Prey selection and use of natural and man-made barriers by African wild dogs while hunting

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The hunting patterns of a pack of African wild dogs (*Lycaon pictus*) were monitored on an 8356 ha reserve in the Waterberg Mountains, Limpopo Province, South Africa. Some members of the pack were radio-collared and the dogs were followed daily by researchers from April 2002 to January 2003. Prey selection and the use of barriers during the wild dogs' hunts were studied. Barriers were defined as objects such as game fences, flowing rivers and dams, which impeded a fleeing prey animal's escape. Kudu (*Tragelaphus strepsiceros*) comprised the majority (60%) of the dogs' kills, although they made up only 14% of the total prey items available to the dogs. Wild dogs in the reserve made 81% of their kills within 20 m of a barrier, although these 20 m zones made up only 1.7% of the total area available to the dogs in the reserve. Being able to factor the use of barriers into their hunts could explain the preponderance of large prey in their diet. Because wild dogs make most of their kills near or at barriers, there are important management implications of having wild dogs in small reserves. These include ensuring that fences are sturdy and monitored for damage which might occur during hunts. The ability of wild dogs to successfully target the larger prey animals may also have an effect on the carnivore/prey balance and should be monitored carefully.

Key words: African wild dogs, prey selection, barriers.

INTRODUCTION

Most studies on the hunting behaviour of wild dogs *Lycaon pictus* have been carried out in large conservation areas (e.g. Mills & Gorman 1997; Andreka *et al.* 1999; Krüger *et al.* 1999). With a trend towards smaller (less than 100 km^2), privately owned reserves introducing wild dogs, it is interesting and informative to consider the prey selection and hunting success of wild dogs within these small reserves.

Wild dogs typically use stamina to run down their prey, which is usually caught after a chase lasting 50 m to 4.6 km (Creel & Creel 1995). In large reserves, the wild dogs' stamina and the prey item's exhaustion are usually the cause of successful hunts. In small reserves, game fences and other barriers such as waterholes and dams would be encountered more often during a chase than they would in large reserves, due simply to factors of scale. If an impenetrable barrier occurs in the path of the fleeing prey, the dogs are able to surround the animal and begin the kill, often before prey is exhausted.

The aim of this study was to monitor the hunting techniques of wild dogs in a small reserve (<90 km^2), focusing on the species of prey selected, and whether the animal was impeded by a barrier. Prey selection is compared with results from other studies. Reich's (1981) postulation (in Krüger *et al.* 1999) that wild dogs adjust prey selection in relation to ease of capture is also considered.

MATERIALS AND METHODS

Study site

This study was conducted at Shambala Private Game Reserve (24°15′45″S–24°22′50″S, 27°54′55″E–28°02′30″E), Limpopo Province, South Africa. Shambala Private Reserve is 8719.8 ha in extent. Of this, 363.5 ha is fenced off for animal breeding, reducing the effective reserve area to 8356.3 ha. The 2.4 m high outer perimeter and breeding camp fences are electrified and regularly maintained. The average annual rainfall is 580 mm and falls primarily in summer. Mean daily temperatures range from a maximum of 30°C during December to a minimum of 1.7°C for July (Bredenkamp & Brown 2000). The area is representative of Acocks' (1988) Sour Bushveld and is dominated

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Table 1. Number and proportion of potential prey animals available to wild dogs, times encountered and contribution to actual kills.

Prey Species	Number and proportion of animals	(%)	Number and proportion of encounters[†]	(%)	Number and proportion of wild dog kills	(%)
Blesbok, *Damaliscus dorcas phillipsi*	50	(3.0)	1	(2.5)	2	(3.4)
Blue wildebeest, *Connochaetes taurinus*	221	(13.2)	8	(20)	3	(5.3)
Buffalo, *Syncerus caffer*	2	(0.1)	0	(0)	0	(0)
Bushbuck, *Tragelaphus scriptus*	2	(0.1)	0	(0)	0	(0)
Bushpig, *Potamochoerus larvatus*	15	(0.9)	0	(0)	0	(0)
Common duiker, *Sylvicapra grimmia*	11	(0.7)	1	(2.5)	0	(0)
Common reedbuck, *Redunca arundinum*	20	(1.2)	0	(0)	0	(0)
Eland, *Taurotragus oryx*	77	(4.6)	4	(10)	0	(0)
Gemsbok, *Oryx gazella*	30	(1.8)	0	(0)	0	(0)
Impala, *Aepyceros melampus*	540	(32.3)	4	(10)	7	(12.3)
Klipspringer, *Oreotragus oreotragus*	10	(0.6)	0	(0)	0	(0)
Kudu, *Tragelaphus strepsiceros*	225	(13.5)	6	(15)	34	(59.6)
Livingstone's eland, *Taurotragus oryx*	22	(1.3)	0	(0)	0	(0)
Mountain reedbuck, *Redunca fulvorufula*	5	(0.3)	0	(0)	0	(0)
Nyala, *Tragelaphus angasii*	15	(0.9)	0	(0)	1	(1.8)
Ostrich, *Struthio camelus*	2	(0.1)	0	(0)	0	(0)
Red hartebeest, *Alcelaphus buselaphus*	8	(0.5)	1	(2.5)	0	(0)
Steenbok, *Raphicerus campestris*	6	(0.4)	0	(0)	0	(0)
Tsessebe, *Damaliscus lunatus*	4	(0.2)	1	(2.5)	0	(0)
Warthog, *Phacochoerus aethiopicus*	120	(7.2)	8	(20)	6	(10.5)
Waterbuck, *Kobus ellipsiprymnus*	50	(3.0)	2	(5)	3	(5.3)
Zebra, *Equus burchellii*	235	(14.1)	4	(10)	0	(0)
Unknown[‡]	–	–	–	–	1	(1.8)
Total	1670	100.0	40	(100)	59	(100)

*Potential wild dog prey excludes white and black rhino, giraffe, and other species not hunted by wild dogs. All buffalo, sable, tsessebe and other herbivores kept in predator-exclusive camps were excluded from analysis.

[†]'Encounters' include only those instances during which the wild dog chased or hunted (not necessarily killed) the animal. The list includes only those hunts observed by researchers, and therefore excludes those animals found killed by the dogs (unless the hunt and the kill were witnessed by researchers).

[‡]'Unknown' animals include those where a kill site was found but insufficient body parts remained for identification to be made.

by open woodlands. The terrain comprises a complex of rocky ridges, the southern areas at a slightly higher altitude than the northern parts. The western half of the reserve is characterized by extremely hilly and rocky terrain. The eastern half is lower-lying and flatter.

Over 1500 mammalian herbivores roam the property, ranging in size from small (klipspringer, *Oreotragus oreotragus*) to large (elephant, *Loxodonta africana*). Table 1 lists those prey species available to the wild dogs at the time of this study. No data on age distributions or sex ratios were available. After spending two months in a release facility, seven wild dogs were released onto the property at the end of April 2002. Ten pups were born in May 2002, of which five survived to the end of January 2003. Other predators on the property included seven lions, four spotted hyenas, an unknown number of leopards and brown hyenas and four cheetah, as well as smaller species such as caracal, African wild cat and black-backed jackal.

Wild dog monitoring

At the beginning of March 2002, three members (the alpha male and female, and another adult female) of the wild dog pack were fitted with conventional radio-collars. There appeared to be no adverse effects of the radio-collars on dog behaviour, and the collared dogs were observed to interact and hunt successfully with the rest of the pack.

Between April 2002 and mid-January 2003, the dogs were tracked on a daily basis using a portable hand-held antenna. A vehicle was used to follow the dogs as far as possible. If no sighting was obtained, the dogs were located on foot. Monitoring of the dogs was based on the assumption of a bimodal pattern of activity exhibited by wild dogs (Fuller & Kat 1990), with intensive monitoring conducted during the early morning and late afternoon when the dogs were most active. Physical constraints prevented night monitoring, though wild dogs are reported to rarely hunt at night in woody habitats (Creel & Creel 1995). Van Dyk & Slotow (2003), in their studies on wild dogs in the Pilansberg National Park, never detected active dogs at night.

Wild dog sightings by researchers (95% of sightings) were supplemented by reports from game scouts (5% of sightings). Game scout sightings were limited to regions close to the boundary fences along which they conducted their daily patrols. These reports were followed up by the researchers to verify the details. The rough terrain of the reserve and highly mobile nature of the wild dogs precluded data collection on occasion. The wild dogs were viewed 314 times during the study period, and a further 45 Global Positioning System (GPS) distribution points were taken based on strong telemetry signal, when visibility was made impossible due to the terrain. At each sighting of the wild dogs, their GPS location, kills, activities and interactions (both intra- and interspecific) were recorded. If dogs were found resting or eating, a single GPS point was taken to mark their position. If dogs were found on the move, two GPS points were taken to indicate the starting and ending points of their movement during the day's study period. Hence, there are more GPS points indicating wild dog position than days of actual study. The area surrounding the den site of the wild dogs is perhaps over-represented in the distribution data set for the dogs as the adults were hesitant to hunt too far from the den site and spent most of their time in a limited area. After the pups became mobile, the area where the dogs raised their youngsters was still favoured for hunting and was visited frequently over the months.

The percentage of all found wild dog kills of different animal species was calculated. This percentage was then compared, using the Chi-square test, with the percentage of the total herbivore population made up by each species. Game numbers were based on the most recent game count (March 2001) conducted at Shambala, supplemented with known information on births and deaths. Data may be biased in that smaller species and young prey animals killed by the wild dogs are less likely to be found by researchers than large kills. This is due to small kills being more difficult to see than larger ones, and larger prey items taking longer to be devoured, increasing the likelihood of seeing the dogs on the kill. The number of small kills may therefore be underestimated. It is likely that the dogs killed at least twice as many times as that recorded for this study. For this comparison, only those herbivore species considered to be potential wild dog prey items were considered. White rhinos (*Ceratotherium simum*), elephants (*Loxodonta africana*), hippopotamuses (*Hippopotamus amphibius*) and giraffes (*Giraffa camelopardalis*) were excluded. Those species actually observed to be encountered most often by the wild dogs while out hunting were also compared to the percentage of kills for each prey species. On a number of occasions, the dogs were found only once they had already made a kill. In these instances, it was not possible to record which species the dogs had encountered during their hunts. For this reason, the number of observed 'encounters' is often less than the number of kills for certain species.

Barriers

In this study, a barrier is defined as any large obstruction or object impeding the escape or efficient movement of a fleeing prey item, namely game fences, flowing rivers, cliffs, large waterholes and hutted camps. All of these barriers (game fences in particular) impede a prey item's escape to such an extent that the wild dogs could surround them and gain easy access to their hindquarters. Creel & Creel (1995) noted that prey items are killed by disemboweling, and our observations support this. In order to disembowel a large animal, the wild dogs generally waited for the animals to slow down or stop (being unable to 'tackle' larger animals), and for this reason the barriers seemed particularly effective in aiding the wild dogs' killing technique in this reserve.

The zone of influence of a barrier was defined as being any area within 20 m of that barrier. This value was decided arbitrarily, but after repeated observation, we propose that within 20 m of a barrier, an animal would be aware of the barrier, and its escape route effectively blocked off or strongly impeded. The animal would be slowed down or stopped, making it easier for the dogs to close off all other avenues of escape, and get an opportunity to grasp it. Further than 20 m from the

Table 2. Chi-square results of prey selection by wild dogs (d.f. = 21).

Species	Observed number of kills	Expected number of kills based on proportion of prey species available	Chi-square value
Blesbok	2	1.71	0.0492 NS
Blue wildebeest	3	7.52	2.7168 NS
Buffalo	0	0.06	0.6000 NS
Bushbuck	0	0.06	0.6000 NS
Bushpig	0	0.51	0.5100 NS
Common duiker	0	0.40	0.4000 NS
Common reedbuck	0	0.68	0.6800 NS
Eland	0	2.62	2.6200 NS
Gemsbok	0	1.03	1.0300 NS
Impala	7	18.41	7.0716 NS
Klipspringer	0	0.34	0.3400 NS
Kudu	34	7.70	89.8299 **
Livingstone's eland	0	0.74	0.7400 NS
Mountain reedbuck	0	0.14	0.1400 NS
Nyala	1	0.51	0.4708 NS
Ostrich	0	0.06	0.0600 NS
Red hartebeest	0	0.29	0.2900 NS
Steenbok	0	0.23	0.2300 NS
Tsessebe	0	0.11	0.1100 NS
Warthog	6	4.10	0.8805 NS
Waterbuck	3	1.71	0.9732 NS
Zebra	0	8.04	8.0400 NS

**$P < 0.001$.

barrier, prey would have greater manoeuvrability and more room to escape. Each recorded wild dog kill was thus examined and its distance from a barrier recorded; if this distance was less than 20 m, the kill was recorded as having been influenced by the barrier.

Again, a simple percentage was calculated, to determine what proportion of the wild dogs' kills at Shambala Private Reserve were made in close proximity to a barrier. Two maps were constructed (Fig. 1a,b). The first (Fig. 1a) plotted the wild dogs' distribution within the reserve during the study period, as well as the position of the known barriers. The second (Fig. 1b) superimposed wild dog kill sites on a plan of all known barriers on the reserve. Of the total area of the reserve available to the wild dogs, the percentage falling within 20 m of a barrier was calculated. The number of kills recorded at or near barriers may be biased due to daily patrols by the game guards along the fences, and cleared vegetation around the reserve's perimeter. This could inflate the number of kills found along the fences in comparison to those found in the more densely vegetated, less frequently patrolled interior.

RESULTS

Prey selection

Of those prey items killed by the wild dogs, 60% were kudu. Kudu made up only 14% of the total number of animals available to the dogs (Table 1). Significantly more kudu were killed by the wild dogs than expected (Table 2), based on the proportion of prey species available.

At Shambala Private Reserve, smaller species such as impala (*Aepyceros melampus*), blesbok (*Damaliscus dorcas phillipsii*), nyala (*Tragelaphus angasii*), mountain reedbuck (*Pelea capreolus*), common reedbuck (*Redunca arundinum*), bush buck (*Tragelaphus scriptus*), steenbok (*Raphicerus campestris*) and grey duiker (*Sylivicarpa grimmia*) were not killed by wild dogs significantly less than expected (Table 2). They made up more than 38% of available prey, yet together constituted only 18% of the diet of the wild dogs during the study period (Table 1). As previously mentioned, it is possible that kills of these smaller prey items were found less often than larger species, due to both ease of sighting and the wild dogs spending longer at larger kills. The proportion of

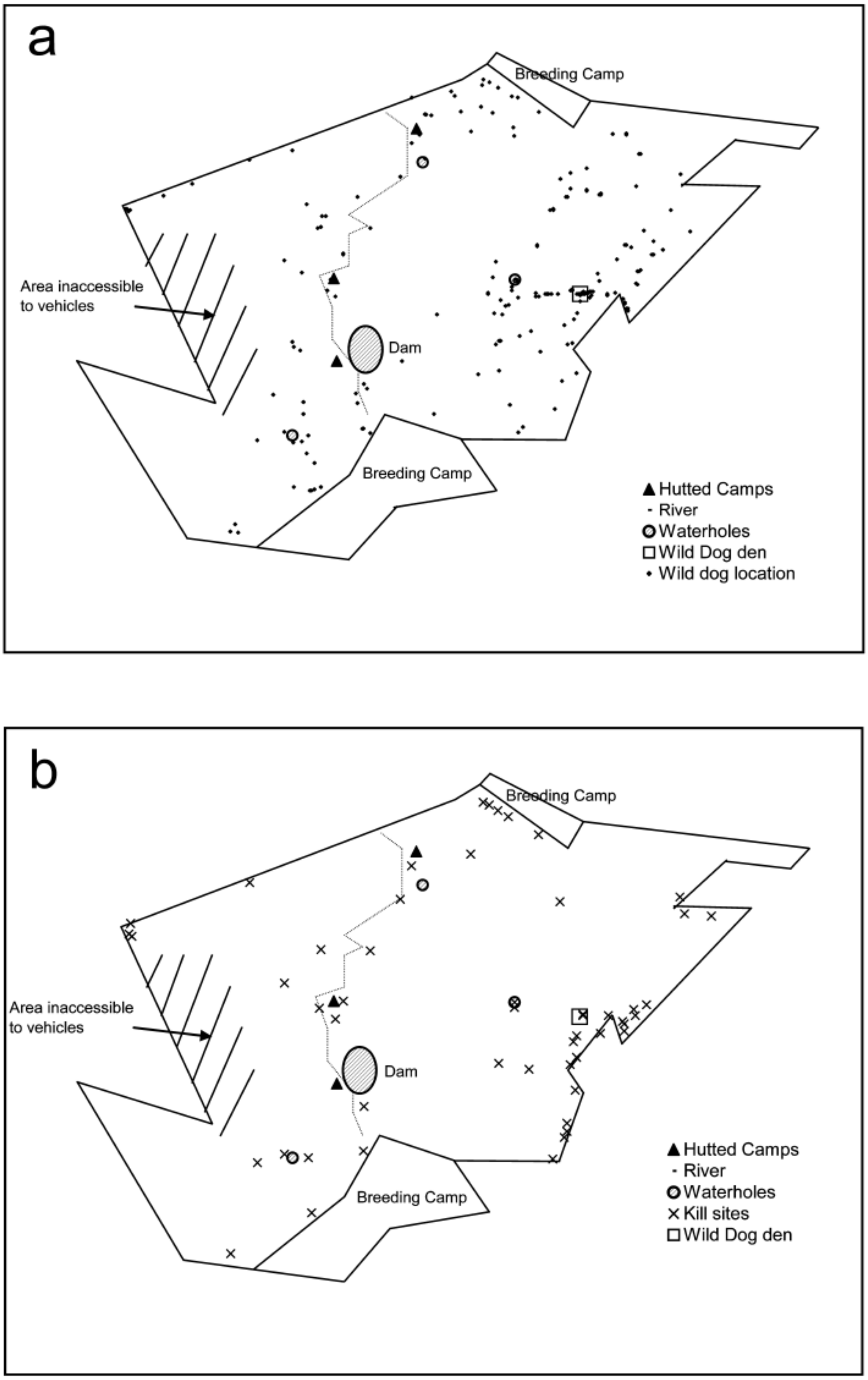

Fig. 1. Map depicting (**a**) the location of the wild dog pack during the study period (n = 359) and (**b**) the location of all recorded kills (n = 57).

Table 3. Number of animals killed by wild dogs at different barrier types.

Species	Barrier type					
	Game fence	Flowing river	Cliffs	Large waterholes and dam	Hutted camps	Open
Blesbok	2					
Blue wildebeest	1	1		1		
Nyala						1
Impala	6			1		
Kudu	23	1	1	1	2	6
Warthog	1			1		4
Waterbuck	3					
Unknown					1	
Total	36	2	1	4	3	11

blue wildebeest killed by the wild dogs was also lower than the proportion (13%) available to the dogs, yet was not statistically significant (Table 3).

Although 60% of the wild dogs' kills were kudu (Fig. 1), the dogs were only observed to encounter kudu 15% of the time (Table 1). Conversely, blue wildebeest, eland, warthog and zebra, species which together constituted only 16% of the wild dogs' kills (Fig. 1) were encountered 60% of the time (Table 1). A total of 16 species were actively hunted (though not necessarily killed) by the dogs.

The smaller species such as impala, nyala, bushbuck and duiker, which are often preferred by wild dogs (Krüger *et al.* 1999), constituted only 14% of the dogs' total diet (Table 1) at Shambala.

The use of barriers

The wild dogs exploited the entire reserve for hunting (Fig. 1), traversing most habitat types within a week. Of the total reserve area available to the wild dogs, approximately 141 ha, or 1.7%, fell within 20 m of a barrier. More than 80% (Fig. 1; Table 3) of all wild dog kills during the study period were made within these areas, with only eleven (19%) of the 57 kills found, made away from a barrier. Only warthog and nyala were caught more frequently without the use of barriers. Of the barriers encountered by wild dogs during hunts, fences play a substantially larger role in hunting success than do other barriers (Table 3).

As previously mentioned, kills made near barriers – especially fences – could have been found more easily than those made on the interior of the reserve, resulting in biased data. With more than 50 km of fenceline available to the dogs as an aid in hunting, they made use of only a fraction of this (±15% of the fenceline) to initiate most (>63%) of their kills (Fig. 1; Table 3).

DISCUSSION

There are three important factors to consider when analysing prey selection. These are: i) the proportion that each species contributes to the total number of suitable prey, ii) the number of times they were encountered and chased, and iii) their contribution to the diet of the wild dogs.

If wild dog hunts were random, one would expect the most common animal species to be encountered more often than others and therefore contribute more to their diet. This was not the case. Although other species were encountered more than kudu during hunting excursions, the dogs did not 'target' them as intensely. The dogs killed significantly more kudu than would be expected (χ^2 = 89.83, d.f. = 21, $P < 0.001$), based on available numbers. For all other species considered in this study, the difference between observed and expected kill numbers was not significant (Table 2).

Krüger *et al.* (1999) also found that wild dogs pursued warthog, blue wildebeest and zebra less successfully than other species. Wild dogs are rate maximizers, selecting their prey in a way that maximizes their long-term rate of energy intake and therefore including prey types in their diet according to their profitability (Krüger *et al.* 1999). Species such as warthog, blue wildebeest and zebra, which are characteristic of grasslands and open woodlands, are not profitable in terms of ease of capture (Krüger *et al.* 1999). A foraging model designed by Krüger *et al.* (1999) predicted habitat-related differences in the diet of wild dogs with nyala, red duiker and bushbuck (closed woodland species) being the most profitable species to hunt. This model could apply to the Shambala wild dog pack where of the closed woodland prey species, kudu were the most abundant (Table 1).

In most feeding studies of wild dogs, the most abundant, local medium-sized to large prey species dominate in the diet (Ginsberg & MacDonald 1990). For example, impala and kudu in the Kruger National Park, South Africa (Mills 1992), Thomson's gazelle and blue wildebeest in the Serengeti, Tanzania (Frame 1986) and nyala and impala in Hluhluwe-Umfolozi Park, South Africa (Krüger *et al.* 1999). This is the case in Shambala where kudu and impala dominate the wild dogs' diet. However, the proportion of kudu in the diet is unexpectedly high (more than four times that of impala), considering the number of times that they were encountered by the dogs. This indicates that the number of kudu eaten was not simply due to the dogs encountering them more often than other species. It could signify dietary preference by the wild dogs at Shambala, similar to what was recorded in Pilansberg National Park, possibly due to increased food demand brought about by growing pups (Van Dyk & Slotow 2003). The use of fences and other barriers by wild dogs as an aid in hunting may also have allowed them to target, and regularly catch, large prey.

The possibility that the wild dogs adjusted prey selection in relation to ease of capture – as postulated by Reich (1981, in Kruger *et al.* 1999) – is a consideration in a reserve such as this where boundaries were often encountered during hunts. Another study has shown that where wild dogs make use of fences and other such barriers for hunting, larger prey species are captured (Van Dyk & Slotow 2003). The ability to catch and kill large prey species with the aid of barriers may contribute to the rate-maximizing hunting strategy employed by wild dogs (Krüger *et al.* 1999), allowing them to maximize their rate of energy intake (by killing a larger animal) without expending as much energy on killing it (due to a shorter chase).

The use of barriers

Though the wild dogs made use of most habitat types during any week, the location of their kills in relation to barriers suggests that their hunting strategy was not random. Although the dogs hunted across the entire reserve, the majority of their kills were made near a few particular barriers. It is unclear why the wild dogs made use of these particular areas; no pattern emerges readily. They appeared to use some corners of the fence repeatedly, but not others. This may be as a consequence of the dogs exploiting these particular barriers for hunting or that animals considered the path towards the barrier as a useful option for escape. Van Dyk & Slotow (2003) also found that wild dogs made preferential use of certain sectors of the Pilansberg National Park fence, when hunting.

With 81% (Fig. 1) of the wild dog kills made within the 20 m zone of various barriers within Shambala Private Reserve, it would seem that barriers play a major role in the hunting success of these carnivores. Whether the dogs actively sought to make use of the barriers during hunting, and directed fleeing prey in the direction of barriers, or whether the small reserve size, coupled with the wild dogs' typically long-distance pursuit of prey, caused a large number of chance interceptions with barriers, is debatable. A disproportionately large percentage of kills occurring close to barriers and fences suggests that the dogs actively sought out these obstacles as hunting aids. Certain areas, especially along game fences, were used more often than others. Examples of favourable kill sites being used more than once lend further weight to this argument: at a ninety-degree corner in the game fence, where a fleeing animal's path would be blocked in two directions, three adult male kudu were killed within metres of each other over a two-month period. In all three cases, it was apparent that the kudu had jumped against the fence and then been killed within metres of the wire. We also observed a hunt near the fenceline where ten of the pack members disappeared into the bush and left the alpha female on the fenceline; a wildebeest was flushed out of the bush and she headed it off, helped soon by the rest of the pack. Observations such as these suggest that the wild dogs actively choose to make use of the barriers while hunting. The overall technique and hunting success of the wild dogs indicate strongly that the dogs prefer hunting kudu, using the numerous barriers afforded in the reserve to help bring down these large and potentially dangerous animals. A kudu was seen being killed by the dogs while its horns were caught up in the game fence, making it easier and safer for the predators to kill their prey. Future studies are necessary to ascertain whether barriers enable wild dogs to catch prey more easily and expend less energy than if they were to catch the same animal through stamina alone. However, from personal observations it would appear that barriers enable the dogs to conduct more energy-efficient hunts.

As noted by Reich (1981, cited in Krüger *et al.* 1999), wild dogs are expected to adjust prey selection in relation to ease of capture, and are unlikely to consider all members of a species of equal profitability under all circumstances. It seems that in Shambala, the wild dogs have adjusted their prey selection, often choosing larger prey such as kudu over smaller prey, due to increased ease of capture in this small reserve. This corroborates other findings that wild dogs are rate maximizers, choosing larger prey when it is made easier to do so (Krüger *et al.* 1999).

The hunting techniques employed by the wild dogs at Shambala Private Reserve, coupled with a small reserve size, suggests that a specialized hunting technique, similar to that of wild dogs in Pilansberg National Park (van Dyk & Slotow 2003) has been developed by the dogs in this reserve. It is also possible, then, that wild dogs in other small reserves could make use of similar techniques to best exploit their environment. The use of barriers by wild dogs at Shambala Game Reserve has practical implications for reserve management. First, strong and efficient game fences are vital if one is to contain wild dogs. If fences are not sturdy enough, large prey items such as kudu are liable to knock them down while fleeing, allowing the wild dogs (and possibly other game) to escape. Fences should be regularly checked to ensure integrity, as repeated hunts ending in a similar area could weaken the fence. Second, herbivore population dynamics could also be affected if the wild dogs utilize the prey species in a pattern inconsistent with that expected (and planned for) by reserve managers.

CONCLUSION

This study provides evidence that prey selection of wild dogs is unrelated to the proportion of each species in the total population. The ability of dogs to 'target' certain species such as kudu may be aided by the use of barriers in hunting, accounting for a large proportion of kills (81%) being made near these barriers. The dogs may have learnt to use barriers to increase the likelihood of killing larger, potentially dangerous animals such as blue wildebeest and kudu. These results have important management implications, especially on small reserves where the effect of wild dogs on herbivore population dynamics and fence integrity needs to be monitored carefully.

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