wildlife systems are harvested only selectively in a way that tries to ensure their underlying structural and functional integrity, and what I would refer to as 'farming' of these systems. Similarly, the 'precautionary principle' (Myers, 1993) also counsels us that conservation or other action should not be undertaken unless it can be shown not to be damaging.

Carnivore biologists, wildlife and farm managers regularly assume that jackal populations can be reduced without significant biological impact. 'Biological impact' is typically defined solely as numerical status: The impact is considered negligible if the jackal populations either maintains or soon recovers to about the same size. Little more than the number of animals is considered, and sometimes not even this standard is maintained. Some biologists seem willing to accept almost any behavioural variation as 'inherent'. Scavenging of dead ungulates is an important supplemental foraging activity by jackals, but should garbage eating, largely solitary maize-field canids really be regarded as jackals? Or are they the products of a lengthy subtle process of altering jackal behaviour through human persecution and habitat/prey displacement? Some examples of 'adaptability 'may instead actually serve as a warning about the pitfalls of watching for numerical signals of endangerment while ignoring virtually all else about the biology of the animals. To understand the impact of heavy ongoing public killing, and short-term government control on jackal populations and why, in general, this makes little biological sense, requires an understanding of jackal social organisation. Social behaviour is strongly influenced by inheritance (Plomin, 1990) and is therefore very much within the realm of biology.

One of the factors that will affect the efficacy of a canid control operation is the behaviour of the target animals. In a species such as the black-backed jackals where there are territorial and transient animals, it is logical to assume that the territorial and hence reproductive individuals may pose the greater risk to some agricultural interests, since the provisioning of pups is a stimulus to depredation, and the removal of the pups may as well end the problem. However, the younger and transient animals would presumably be easier to capture than territory holders within the interior of their ranges. Thus jackal control operations would be most effective after dispersal and immediately before the whelping season. Any mortality would then be additive and also limit production the following season.

Black-backed jackals are territorial animals, and territories being specific defended areas, are often considered as spatially consistent throughout the life-span of an individual (e.g. Brown & Orians, 1970; White & Garrott, 1990). However, in some circumstances territory size and configuration may be adjusted to incorporate changes in occupancy of neighbouring territories or changes in the distribution of certain limiting resources (Kruuk & Macdonald, 1985; Doncaster & Macdonald, 1991). Relative values of mortality for dominant animals rather than overall values are likely to be of greatest significance for territory stability since these are the individuals which spend most of their time in active territory maintenance and defence. (White, *et al.*, 1996). Hence any mortality of dominant animals will act to destabilise existing social hierarchies, and consequently, surviving animals may make opportunistic adaptations to their behavioural patterns to exploit resources in neighbouring territories made available by the death of a dominant animal. In cases where mortality rates of dominant animals are high, such destabilisation will be more frequent, and spatial organisation will be unstable as a result.

Heavy, indiscriminate harvest or control of a highly social species could hardly be expected not to reduce and fragment its sociality and eventually produce less selectivity in other important aspects of behaviour (Haber, 1996). Similarly it is difficult to imagine that such killing would not add greatly to the natural variations in territory boundaries and overall territory mosaics and that it would not simplify homesite traditions within these territories. Greater variability in prey kill rates and territory-size versus group-size relationships is probably also explained to a large measure by social changes and by the increased availability of temporary vacancies within territorial mosaics, which allows for more expansion of both surviving and new territories. It is difficult to dissect the impacts of jackal exploitation because detailed comparative information on behaviour from both exploited and protected jackal populations is scarce. Major differences in prey types can greatly influence the degree of sociality (Bowen, 1981) and consequently, foraging behaviour.

Under conditions of moderate to heavy exploitation, with frequent replacement of key individuals, it would be difficult for jackals to maintain stable, well-defined dominance relationships such as has been reported in other studies (Ferguson, 1978; Moehlman, 1983, 1986; Rowe-Rowe, 1986; J.D. Skinner, pers. comm). There would likely be more overall variation in most relationships, dominance and otherwise. Territorial behaviour and hunting would be determined more by interactions of various jackals than by the behaviour of the same core of high-ranking group members. Competition would be less restrained, and when group size continued to increase, there would probably be less of a difference in consumption rates among adults, lower average per-adult rates of consumption per prey kill, and shorter refractory periods leading to more time spent hunting, a continuing increase in kill rates, and probably more of a tendency for the group to try and expand its territory (Haber, 1996). With heavy exploitation, especially ongoing harvest, there is bound to be much less opportunity for well-established groups to persist in relative isolation from each other.

Additional kill rate differences reported for exploited populations might involve subtler social or other types of distortions. Hayes *et al.* (1991, in Haber, 1996) suggested that the sharp increase in kill rates (by wolves *C. lupus* on moose *Alces alces*) they observed for groups reduced to pairs following heavy control was due to two factors: 1) The unusually large territories that colonising pairs were able to occupy initially provided them with an increased selection of potentially vulnerable prey. 2) Higher per-kill losses to competitors, especially ravens, prompted them to spend more time hunting. It is also quite plausible that heavy broadcast harvest or control implies a greater likelihood that pairs can settle into area and hunt sizeable territories with less risk of attack from nearby established groups.

In those situations where jackals have been shown to depress ungulate population levels, the most frequent management response is to kill the jackals. But jackals, like many canids can be very productive (Van Heerden, 1988). Yearly variations in reproductive output may primarily be a function of changes in pregnancy rates, especially yearlings, in addition to changes in litter size, and post-natal survival of young pups may have an important influence on recruitment. In many areas canid populations may be food-limited, and this may be a major factor limiting pup survival. An increase in the proportion of young animals is frequently recorded in canid populations following substantial levels of harvest. The combination of density-dependent effects on reproduction, mortality, and dispersal makes it nearly impossible to reduce abundant canid populations in anything except local areas. For example, a wolf pack usually produces one relatively large litter of five to six pups. When populations are not saturated, 22-41% of all wolf packs produce multiple litters (Harrington *et al.*, 1982; in Ginsberg & Macdonald, 1990). In other areas, only 10% of the packs may produce multiple litters. Hence reducing wolf numbers may result directly in a large number of young wolves (Ballard, Whitman, & Gardner, 1987). What this means is that even when suffering an annual mortality of 50%, a wolf pack can remain stable in its numbers. Storm (1977) also found that when the density of foxes was reduced to 0.04 km^{-2} by control, dispersal was responsible for repopulating areas to a density ten times that level within four years. Thus, although reduction may result in reduced numbers, it can also lead to several new waves of immigration and an increase in births. Nature abhors a vacuum, and carnivores appear to be no exception to natural laws. Jackals are frequently killed as control measures in areas where ecological factors such as abundant food have made them a pest. But for every predator killed, there may be another just waiting to move into such prime habitat. A local lethal control for wolves in Canada did not decrease wolf numbers but led to an increase in immigration with new wolves moving into the area to compensate for artificially low densities (Ballard *et al.*, 1987). This clearly shows that even total removal will only result in a temporary respite from canid predators unless an area is completely isolated.

Other likely impacts of harvest and control include disruption of learning, increased population-wide mixing, and different within- and between-group genetic patterns, all of which would be difficult to identify with the sketchy comparative information available. However, these impacts might be among the most important. Disruption in the flow of learning from generation to generation would result in fewer, simpler learned behavioural traditions and in general a diminished role of these behaviours (Haber, 1996) that help adapt individual family groups to the specific resources and other unique features of each area.

Jackals commonly live 6-7 years or more in well-established family groups subjected to little or no hunting or trapping (Lombaard, 1971; Moehlman, 1983, Rowe-Rowe, 1986). In contrast, few jackals live for more than 4-5 years in exploited populations. This implies a high rate of turnover and young age-structure. Consequently there is much less opportunity for jackals in these populations to accrue and transfer information from one generation to the next via the prolonged dependency period and complex learning sequences important to jackals under natural conditions (Moehlman, 1983, 1986).

Jackal social behaviour may be remarkably adaptable, but the adaptations are primarily for food acquisition, not defence against sustained, heavy predation. It does not necessarily follow that jackals will be able to survive heavy exploitation and control just because they have held their own numerically against heavy killing for the past century or so. A few decades of heavy killing amount to the blink of an eye compared with the far longer period of evolutionary time over which jackals have evolved in response to the opposite pressures.

It surely is surprising how we seldom practice what we preach. We have managed to artificially select for particular breeds of stock in agriculture for centuries, but we shy away from the fact that by killing jackals for control purposes, we may be unwittingly doing the same. In the longer term natural selection operates against controlled killing: only jackals that survive the cull can breed, which selects for individuals less easy to kill. And these may well be the extant jackal populations that we find most difficult to control today because, relative to those who perished, their behavioural repertoire allows them to withstand the vagaries of human persecution.

Effects on Animal Population Densities

The effects of control on canid numbers are particularly difficult to evaluate, since there are a few absolute and relatively few reliable comparative density estimates for canids. Hence there have been few attempts to measure long- or short-term canid population changes. Density estimates based on the number of social groups per square kilometre are generally of little use for evaluating the effects of control unless the actual number of animals is known.

The primary objective of predator reduction was to safeguard domestic livestock and poultry, but also to promote human safety and to benefit game species (Reynolds & Tapper, 1996). As time went by, and larger predators became increasingly uncommon or even extinct, attention shifted to smaller predators. It is possible that in general the removal of top predators allowed smaller predators to increase numerically and expand their geographical distribution, because predation within 'guilds' of predators (or 'intra-guild predation') is increasingly proving to be important in shaping predator communities (Polis, Myers, & Holt, 1989; Palomares, Gaona, Ferreras, & Delibes, 1995). In any case, small predators certainly benefited from changes in land-use.

Large mammalian carnivores may help control populations of medium-sized, opportunistic predators in landscapes with some degree of habitat fragmentation. Soule' (1988) suggested that mesopredator release is a general phenomenon and that smaller omnivores and predators undergo population explosions, when large dominant predators are extirpated. In Yellowstone National Park (Wyoming, USA), coyotes *Canis latrans* expanded in population after extirpation of wolves (*C. lupus*) and assumed many of the ecological characteristics and functions, including pack formation and predation on large ungulates (Noss, Quigley, Hornocker, Merrill & Paquet, 1996). Furthermore, in at least one instance (Sargeant *et al.*, 1994, in Reynolds & Tapper, 1996) it is clear that the destruction of coyotes (*C. latrans*) to protect livestock in the North American prairie pothole region changed the distribution, abundance and predation impact of yet another smaller canid, the red fox (*V. vulpes*). In a similar vein, in sub-Saharan Africa, black-backed jackals have also been implicated as being capable of assuming the predatory role of large African pure predators, where the latter have been extirpated (Estes, 1967). In particular, an increase in the numbers of caracals (*C.caracal*) after extensive eradication campaigns of jackals has been observed in southern Africa (J.D. Skinner, pers. comm.), simply because the latter usually suppresses the population of the former through intra-guild predation.

Although the idea of 'predator pits' (Newsome, 1990), i.e., that there is a limited range of population densities at which a predator can control a prey population remains theoretical, it is of extreme practical importance for the control of canid populations since injudicious control may result in unwanted numbers of other pests. Newsome, Parer & Catling (1989) found no effect of fox predation on rabbit population declines that were due to arid conditions and poor pastures. However, after rabbit numbers collapsed, foxes were important in suppressing population growth. Newsome *et al.* (1989) then introduced the concept of environmentally modulated predation. Sinclair, Olsen & Redhead (1990) also came to very similar conclusions with mouse (*Mus domesticus*) populations in Australia; at lower prey densities, the impact of predators was density-dependent and regulated prey densities, whilst at higher densities the total predator response was inversely density-dependent and predators were unable to regulate the mouse population.

Furthermore, generalist predators may have a stabilising influence on prey numbers, since they include a considerable proportion of rodents in their diet only when rodents are common, and switch to other prey during periods of rodent scarcity (Andersson & Erlinge (1977).

Epidemiology of Jackal Rabies

Since black-backed jackals have also been implicated in the transmission of rabies in southern Africa (e.g. Meredith, 1982; Bingham & Foggin, 1993; Alexander, *et al.*, 1994), the transmission of the rabies virus from infectious to susceptible jackals is a direct consequence of the social behaviour of the infectious individuals. An understanding of the ecology of the reservoir animal population is basic to the development of an effective rabies control programme. The persistence of rabies and the success of attempts to control it depend fundamentally on a measure known as the contact rate (Bacon & Macdonald, 1980; Macdonald, 1980a, 1982). The contact rate for a population is the average number of susceptible individuals infected by each diseased animal (Prozesky, 1982; Bailey, 1975, in Ginsberg & Macdonald, 1990; White, Harris & Smith, 1995). Although radio-tracking has enabled the movements of jackals to be studied in detail, quantifying the contact behaviour of such an elusive species as the black-backed jackal requires more than one individual to be radio-tracked continuously and simultaneously with a high degree of accuracy. The need for many animals in a relatively small area to be captured and radio-collared, combined with the fact that simultaneous, continuous radio-tracking is a very labour-intensive operation, has meant that such work has not been undertaken so far on any vertebrate host (White *et al.*, 1995). Contact rate is not constant, but a complicated function of the social organisation and density of vectors, and thus of the frequency of meetings between them. From basic biological premises, many factors could influence the rise and fall of the disease: the number of jackals, the density of the population, their contact rate; the virulence and incubation period of the infection (Bacon & Macdonald, 1980; Macdonald & Bacon, 1982; Prozesky, 1982), etc. Using computer simulations it is possible to get a fair idea of what is actually happening in nature. But most of these parameters (e.g. reproductive rate and contact rates) depend on vector (in this case, jackals) behaviour; if we are to understand how jackal rabies spreads, and how, rationally, to stop it spreading, we must understand jackal sociobiology.

Human Perceptions

People possess certain basic values toward animals and nature that inevitably affect their perceptions of individual species. Second, people's attitudes are significantly influenced by the physical and behavioural attributes of a species, including the animal's size, perceived intelligence, morphology, mode of locomotion, cultural and historical associations, and other factors. Third, people's knowledge and understanding of a species can influence attitudes, including factual, conceptual, and conservation awareness. Finally, perceptions are affected by past and present interactions with particular species, including conflict, recreational use, property relationships, and management status (Kellert, Black, Rush & Bath, 1996).

Why should carnivores be conserved if their activities conflict those of man? Ginsberg & Macdonald, (1990) offered an appealing explanation: "Perhaps it is insight into their individualism won through our association with domestic dogs, perhaps it is the ability of some of them to withstand the worst that man can throw at them, perhaps it is that we see some reflection of ourselves in their opportunism, or perhaps it is simply the transfixing elegance of their jaunty grace. Whatever the pot-pourrie of reasons that blend into their appeal, the 34 species that comprise the family Canidae are special. They are special because they have, as perceived friend and foe, preoccupied the imaginations of mankind for millennia. They are special because the breadth of their adaptations makes them enthralling to science. They are special because the contradictory facets of their relations with people perplex the conservationist. The possibility that we are heedlessly, perhaps needlessly, mismanaging many of them is saddening; the probability that our negligence will force several more to extinction should fill us with bottomless dismay".

The relationship between jackals and humans has never been amicable due to predation on game and livestock. Farmers and ranchers have consistently expressed the most negative attitudes towards predators, a sentiment generally motivated by fear of economic loss. Still, perception is often stronger than reality, and depredation by any predator of an individual rancher's stock can inflict severe emotional, financial, and political consequences. The path of least resistance to a state resembling harmonious coexistence of predators and livestock producers involves limiting the opportunity for conflict. Improvement in animal husbandry may not be costly and may produce significant results. Proper disposal of livestock carcasses, either those killed by predators or those resulting from other causes of natural mortality, appears to reduce subsequent predation. Confining animals at night, or during their infancy, when they are most vulnerable, also reduces losses to predation. Proper disposal of garbage limits jackals access to otherwise easily accessible food resources, eventually restricting the ability of jackal populations to increase.

Why are so many losses that appear to be due to natural causes, or other predators blamed on a particular species like lions and wild dogs? In many cases, the blame for such misreporting is, in part, due to abuses of policies developed to protect those larger carnivores. In many parts of the world, where large predators are rare or endangered, farmers and game ranchers are compensated for losses due to lions and wild dogs (e.g. in Botswana and Zimbabwe), but not for other causes of livestock mortality. Hence kills known to have been made by black-backed jackals, foxes, and feral dogs are called wild dog kills so that a farmer can collect compensation (Ginsberg & Macdonald, 1990; Reynolds & Tapper, 1996; pers. obs.). However, compensation is not a form of predator control, but a form of governmental recognition that the costs of predation should be borne by the public at large. Compensation spreads the risk to individual farmers, which can be considerable even if regional losses are low. As noted above, compensation without confirmation of canid depredation can lead to abuse of the system, rather than justified claims for compensation.

Some carnivore species, such as lions have been protected to the point that they are threatening trailists in national parks or people living in proximity to parks. Still, others like black-backed jackals have adapted so well to human development, which often removed their competitors and enemies, that they are now more numerous than ever. So, we are entering an era which may be more contentious than in the past because when carnivores interfere with human activities, they aren't merely an aggravation like impala eating grain on fields; they also eat livestock (Mills, 1991). In most cases, conflicts of people with carnivores represent a more serious and urgent problem to management agencies than other kinds of complaints. This may clearly more than offset the creature's charisma, an attribute sometimes advanced for their conservation. When these factors are added to the growing trend towards wildlife management by public referendum, inequities and conflicts are inevitable. For example, the multitude of voters in cities who are unaffected by any of the negative impacts of carnivores can simply outvote rural residents who bear the brunt of the damage. It is ironic that this simple majority-rule type of wildlife management is basically the same approach that extirpated carnivores many years ago. There may not have been public referendums at that time, but there were bureaucrats acting contrary to scientific opinion but bending to public will.

Any effort to conserve biodiversity is bound to be difficult at a time when the human population is growing exponentially, and everyone worldwide wants to live like the rich, extravagant members of our species in most parts of the Northern Hemisphere. Conservation requires compromises and concessions from everyone and is nearly always accompanied by biological tragedy (Noss, 1996). Even the most stubborn optimists know in their hearts that unless some plague or other factor brings human population and consumption down to sustainable levels, and unless the prevailing attitudes of humans towards nature changes radically soon, mass extinction is probably unavoidable. Some species will almost certainly go extinct whether or not we try to save them; other species may go extinct if we do nothing to help them but may survive regardless of what we do. So, it makes sense to focus conservation programmes on the middle group of species, those that are in trouble but have a good chance of surviving if we help them.

The ultimate challenge is changing human attitudes, and the proximate challenge is offering these animals sufficient security until human attitudes change. But changing human attitudes through education may take generations to have an effect inasmuch as attitudes towards the animals have been moulded for hundreds of years. Conservation of carnivores and other demanding species will always be inconvenient (Noss, 1996). It will always be violently opposed by some people, and therefore politically volatile. Conserving animals that are capable of spreading disease, killing, and eating us and that need large, wilderness areas requires great commitment on the part of conservation biologists, activists, land managers, and political leaders, and a good bit of tolerance on the part of the people who live, work, and play in carnivore habitat. Hence the predatory activities of black-backed jackal on domestic stock has functioned as a particularly powerful barometer of changing and conflicting attitudes towards wildlife in most parts of Sub-Saharan Africa. It is evident that the management of MNR and livestock owners perceived that they had a significant problem with predation on smaller ungulates and livestock, respectively. An economic loss of this magnitude while perceived as a problem by small livestock owners, may not be great enough to warrant action by the government. Such a programme might be more costly than the total annual loss to the herds, though from the standpoint of public relations such a programme may be desirable. Most methods of jackal control are available albeit at a cost.

The following criteria are a suggested blueprint for the conservation and management of black-backed jackals in particular, and other mammalian predators, in general. First, field research must play a primary role. Without baseline information on the status of the species, its principal prey, and its range and habitat requirements, sound conservation planning and management are impossible. Secondly, once baseline biological data are available, it then becomes essential to expand the conservation equation to include relevant cultural, economic, and political factors. Conservation does not occur in a vacuum, and understanding the broader context is essential to long-term success. Thirdly, based on such a broad understanding, it is then possible to design and implement more comprehensive approaches to conservation. Finally, there should be monitoring and feedback. Good conservation is a dynamic process. Techniques must be developed and personnel trained to replicate initial surveys and provide updated information, not only on status of the predatory/prey populations, but also on habitat conditions, and the broader socio-economic context. Such information must then be made available to decision-makers so that they may adapt their management plans and practices. Without such monitoring and feeback, conservation is reduced to mere crisis management. But conservation biology or wildlife management should not become a science of doom.

The foreregoing discussion illustrates two points: a) that there are substantial management problems concerning species such as jackals which are not endangered, and b) that modern techniques offer ecologically exciting solutions to wildlife management problems. I fully recognise that the particular propositions I have propounded have far greater conceptual than prescriptive power. However, prescriptions and cookbook approaches should be avoided in conservation biology and wildlife management because the systems with which we work are specific and endlessly varied in time and space. No single detailed prescription can be of much use for more than a single system.