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FEEDING ECOLOGY OF LEOPARDS (*PANTHERA PARDUS*) IN THE WESTERN SOUTPANSBERG, REPUBLIC OF SOUTH AFRICA, AS REVEALED BY SCAT ANALYSES

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Abstract. The feeding biology of leopards in the Lajuma Mountain Retreat (Soutpansberg), South Africa was examined by applying scat analysis. We investigated 179 scat samples for undigested hair of prey animals. Additional sources of information were other remains such as hooves, teeth, nails, and bones. Applying this technique we discovered 13 different species of prey – exclusively mammals. Two species of *Bovidae*, namely the bushbuck (*Tragelaphus scriptus*) and the common duiker (*Sylvicapra grimmia*), accounted for the majority of the leopard's prey. One primate, the vervet monkey (*Cercopithecus aethiops*), and the rock hyrax (*Procavia capensis*) were also a major component of the leopard's food. The share of rodents (Rodentia) was surprisingly small, especially if taken into account that they were abundant in the study area. Leopards showed a preference for middle-sized (20–70 kg) and small animals (5–20 kg).

Key words: *feeding ecology*, *leopard*, *prey spectrum*, *scat analysis*.

INTRODUCTION

Due to their ecological flexibility, leopards have survived in some areas in Africa and Asia that were depleted of other big carnivores long ago (Norton *et al.* 1986). With the exception of the driest deserts, leopards can still be found in the majority of protected areas in Africa, including our study site in the Western Soutpansberg (Sunquist & Sunquist 2002). These mountains probably contain one of the highest densities of leopards in South Africa (Stuart, pers. comm.). As the Soutpansberg's top-predator, leopards play an important ecological role. By keeping the abundance of potential prey below the carrying capacity of the ecosystem, this predator contributes to sustaining the ecological balance of the ecosystem.

Furthermore, the leopard represents an important economic factor. Ecotourism is widespread in the Soutpansberg, with leopards being a very popular photo subject for tourists. According to a recent survey, tourists are willing to spend the highest single amount of money on a leopard encounter (Nemangaya 2002). Scientific work is an important prerequisite for a proper local management of leopards, which are in turn of great importance for long-term sustainable ecotourism in the area.

In areas where leopards and cattle-breeding coincide, the analysis of feces can help to mitigate potential human-wildlife conflicts by giving clear and unbiased results concerning the killing of livestock. Analysis of feces allows the determination of possible prey preferences, which in turn might help to facilitate decision-making in relation to the reintroduction of prey species (Power 2002). By elucidating the prey range of leopards in the Soutpansberg we aimed to answer the following questions concerning their ecological and economical role: What species are taken by leopards? What is the leopard's preferred prey? Do leopards prey on livestock?

The feeding ecology of leopards can be studied by applying direct observation, radio-telemetry, documentation of kills, and the analysis of scats. Leopards prefer habitats with dense vegetation providing cover while hunting (Sunquist & Sunquist 2002). Combining this with the fact that they mostly hunt at night, direct observations of leopards are difficult to achieve. In addition, finding kills in a densely wooded area is problematic when vultures are absent, which in open areas indicate carcasses of big game (Bailey 1993). Data that are only based on kills are generally biased towards bigger prey, since smaller car-

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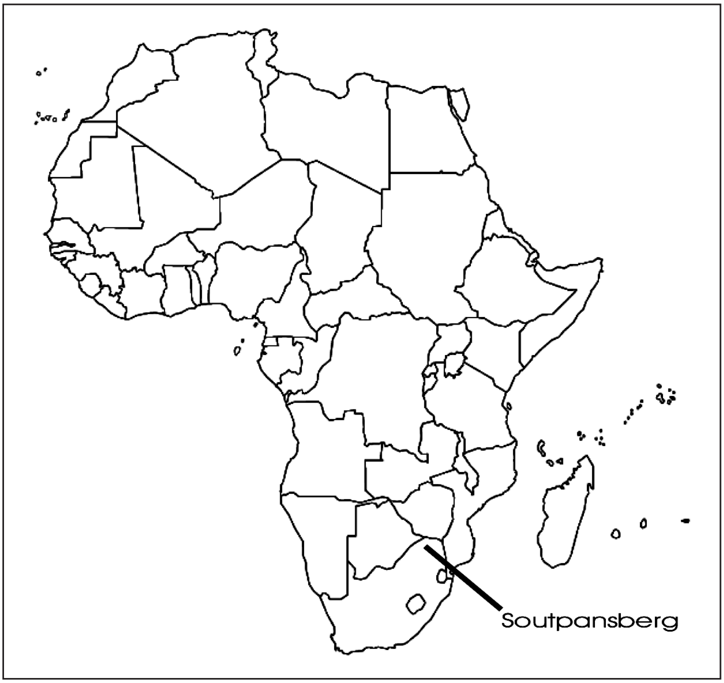

FIG. 1. Study area in South Africa.

casses are usually completely devoured, leaving no visible signs behind. Hence the application of radio-telemetry should not be used as the sole technique in investigating the feeding ecology of leopards, although this method enables researchers to track leopards feeding on large prey items (Bailey 1993).

The best alternative avoiding these problems is the analysis of feces. This 'hands-off technique' can be applied independently of the prevailing vegetation pattern, since leopards prefer dropping their feces on surfaced hiking trails or roads (Bodendorfer 1995). As vultures are not present in the area of our analysis, and large parts of the landscape are covered with dense bush or forests, and also no leopard could be supplied with a radio collar, priority was given to the analysis of scats for the research presented here.

STUDY SITE AND METHODS

The Soutpansberg is the northernmost mountain range in South Africa, located in the Northern Province. The mountains extend from 23°05'S, 29°17'W as far as 22°25'S and 31°20'W, stretching approximately 100 km from south to west. They are situated in the south of the Limpopo plain between the Kalahari in the west and the Kruger National Park in the east (Fig. 1). The peak Lajuma (1748m) is the highest point of this mountain range. The base of Lajuma lies 300 m above sea level. The Lajuma Mountain Retreat, measuring about 430 hectares, is sited in the western part of the Soutpansberg. It has an average annual rainfall of 700 mm. The altitude of Lajuma Mountain Retreat is between about 1200 m and 1748 m.

Collection of the feces. During a time period of four years (1999–2003), 179 feces of leopards were collected, dried, and kept in plastic bags for further analysis. The samples were mainly found and collected on surface hiking trails or roads. The single hiking trails were patrolled regularly (daily) in order to find new feces. According to Hoppe-Dominik (1981), leopard scats can be easily identified due to their diameter and weight as well as their smell and shape. In order to avoid confusion with scats of other predators, only feces with a diameter of at least 20 mm were included in the analysis. Confusion with feces of brown hyena (*Hyaena brunnea*) or caracal (*Felis caracal*) was ruled out by setting this minimum scat size as well as by the fact that hyenas defecate in special latrines. The absence of lions (*Panthera leo*) in the area allowed the inclusion of all larger feces in our investigation.

Characterization of leopard feces. Following the procedure described by Hoppe-Dominik (1981), the feces were sun-dried, followed by separation of organic components from other material for subsequent examinations. All hair, hooves, claws, teeth, nails, and bones were separated for the analysis. Feces were manually carefully cleaned and all prey remains relevant for identification isolated, while wearing rubber gloves and a face mask. Very hard scats could be broken up using a heavy tool with great care to avoid destroying prey remains. Hair and other significant material was cleaned, air-dried, completely separated from impurities, and stored in plastic bags. Three different hair types could be distinguished: bottom, sensory and kemp hair. Kemp hairs, that build a distinct layer and form the pelage of the animal were decisive for the analysis. Kemp hairs are characteristic in terms of color and shape for each species. Kemp hairs were separated from the bulk of other hair types. This work cycle was performed either with hair soaked in a bowl of water or with dry hair, which was less time-consuming. The characteristic kemp hair was examined using a binocular microscope. The identification was made using the characteristics typical for each species: coloring, shape, and band pattern. Other remains in the feces, like bones and teeth, were mainly used to identify the rock hyrax (*P. capensis*). Prey remains were determined by comparison with a reference collection book (Hoppe Domink, unpubl.) on animal hair of the Comoé National Park (Ivory Coast), by means of data from a M.Sc. thesis (Bodendorfer 1995), and by reference to hair samples collected in the study area. Only samples containing at least 10 kemp hairs per prey species were included in the analysis.

Quantification of the data. Prey contents can be calculated as relative frequencies, i.e., the frequency at which a certain item (f) is found in relation to the total number of items (R).

Relative frequency = number of items of one species / total number of items x 100. A conversion into biomass has been suggested by Floyd *et al.* (1978), but it is not advisable to conclude food intake directly from remains or from their relative frequency in the scats, since small animals have a proportionally larger skin surface. This would lead to an overestimation of small compared to large prey in the feces. In addition, small prey animals are more often devoured completely, which increases the excretion due to the higher intake of indigestible bone material compared with large prey animals. Floyd *et al.* (1978) carried out experiments with wolves (*Canis lupus*) and calculated an index to compensate for the discrepancy between the overrepresented small and underestimated larger prey animals. Although some studies used Floyd's index (Bodendorfer 1995), we preferred to use Ackerman's index in our analyses to calculate the share of biomass (Ackerman *et al.* 1984). This index was developed with cougar (*Felis concolor*) data and appear to be more adequate to our case:

$$\mathbf{Y} = 1.98 + 0.035\,\mathbf{X}$$

with **X** corresponding to the mean weight of the prey animal and **Y** to the intake of biomass in kg. The mass relation is shifted clearly to bigger prey, leading to more meaningful results.

According to Emmons (1987), a leopard weighing 50 kg consumes on average 2.125 kg meat per day leading to a total food intake of 776 kg meat per year. As about one third of the prey animal will be excreted as indigestible, a leopard has to hunt 1165 kg biomass per year in order to cover its nutritional demands. It has to be kept in mind that a predator produces significantly more feces when eating big prey animals even though the excretion rate of small prey animals is higher.

Food preference was based on prey species that are abundant in the Lajuma Mountain Retreat. The occurrence of these species in the study area was ranked by Prof. Dr. Ian Gaigher, based on more than a decade of experience on site from 1–12 (Table 3). The frequency of occurrence in the scats was also ranked. An index of preference was obtained by dividing the ranking in the environment by the ranking in the scats.

RESULTS

Relative frequency of the prey animals. In the 179 scat samples analyzed from the study area, a total of 13 mammal prey species could be detected. The three most abundant prey animals were the bushbuck (45.3 %), the common duiker (11.2 %), and the rock hyrax (11.2 %), which accounts for 67.7 % of the prey. Porcupine (0.6 %) and giant rat (0.6 %) could only be found in one single sample each (Table 1). The Artiodactyla accounted for 65.4 % of all prey animals. Primates had a share of 17.9 % and were the second largest group of prey. Hyraxes (Hyracoidea) made up 11.2 %, forming the third largest group. Rodents (Rodentia) made up a small portion, accounting for only

TABLE 1. Relative frequency of prey in leopard feces (n = 179) in the Lajuma Mountain Retreat, Soutpansberg, South Africa; (r) = scat containing this species, (r/n) = relative frequency.

Order/Family/Species	Number of scats	Percentage	(r)	(r/n)
Primates	32	17.9		
Samango monkey (*Cercopithecus mitis*)			2	1.1
Vervet monkey (*Cercopithecus aethiops*)			18	10.1
Baboon (*Papio cynocephalus ursinus*)			12	6.7
Lagomorpha	7	3.9		
Rock rabbit (*Pronolagus* sp.)			2	1.1
Cape hare (*Lepus capensis*)			5	2.8
Hyracoidea	20	11.2		
Rock hyrax (*Procavia capensis*)			20	11.2
Rodentia	3	1.7		
Giant rat (*Thryonomis swinderianus*)			1	0.6
Porcupine (*Hystrix africaeaustralis*)			1	0.6
unknown species			1	0.6
Artiodactyla	117	65.4		
Bushbuck (*Tragelaphus scriptus*)			81	45.3
Common duiker (*Sylvicapra grimmia*)			20	11.2
Red duiker (*Cephalophus natalensis*)			11	6.1
Bushpig (*Potamochoerus larvatus*)			5	2.8

1.7 % of the prey. By regrouping the prey species according to their size, it could be shown that it was 'middle-sized' species that were most often preyed upon by leopards (54.7 %). This group contains, e.g., bushbucks and baboons. The second place (25.1 %) is taken by the 'very small' prey animals like rock hyrax and vervet monkey. The 'small' prey animals, e.g., red and common duiker, were found third in place. According to our analysis porcupines and giant rats are rarely killed and eaten by leopards in the study area. There was no proof of 'big' prey animal remains like kudu (*Tragelaphus strepsiceros*) or domestic cattle

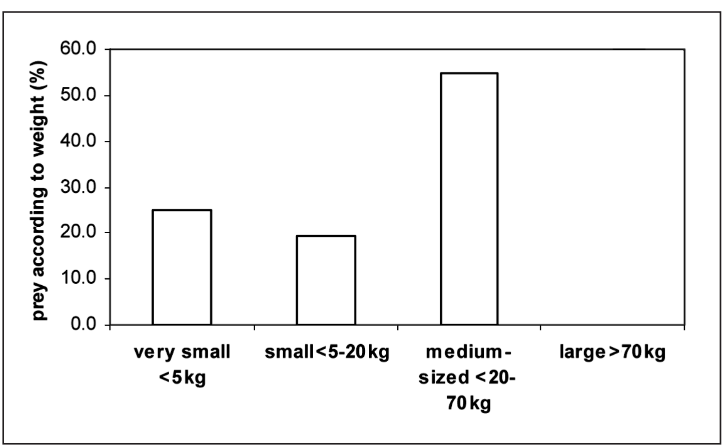

FIG. 2. Relative frequency of prey animals according to their size in the Lajuma Mountain Retreat, Soutpansberg, South Africa.

TABLE 2. Biomass and annual requirement of prey in the Lajuma Mountain Retreat, Soutpansberg, South Africa (undetermined rodents are not included) and presentation of the discrepancy between the relative frequency and the share of the biomass.

Species	Relative frequency (%)	Biomass (%)	Animals per year
Bushbuck (*Tragelaphus scriptus*)	45.3	52.7	16.4
Rock hyrax (*Procavia capensis*)	11.2	8.3	27.7
Common duiker (*Sylvicapra grimmia*)	11.2	10.5	6.3
Vervet monkey (*Cercopithecus aethiops*)	10.1	7.7	18.6
Baboon (*Papio cynocephalus ursinus*)	6.7	6.5	3.5
Red duiker (*Cephalophus natalensis*)	6.1	5.3	4.8
Bushpig (*Potamochoerus larvatus*)	2.8	4.3	0.7
Rock rabbit (*Pronolagus* sp.)	2.8	2	11.8
Cape hare (*Lepus capensis*)	1.1	0.8	4.3
Samango monkey (*Cercopithecus mitis*)	1.1	0.9	1.5
Porcupine (*Hystrix africaeaustralis*)	0.6	0.5	0.3
Giant rat (*Thryonomis swinderianus*)	0.6	0.4	0.8

in the samples, although they were present in the area (Fig. 2).

The amount of medium-sized and large prey animals were transferred, applying Ackerman's *et al.* (1984) calculation of biomass, resulting in an increase in their proportional share (Table 2). The percentage of the bushbuck, e.g., increases by 7.4% points, while the proportion of the rock hyrax is reduced by nearly 30% (from 11.2% to 8.3%). Calculating the annual demand of a leopard weighing approximately 50 kg leads to the following results: a leopard in the Lajuma Nature Retreat would kill about 28 rock hyraxes, 19 vervet monkeys, and 16 bushbucks annually.

Estimate of prey preference. Table 3 illustrates that leopards in the study might have a preference for bushbucks, common duiker, and vervet monkey. It also shows that other widespread species like porcupines or baboons are being taken less frequently.

TABLE 3. Preference of prey in the Lajuma Mountain Retreat, Soutpansberg, South Africa (giant rat and undetermined rodents are not included due to their low frequency); A = Rank in environment (Gaigher, unpublished data), B = Rank in scats, (A/B) = Preference index.

Species	A	B	(A/B)
Rock hyrax (*Procavia capensis*)	1	2.5	0.4
Bushbuck (*Tragelaphus scriptus*)	2	1	2
Baboon (*Papio cynocephalus ursinus*)	3	5	0.6
Porcupine (*Hystrix africaeaustralis*)	4	11	0.36
Common duiker (*Sylvicapra grimmia*)	5	2.5	2
Red duiker (*Cephalophus natalensis*)	6	6	1
Samango monkey (*Cercopithecus mitis*)	7	9.5	0.74
Vervet monkey (*Cercopithecus aethiops*)	8	4	2
Bushpig (*Potamochoerus larvatus*)	9	7.5	1.2
Rock rabbit (*Pronolagus* sp.)	10	9.5	1.05
Cape hare (*Lepus capensis*)	11	7.5	1.47

DISCUSSION

Methodology. The analysis of feces is a good alternative to direct observations in studying the feeding ecology of large carnivores. The Lajuma Mountain Retreat is widely covered with dense bush and forests, which hamper direct observations and the detection of kills. Feces sampling allows for comprehensive data collection, despite this vegetation pattern. However, applying feces analysis comprises other obstacles. Analyzing scats does not allow determining which prey has actually been killed, but only gives information about which animals have been ingested, including those that have been scavenged upon. While direct observations tend to over-represent bigger prey, the analysis of feces is biased towards small prey items. This problem can be overcome by applying the method of Floyd *et al.* (1987). The number of feces containing remains of small prey is greater than that of larger prey, because small species have a proportionately greater skin surface, leading to an increased excretion of feces. Although the application of Floyd's transfer partially overcomes this problem it is rarely used (Bailey 1993). Hence, we would like to strongly advise the application of the conversion leading to more reliable results in feeding ecology studies of large predators.

In most studies, samples have been collected on hiking trails and paths (Bodendorfer 1995, Norton 1986 &, Power 2002). Do leopards really prefer hiking trails and paths or are feces simply easier to detect here? We assume that leopards actually prefer to leave their scats on more open terrain, taking advantage of this setting for improved scent and visual marking. However, even if leopards do not prefer to defecate on paths, feces are easier to detect here compared to those in forests or savannas. This will most likely not bias results, since it is highly improbable that feces on paths and trails contain substantially different prey items from scats left behind at other locations.

We suggest combining scat analysis, direct observation (where possible), and radio-tracking for best results in comprehensive leopard studies. The analysis of feces combined with other techniques shows the following advantages:

– The analysis of feces prevents biases of actual prey eaten. Small prey is not overlooked.
– Direct observations answer questions about the leopard's mode of feeding, and provide information on condition, sex, and age of the predator and its prey.
– Radio-tracking provides additional information on spatial and temporal habitat use.

Furthermore feces sampling proves to be useful in other contexts. Genetic material in scats can be used in phylogenetic analysis and provides additional information on population structure and ecology (Uphyrkina *et al.* 2002). This is of considerable importance for threatened taxa such as the big cats, which only survive in isolated, scattered, and sometimes very small populations that are prone to inbreeding. Genetic information on leopards is therefore of great interest for conservationists and protected-area managers.

Feces analysis allows us to identify leopards individually, which in turn helps to determine population size and composition, as well as spatial habitat use. Based on these results, relevant management measures can be taken and the future existence of even small populations ensured, given that adequate prey is available (Ernest *et al.* 2000). Analysis of feces might also enable us to detect elusive or small prey species, especially in dense habitats (Mowat *et al.* 1999).

Prey spectrum. The prey spectrum of the leopard in the study area contained 13 different species of mammals – a relatively small number compared with other leopard studies (Bodendorfer 1995: 34 mammal species, n = 340; Power 2002: 25 mammal species, n = 225). A reason for the small prey spectrum of leopards in the Lajuma Mountain Retreat might be the fact that many potential prey animals have been exterminated by man, such as the impala (*Aepyceros melampus*), blue wildebeest (*Connochaetus taurinus*), hartebeest (*Alcelaphus buselaphus*), common eland (*Tragelaphus oryx*), and common reedbuck (*Redunca arundium*). In the Comoé National Park the share of reptiles and birds accounted for 2.7 % of the total prey spectrum of the leopard (Bodendorfer 1995). In contrast, no snakes and birds could be proved in our samples. The lack of reptile and bird remains suggests that the leopard rarely feeds on them, either because mammalian prey is so abundant and/or because reptiles are rarely encountered and birds are difficult to ambush in the prevalent habitat. Power (2002), who examined in his study the entire Soutpansberg area, could not detect remains of reptiles and found bird remains in only 0.4 % of the analyzed samples.

There was a complete lack of carnivores in the scats analyzed, which might reflect their low abundance in the study area.

Prey preferences. Not all available prey is taken and species fed upon might be rarer or more common in the scat than in the study area, suggesting a preference for certain species and avoidance of others.

Leopards in our study site seem to avoid certain species, such as the aardvark (*Orycteropus afer*) and porcupines, both of which are common in the study area. The reason for this might be an indication for diurnal activity in leopards in the area. Two other groups of animals that were under-represented in our study are pigs and baboons. All of these species share fierce defensive reactions and thus make a successful and secure hunt more difficult. Leopards were actually specialized porcupine hunters in other study areas (Sunquist & Sunquist 2002), with traditional prey-specific hunting techniques being passed from leopard mothers to their offspring. Leopards that are not specialized hunters of these species might try to avoid preying upon them and might only hunt them in times of shortage of other prey (Sunquist & Sunquist 2002). The low frequency of giant rat remains in the scats is amazing, since the animals are a preferred prey of leopards in the Comoé NP in Côte d'Ivoire (unpubl. results).

Species consumed more often than expected were bushbuck, common duiker, rock hyrax, and vervet monkey, which belong to the group of small and medium-sized prey that can easily be killed. The bushbuck is the most rewarding prey in terms of relation of hunting effort to amount of meat returned. From an energetical perspective it is most advantageous for a leopard-sized hunter to kill and feed on prey of this size (Sunquist & Sunquist 2002). Taking into account that medium-sized ungulates inflict a comparatively low number of injuries to the predator adds to the advantage. However, small and very small prey animals, that were quite abundant, were also part of the prey spectrum. Large animals were only rarely encountered in the study area. The only antelope present in this category is the greater kudu (*T. strepsiceros*). Leopards are capable of killing kudus, but the species seems to be rather rare. We did not find any remains of domestic animals in the samples. One reason for this is the lack of cattle breeding within the study area. However, cattle breeding occurs in the eastern area adjacent to our study area. This area includes entirely the hunting ground of the studied leopards. Leopards can obviously cover their entire nutritional needs by hunting wild animals and are not tempted to take livestock.

Number of prey individuals. In terms of numbers of individuals taken, rock hyraxes, vervet monkeys, and bushbucks are most often consumed by leopards. Due to their slow reproduction, with only one young per term, vervet monkeys and bushbucks will most likely be more affected by leopard predation compared with rock hyraxes, which give birth to 2–3 young. Vervet monkeys live in troops of 20 or more individuals but are not able to defend themselves against leopards (Stuart & Stuart 1997). The fact that rock hyraxes and vervets are diurnal might clue that leopards are active during the day in the study area, or prove that vervets choose sleeping sites that are easily accessible for leopards during the night.

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