

Unusually High Predation on Chacma Baboons (*Papio ursinus*) by Female Leopards (*Panthera pardus*) in the Waterberg Mountains, South Africa

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Key Words

Predation rate · Chacma baboon · Leopard

Abstract

Leopards do not preferentially favour baboons as prey, but they are considered the primary predators of baboons across Africa. Even in areas where baboons are abundant, their contribution to leopard diet seldom exceeds 5% of biomass. It is suggested that the extreme aggressiveness of baboons, group vigilance and their high mobility when escaping may limit leopard predation. Male baboons are particularly aggressive, and retaliation often leads to the death of the leopard. However, evidence suggests that leopards may learn to catch and kill certain dangerous prey. This study reports predation on chacma baboons by 3 female leopards on a private game reserve in the Waterberg Mountains of South Africa. Potential leopard feeding sites were identified using global positioning system (GPS) location clusters obtained from GPS collars. Over a 5-month period, we investigated 200 potential leopard feeding sites and located 96 leopard feeding/kill sites. Baboons constituted 18.7% of the leopards' biomass intake. The majority of baboons preyed upon were adults and 70% of the kills were diurnal. In terms of the measured variables, there were no significant differences in the way the leopards preyed upon baboons, compared to the rest of the prey species.

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Introduction

Studies on the predation of primates are scarce and frequently restricted by small sample sizes [Isbell, 1994; D'Amour et al., 2006; Morino, 2010]. Simple biological fact (e.g. primates are rarely preyed upon) interacts with logistical realities (e.g. data on the subject are difficult to collect) and leads to this scarcity of knowledge

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0015-5713/12/0836-0353\$38.00/0

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on predation of primates. Given this, it is not surprising that most studies on the predation of primates by carnivores rely on indirect evidence and opportunistic reports [Isbell, 1994; Morino, 2010]. This is unfortunate because predation is likely to have an important impact on population dynamics of primates, which tend to have relatively slow life histories [Charnov and Berrigan, 1993].

Leopards (*Panthera pardus*) have a diverse diet and will prey on animals ranging in size from insects, rodents and birds to large ungulates [Bothma and Le Riche, 1984; Skinner and Chimimba, 2005; Hayward et al., 2006]. However, the level of specialization in a leopard's diet is unclear. Bailey [2005] reports more than 90 different species in the leopard's diet, while Balme et al. [2006] suggest that leopards might be more specialized than previously thought, especially with regard to the selection of hunting habitat. It appears that leopards prefer to prey on animals that occur in small herds, in dense habitats, and which present a minimal risk of injury, such as impala (*Aepyceros melampus*), which is generally the most frequently taken prey (preyed on in 100% of study areas where they occur) [Hayward et al., 2006].

A misconception about leopards is that they prefer baboons as a prey item [Hunter, 1999]. Even in areas where baboons are abundant and are likely to be encountered frequently, they are avoided by leopards [Hayward et al., 2006]. Baboons exhibit several characteristics likely to limit leopard predation, most notably extreme aggressiveness and high mobility when escaping onto the smaller branches of trees [Bailey, 2005]. Male baboons are particularly aggressive, and retaliation often leads to injury or even death of the leopard [Cowlshaw, 1994]; on rare occasions when leopards do hunt baboons, it usually occurs at night while the baboons are at rest [Busse, 1980]. Numerous studies from South Africa illustrate this avoidance of baboons by leopards. In the Baviaanskloof region, leopards did not prey on baboons at all, despite them being abundant throughout the study area [Ott et al., 2007]. In the Cederberg Mountains, baboons comprised only 6.4% of the leopard's biomass intake [Martins et al., 2011]. In the Soutpansberg Mountains, baboons comprised between 4.2% [Chase-Grey, 2011] and 6.7% of the leopard's biomass intake [Schwarz and Fischer, 2006], and in the Waterberg Mountains, baboons contributed to less than 2.7% of all kills found [Grimbeek, 1992; Swanepoel, 2009]. Savannah primates – like baboons – are preyed on so infrequently that they are often left off the prey lists by researchers of terrestrial carnivores such as leopards [Isbell, 1994].

Here, we report unusually high predation on chacma baboons (*Papio ursinus*) by female leopards in the Waterberg Mountains of South Africa and evaluate temporal features associated with baboon kills to determine if leopards hunt baboons differently than other species. This is one of the very few studies on the predation of primates by carnivores where we could focus on the predator instead of the prey, and this allowed us to record all the kills made by the study leopards and not just occasional kills in a specific troop of baboons.

Methods

Study Area

The study was conducted on Welgevonden Private Game Reserve in the Waterberg Mountains of South Africa (24°18' S, 27°50' E). Eighty percent of the reserve is mountainous with numerous deep valleys and ravines [Kilian, 2003]. Although the reserve is encircled by a bound-

ary fence, leopards are still able to move freely between neighbouring properties. At the time of the study, the density of leopards on the reserve was approximately 4.5 adult leopards/100 km², as determined by mark-recapture models applied to camera trapping data [L.H. Swanepoel, unpubl. data].

The reserve hosts more than 50 mammal species, including various carnivores such as lion (*Panthera leo*), brown hyaena (*Hyaena brunnea*), black-backed jackal (*Canis mesomelas*) and cheetah (*Acinonyx jubatus*). A high diversity of herbivore species exists, ranging in size from giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) to smaller antelope such as waterbuck (*Kobus ellipsiprymnus*), mountain reedbuck (*Redunca fulvorufula*) and steenbok (*Raphicerus campestris*). The most abundant species on the reserve is impala (*A. melampus*). The mountainous terrain of the reserve provides an ideal habitat for baboons and, during the course of the study, there were approximately 25 troops on the reserve, with some comprised of as many as 100 individuals as determined by annual aerial censuses.

Leopard Capture and Collaring

Leopards were captured using soft-hold foot snares [Frank et al., 2003] and immobilized with an intramuscular dose of teletamine-zolazepam (Zoletil® 100, Virbac RSA Pty Ltd., Centurion, South Africa; 4–5 mg·kg⁻¹). Condition and morphological characteristics were assessed whilst the leopards were sedated. After collecting biological samples, leopards were fitted with remote drop-off global positioning system (GPS) collars (Followit Tellus, Lindesberg, Sweden). Once fully recovered, leopards were released within close proximity to the capture site. Capturing and collaring was conducted under the University of Pretoria Animal Use and Care Committee ethics clearance protocol AO 22-06 with all its amendments and Limpopo standing permit (No. S13631) for scientific institutional research. All collars were released from the leopards on completion of the study.

Locating Leopard Feeding Sites

Collars were programmed to download GPS points every 2 h (except at noon) and upload them to a server via cellular phone networks whenever the animal was in range of a tower. Leopard feeding sites were located in the field using GPS cluster analysis [Tambling et al., 2010; Martins et al., 2011]; this was achieved by manually inspecting GPS spatial clusters using ArcGIS v.9.2 (ESRI, Redlands, Calif., USA). Clusters were navigated to using a hand-held GPS device (Garmin eTrexVenture® Cx, Garmin International, Kansas, Mo., USA) and searched for prey remains for a maximum of 30 min. When present, prey remains were photographed and collected for later identification. Prey was identified by microscopic examination of cuticular hair scale patterns and cross-sections [Dreyer, 1966; Keogh, 1979, 1983; Buys and Keogh, 1984] and compared to reference samples housed at the Centre of Wildlife Management, University of Pretoria, South Africa. Prey remains were analysed to determine gender, age, and consequently mass of prey species. Together these data were used to estimate prey biomass intake of the leopards. We categorized rarely eaten species, Jameson's red rock rabbit (*Pronolagus radensis*), banded mongoose (*Mungos mungo*), rock hyrax (*Procavia capensis*), common duiker (*Sylvicapra grimmia*), African civet (*Civettictis civetta*) and bird species, in one category labelled 'other'. Three occurrences of scavenging, indicated by the lack of typical signs of a leopard feeding/kill site (e.g. plucked hair, blood, drag marks, fighting circle) and 2 unidentified prey species, have been excluded from the analysis.

Statistical Analysis

Time of kill was taken as the first GPS location of a confirmed leopard feeding site and was categorized into day and night (8 a.m. to 6 p.m. = day) for statistical analysis. A 2-sample Kolmogorov-Smirnov test was used to determine if the distribution of the time of kills shows a significant difference from uniformity. A binomial test was used to determine whether leopards selected for a specific gender of baboon, and Pearson's correlation test was used to measure the correlation between the number of baboon and non-baboon kills each month. Statistical analyses were conducted with R v.2.10.1 (R Development Core Team, 2011).

Table 1. Prey item remains located at leopard feeding sites using GPS location clusters

	Scientific name	Number	Percent of kills	Percent of biomass
Impala	<i>Aepyceros melampus</i>	18	20.2	20.4
Baboon	<i>Papio ursinus</i>	18	20.2	18.7
Klipspringer	<i>Oreotragus oreotragus</i>	11	12.4	5.6
Plains zebra	<i>Equus quagga</i>	8	9	12.2
Mountain reedbeek	<i>Redunca fulvorufula</i>	7	7.9	7.2
Kudu	<i>Tragelaphus strepsiceros</i>	4	4.5	25
Bushpig	<i>Potamochoerus larvatus</i>	2	2.2	4.8
Common reedbeek	<i>Redunca arundinum</i>	1	1.1	2.6
Other	-	20	22.5	3.5

Results

GPS data were collected from 3 female leopards. Over a period of 5 months, 200 potential leopard feeding sites as indicated by GPS clusters were visited, and 96 actual leopard feeding sites were located. Impala (20.2%), baboon (20.2%) and klipspringer (12.4%) were the species most frequently preyed upon, while kudu made the biggest contribution to the leopards' biomass intake (25%; table 1).

There was no selection by the study leopards for a specific gender of baboons among the small number of individuals for which gender could be determined (binomial test; $n = 8$, $p = 0.64$). With the exception of 1 subadult, all the baboons preyed on were adults. Over time, the distribution of baboon kills showed no significant deviation from uniformity ($n = 19$, $p = 0.4$, $D = 0.2$; fig. 1), but the distribution of combined leopard kills did differ significantly from uniformity ($n = 81$, $p = 0.02$, $D = 0.2$). There were no significant relationship between the number of baboon kills and the number of non-baboon kills each month (Pearson's correlation; $n = 6$, $r = 0.32$, $p = 0.56$; fig. 2).

Discussion

While an overwhelming majority of literature on leopard diet confirms they prefer to prey on medium-sized ungulates that afford them minimal risk of injury [Hayward et al., 2006], there is evidence suggesting leopards may catch and kill certain dangerous prey, as has been shown in several other carnivore species [French and French, 1990; Richardson and Andriashek, 2006; Power and Compion, 2009]. Leopards in the southern Kalahari have acquired the skill to kill porcupines by ambushing them just as they emerge from their burrows [Bothma and Walker, 1999]. A well-observed leopard in the Ngorongoro Crater preyed on 11 jackals in less than a month [Hunter, 1999] and in arid regions of southern Africa there are records of leopards killing cheetahs [Bothma and Walker, 1999; Hunter, 1999]. However, throughout the literature, it is clear that leopards do not favour baboons [Hayward

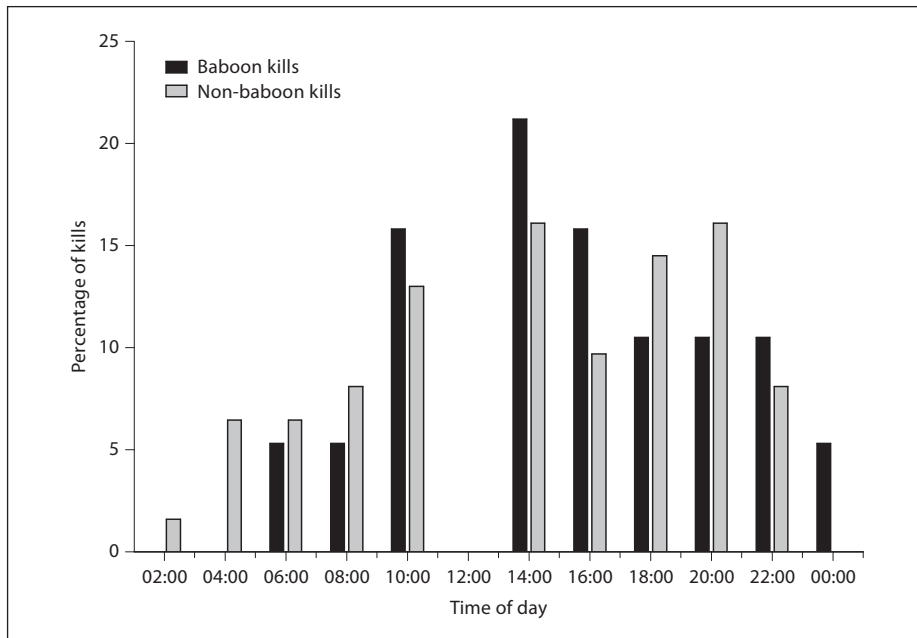


Fig. 1. Comparison between the time of baboon (*P. ursinus*) kills and the rest of the kills made by female leopards (*P. pardus*) on a private game reserve in the Waterberg Mountains. GPS locations were downloaded every 2 h, except at noon, which explains the lack of data at 12:00 and high value at 14:00 h.

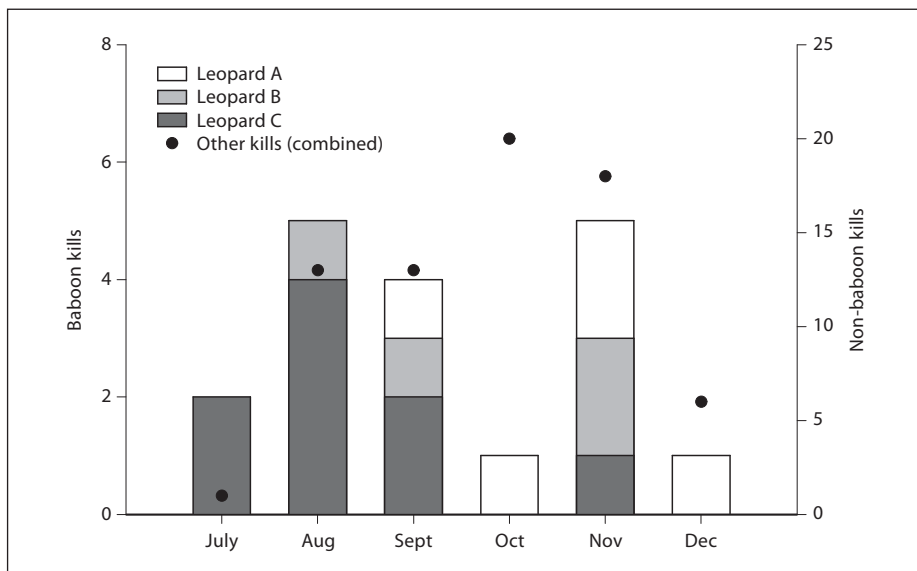


Fig. 2. Baboon (*P. ursinus*) kills by each leopard (*P. pardus*) per month (bars) and non-baboon kills by all leopards combined per month (dots).

Table 2. Weight, developmental stage and baboon capture data of the study leopards

Leopard	Weight, kg	Description	Percent of diet comprised of baboons
A	30	young subadult female	31.5
B	43	adult female	8.8
C	41	adult female with young cubs	23.5

et al., 2006; Ott et al., 2007]. In this study, 20.2% of the leopards' diets and 18.7% of their biomass intake consisted of baboons (table 1), the highest values of predation on baboons ever recorded.

Cowlshaw [1994] investigated patterns of predation in baboons and found that leopards are more likely to take adults than juveniles and more likely to take males than females. It was speculated that adult male baboons are more preyed on by leopards than any other age-sex class because they tend to spend more time on the periphery of the troop and further away from their nearest neighbour. Adult males also undertake solitary periods while transferring between troops. While leopards in our study also focussed heavily on adults, we found no preference for one gender over the other.

Attempts to explain how the leopards managed to kill such a high number of baboons are speculative. Busse [1980] suggested that leopards only attack baboons at night or at dusk, likely because nocturnal hunts on baboons may be more successful [Cowlshaw, 1994]. However, 70% of all kills on baboons in this study were made during the day (fig. 1), thus questioning the widely accepted notion that leopards are primarily nocturnal. The lack of temporal differences in baboon and non-baboon kills suggest that the leopards in this study likely hunt baboons opportunistically, or at least in patterns similar to how they hunt their prey as a whole. However, deviation from uniformity of the combined kills (baboon and non-baboon) suggests that the leopards did not hunt prey at random. The non-significant distribution from uniformity in the baboon kills can possibly be attributed to small sample size; however, the distribution in figure 1 is atypical for leopards [Hayward and Slotow, 2009], and it should therefore be considered that this may be learned behaviour by the local leopard population. The high predation on baboons at this study site can also possibly be attributed to an optimal number of baboons; small isolated groups would be too hard to find, while a large population, with large group formations, would potentially be too dangerous to hunt.

For a leopard to catch and kill a baboon still requires a certain level of skill that is likely to vary among individuals, as has been shown among not only leopards [Bothma and Walker, 1999], but also other carnivores hunting dangerous prey [Power and Compion, 2009]. Leopard A (a young subadult female), despite being inexperienced (table 2), successfully caught and killed 5 adult baboons (fig. 2). This leopard was at the age where she would have only very recently left her mother, it is possible that she acquired this skill while still learning to hunt. Genetic tests revealed no maternal or sibling relationship between the study leopards, so this theory was beyond

evaluation in this study. However, this raises the question of how leopards acquire skills to kill dangerous prey and to what extent such skill is passed on to members of the population, and this should be studied in the future.

We acknowledge that a shortcoming to our study is the inability to interrogate the effect of leopard predation on baboon population structure and density. Unfortunately we could not gather such data because of logistical constraints, difficult terrain and skittish baboon troops. However, we have shown the highest level of predation on baboons by leopards to date, which could possibly have significant effects on the population structure of these baboon populations. Significant research is needed to determine the demographic effects of this predation on baboons as well as the behavioural implications of predation of such a dangerous prey item by leopards.

Acknowledgments

This project was funded by the Wilson Foundation and the Centre for Wildlife Management at the University of Pretoria. Darien Simpson and Anton van Loggerenberg assisted in the capture of leopards. Special thanks go to the management team of Welgevonden Private Game Reserve for assistance during field work. We thank Justin Boyles for valuable input into this paper. Comments and suggestions from Matt Hayward and one anonymous reviewer significantly improved it.

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