SUMMARY

The objective of the present study was to investigate black-backed jackal behavioural ecology at Mokolodi Nature Reserve (MNR), Botswana, with particular emphasis on movements and jackal predation on impala. An offshoot of the present study also sought to explore the prevalence of jackal rabies in MNR and adjacent agricultural areas. Radio telemetry (supplemented by direct observations) was selected as the tool for studying behaviour, movements, social organisation, and also to assist in estimating jackal density in the reserve. Faecal analysis (supplemented by analysis of stomach contents), based on the identification of prey remains in faeces, was chosen as the method to determine jackal diet.

Spatial Utilisation and Activity

Jackal behavioural activity patterns were investigated during standard circuit surveys, through focal animal sampling, and opportunistically. The number of black-backed jackals fluctuated between months and on a seasonal basis (Table 1 & Figure 1). Generally it increased throughout winter and decreased during summer. Fewer jackals were seen between October and February. "Hunting/foraging" (28.7%, n = 181) was observed significantly more often than any other behavioural activity, followed by "locomotion" (23.8%), "flight" (21.2%), "resting" (14.4%), and "interactions", in that order.

Jackals in MNR exhibited a bigeminous activity pattern (crepuscular and nocturnal periods). Periods of activity occurred from 17h00 to 22h00, and also from 05h00 to 08h00, with peaks around 18h00 and 06h00. In general, the frequency of occurrence of each activity type differed according to the part of day (24-h period) it was recorded. Peaks of activity suggested that jackals synchronised their activity with the activity of their animal prey, and the relative inactivity of their major predator (man) as field observations revealed. The apparent persecution of jackals by farmers in the surrounding areas could account for the enhanced vigilance behaviour of the former. There was a seasonal change in the general activity periods of jackals at MNR and this was probably for

thermoregulatory purposes. Total activity was more pronounced for winter (27.2%), followed by spring (21.7%) and autumn (20.8%). The two summers (1995-96 and 1996-97) revealed similar proportions of total jackal activity.

Home-range size was determined through radio-tracking of known individuals, and the programme CALHOME (Kie et al., 1994) was used to analyse range-size using the minimum convex polygon (MCP) method (Mohr, 1947). The mean aggregate home-range size for the 3 radio-collared animals was 15.9 km^2. Seasonal home-range sizes differed between seasons with a tendency for range expansion during the dry winter months. Mean seasonal home-range size was also highest for the winter period (20 km^2). On the basis of social organisation (Rowe-Rowe, 1982) and the mean of the minimum seasonal home-range estimate of 8.2 km^2 it is suggested that MNR supports a jackal population of at least 13 individuals - a density of 0.4 jackals/km^2. The overall seasonal density estimates based on nightlighting sessions (Meia & Weber, 1992, 1996) lay between 0.1 and 1.8 individuals per km^2.

Black-backed jackals in MNR utilised wooded cover for denning, predator avoidance, and foraging purposes. They did not use habitats according to their proportional availability in any season. In all seasons jackals used open savanna grassland, Croton/Combretum tree savanna, and seasonal floodplains less than expected from their availability, and used tree and bush savanna, semisweet mixed bushveld and agricultural areas much more than expected, the latter increasingly so during the spring and summer months. Agricultural areas were used more than expected during both the 1995/96 and 1996/97 summer seasons, and less than expected during the intervening autumn, winter and spring seasons.

More jackals were killed by trapping and hunting outside of their home ranges than along the periphery and no residents were killed within their respective home ranges. This suggests that young dispersing jackals may be more susceptible to hunting than resident jackals because they are away from familiar terrain. However, avoidance of roads and

hunters during daylight hours are learned responses, and younger jackals may be more susceptible to hunting primarily in early autumn. Vulnerability may be more a function of lack of experience rather than unfamiliarity with the surrounding territory (Roy & Dorrance, 1985). Extra-territorial excursions were commonly witnessed in this study area particularly those directed towards the surrounding farming areas and human settlements. Food stress upon groups entailed hazardous extraterritorial movements and may have caused some human-related deaths (i.e. concealed natural mortality). Possibly, human-caused mortality altered group dynamics of some families but not sufficiently to invalidate the description of jackal social organisation discussed in the present study.

In the family pairs of jackals observed in the present study, the home ranges of individuals did not overlap totally, but corresponded more closely to the situations observed by Ferguson et al., (1983) who noted that subordinate individuals only use a small part of the group range. There was no overlap between the ranges of adjacent pairs, but it appeared that jackals entered the range of adjacent groups to access some rich feeding patches such as anthropogenic food sources and carcasses.

Foraging Ecology

Potential animal and plant food available to jackals varied throughout the year because of its seasonal character. Jackals were observed foraging during 37.1% of 786 hours of focal animal observations (including 62.9% of those in which the jackal was foraging when the observation began) and opportunistically in many other instances. It is quite evident that jackals strayed from their territories to devour fresh kills or carrion elsewhere. Hunting accounted for 76.0% (n = 355) of all foraging observations. Scavenging was observed 43 (9.2%) times, while gathering accounted for 14.8% (n = 69) of all feeding observations. Jackals were observed attempting to kill prey on 355 occasions, successfully killing and eating prey on 101 (28.5%) occasions. Of all feeding instances, 21.1 % were kills of rodents. Catches of rodents accounted for 36.6% (n = 45) of all successful hunting attempts.

During the calving/lambing season of ungulates, pairs of jackals could be seen moving among the females presumably inspecting them for signs of lambing. Jackals at MNR fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In addition, concealed lambs were killed by pairs of jackals searching through impala lambing grounds, probably using olfactory cues. Impala lambs were captured due to total exhaustion after persistent attacks, by being bitten under the neck, and then persisting with the pressure. Mostly, the jackals waited until the female had given birth and then worked as a team; one of the pair distracting the female, while the other attacked the young. However, attacks on parturient impala dams were also documented. Frequently, only lamb remains in the form of uneaten portions of legs were found. Most causes of lamb mortality were difficult to determine in MNR because remains of lambs (when there were any) were located a long time after the lamb's death and were badly mangled and had begun to decompose. Jackal predation on neonatal impala as well as on yearlings and emaciated or senile adults, indicates jackal potential to limit impala population increase in MNR, particularly through natal recruitment, but this merits further investigation. At a conservative estimate, overall, at least half of the annual calf crop fell prey to jackals during the 1996/97 lambing period alone. The number of impala lambs that succumbed to jackal predation therefore constitutes a significant proportion of the impala population, and in conjunction with other natal and adult mortality factors, can considerably limit, or even depress population levels.

Furthermore, scat analysis revealed that mammals were the most common food resource (32.4%, n = 518), followed by anthropogenic items (14.8%), fruits (12.9%), invertebrates (10.8%), birds (8.5%), unidentified items (3.5%), and reptiles (1.4%). Jackals changed their diets when prey species became vulnerable to predation. For example, impala lambs were most vulnerable when less than two weeks old. Jackals took advantage of this vulnerability, as field observations suggested. Seasonality of prey occurrence in scats was pronounced for small mammals, miscellaneous fruits and invertebrates: Small mammals (mostly rodents) were more frequently eaten in the dry season and fruits during the wet season.

Because little to no detailed information is available on the interrelationships between jackals and prey prior to the increase in modern man's influence on wildlife and habitats, the

character of that relationship under pristine conditions remains to a large degree speculatory. As human encroachment and agriculture continue to reduce wildlife habitat in Botswana and much of sub-Saharan Africa, management decisions must be founded on a precise understanding of wildlife ecology and population dynamics. In particular, one important aspect of ungulate ecology is the extent and causes of lamb mortality. Although it is usually impractical to eliminate or even reduce the major factors in lamb mortality, an understanding of these factors is necessary to further our understanding of herd dynamics and improve the predictive capabilities of wildlife managers (Kunkel & Mech, 1994). Although the general effects of predation on ungulate populations are difficult to assess without intensive studies, monitoring prey with radio telemetry is a more direct method of measuring losses to predation. Collaring dams and lambs for prompt relocations of dead and live animals as indicated by radio signals (mortality sensors) can provide better tally of losses to predation or other mortality factors, thus improving diagnostic opportunities.

Jackal foraging ecology reflects the availability of a wide variety of food items and the differential vulnerability of prey. Given the addition of anthropogenic food resources and altered habitats in human settlements, black-backed jackals' diet at MNR was more diverse and differed from that reported in relatively undeveloped areas (Wyman, 1967; Hall-Martin & Botha, 1980; Smithers, 1971; Lamprecht, 1978a; Rowe-Rowe, 1983). Direct observational data and scat analysis reported here indicate that jackals are opportunistic feeders, that eat carrion as well as practically any animal they can easily overpower. Jackals are highly adaptable animals being able to exist as predators on small game and livestock, scavengers, eat insects or rodents, and as indicated in the present study, also feed on anthropogenic food sources, wild fruits and agricultural crops. The relative importance of scavenging and predation in the lives of jackals varies according to both time and place. Where pure predators and their prey are plentiful, jackals may live largely as scavengers if they themselves are not too numerous to engage in intraspecific competition (Estes, 1967). Where pure predators are scarce, as is the case in MNR, jackals become very active hunters; in fact they have been implicated to even partially fill a pure predator's vacated niche. Like other predators, jackals behave so as to maximise their fitness, which is often done by maximising their net energy intake. In fact, a predator's prey choice is not only a consequence of prey energy content, but

it also depends on the predator's success in finding, handling, and consuming its prey. Other studies on jackals' diet have revealed similar feeding behaviour (e.g. Wyman, 1967; Bothma, 1971; Smithers, 1971; Rowe-Rowe, 1976), albeit with some deviations from the findings of the present study.

Social Behaviour and Organisation

Direct observations revealed that there was little evidence of jackal groups and I believe social structure in MNR mostly comprised solitary residents, transients, and members of resident pairs. Jackal groups were uncommon probably because of heavy persecution by humans and a food base independent of large prey. Hunting of jackals by man may depress group sizes both directly and by creating vacant territories and so reducing the costs of dispersal. Seasonal variation was also observed in the number of single animals, two's, and groups of 3 to 4 individuals. Seasonal differences were quite pronounced for single animals and groups of two, and followed a pattern that was related to reproduction and social behaviour. Family groups usually consisted of two parents and from 1 to 3 young. Most sightings of single animals were recorded during autumn. Pairs were most numerous in winter and this was probably the pairing-mating season, as the first cubs were seen during August-September

Social encounters within pairs or family groups included social grooming, play fighting, and running play. Intra-group aggression was in connection with incidents involving ano-genital sniffing of females by males, and sometimes some attempts at mounting. The social status of helpers was always submissive with respect to the parents, and these subordinates did assist their same-sex parents in territorial defence against same-sex conspecific intruders. 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, and between two strange males. Encounters between neighbours were less aggressive than between apparently strange groups.

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 adjacent pairs; 3) frequent inter-group boundary chases and clashes; 4) scent marking behaviour; and, 5) vocalisations. 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 whelping and rearing of pups (breeding dens).

Finally, the importance of understanding jackal social behaviour and organisation in the epidemiology of jackal rabies is also underscored. Furthermore, conservation and management options are discussed in relation to their likely impact on jackal behavioural ecology, effects on the ecology of other species, and the role of the human dimension. Broadcast killing of jackals clearly is of limited value in the long-term. And the paradox remains - that an attempt to reduce jackal impact through reducing numbers may so disrupt the jackals' social milieu, by creating vacua and promoting movement - and this could theoretically increase jackal impact even at lowered densities. Some recommendations and suggestions are then offered for a holistic approach to the conservation and management of predator populations.

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Mokolodi Nature Reserve

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