

Kill rates and food consumption of leopards in Bardia National Park, Nepal

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This is the first study presenting data on kill rates and food consumption among Asian leopards *Panthera pardus* Linnaeus, 1758. In Bardia National Park, Nepal, we found leopard kills by searching within areas with clusters of locations from radio collared leopards (2 males and 1 female with 2 cubs aged 4–9 months). We used two tracking schemes, 24-h intensive radio-tracking and daily monitoring, and we defined food consumption as the product of average prey live weight and proportion consumed. The three leopards consumed 89.2 kg of meat from five chital *Axis axis*, one domestic dog and two birds during 19 days of 24-h intensive tracking, rendering an average (\pm SE) daily food intake of 4.7 ± 0.3 kg *per capita*. Twenty-five prey items (14 chital, one muntjac *Muntiacus muntjak*, four primates and six birds) were found during 180 days of daily monitoring of the female. All edible biomass was consumed in all kills, except for three chital, and the rate of kill consumption was positively related to the age of her cubs. The average daily food consumption of the female was 4.0 ± 0.3 kg/day, the kill rate (days/kill) including all prey categories was 5.6 ± 0.4 days, and the kill rate of ungulates was 10.6 ± 0.7 days. Our food consumption estimates are higher than reported from arid African environments. We suggest that the high food consumption rate in our study is a consequence of a release from time-energy constraints due to high prey abundance.

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Introduction

Knowledge of the food requirements and the rates that food is consumed among predators is a prerequisite for understanding predator-prey interactions and for estimating the impact and role of predation on prey species. For large car-

nivores, information on food consumption and requirements is particularly difficult to obtain, and estimates of predation impact are therefore often based on data from other studies (eg Karanth *et al.* 2004), or on estimates of the metabolic requirements of the predator species (eg Emmons 1987, Laundré 2005). However, field observations of kill rates of several large carni-

vores show pronounced intraspecific variation, with values commonly exceeding predicted kill rates from estimates of metabolic requirements (see review by Jeschke 2007). Hence, the commonly used methods of estimating predation impact should be applied with caution, because the assumptions on which they are based may be incorrect, or may require further examination. This should be particularly relevant when dealing with species that occupy environments with large differences in the composition and density of prey.

The adaptive ability of leopards *Panthera pardus* Linnaeus, 1758 is reflected by their wide distribution, which extends throughout large parts of Africa and Asia. Pronounced regional variations in availability of prey, both with respect to abundances and prey sizes, produce differences in several aspects of their behavior, including space use and feeding habits (see reviews by Odden and Wegge 2005 and Hayward *et al.* 2006). In view of the marked contrasts among leopard habitats, information on their kill rates and food consumption is severely limited. Current data are mainly from semi-arid and woodland savannah habitats in Africa (Bothma and le Riche 1986, Bailey 1993, Stander *et al.* 1997), while no studies of this kind have yet been conducted in Asia. In this paper, we present data on kill rates and food consumption of Asian leopards with the aim of improving the general knowledge of leopard feeding habits and their interactions with their prey.

Methods

Study area

Our study area was situated in the south-western part of the Bardia National Park in lowland Nepal (ca 100 m.a.s.l.), bordered by human settlements in the east and the Geruwa River in the west. The climate was subtropical monsoonal with heavy rainfall from July to October. The vegetation consisted mainly of Sal forests *Shorea robusta* and patches of grasslands dominated by *Imperata cylindrica* in the east. A patchwork of *Saccharum* spp. grasslands and a variety of successional forest types dominated the vegetation along the river. Among the ungulates in the park, chital *Axis axis* and hog deer *A. porcinus* were the most abundant; muntjac *Muntiacus muntjac*,

barasingha *Cervus duvaucelii*, sambar *C. unicolor*, nilgai *Boselaphus tragocamelus*, and wild boar *Sus scrofa* occurred in lower numbers (Støen and Wegge 1996). Tiger *Panthera tigris* was the most abundant carnivore; striped hyena *Hyaena hyaena* and dhole *Cuon alpinus* were less common (Heinen and Kattel 1992, Wegge *et al.* 2004).

Capture and radio monitoring

Three leopards, one adult female and two adult males, were captured in box traps and radio-collared during 1999–2001 (Odden and Wegge 2005). The female (F1) and one of the males (M1) were monitored for a period of approximately two years, whereas the other male (M2) was followed for 3 months. We used two radio monitoring programs: (I) 24-hour intensive tracking sessions (F1 = 13 days, M1 = 4 days, M2 = 2 days), with precise radio fixes every hour, and (II) daily radio tracking for periods of minimum 10 days. The first five sessions of 24-hour intensive tracking of F1 were done on consecutive days, whereas the following sessions were not. Further details are given in Odden and Wegge (2005). We were not able to follow the two males for periods long enough to be included in the daily radio tracking scheme, thus only F1 was included. F1 was tracked daily for 180 days during eight periods in the dry seasons of two consecutive years (October 1999 – March 2000 and January 2001 – March 2001). She gave birth to two cubs in June 1999 and two cubs in August 2000, and was therefore with dependent young aged four to nine months during the two main sampling periods. We allowed occasional gaps of a maximum of one day in the daily monitoring plans. However, such interruptions only occurred in 9% of the days included in the analyses.

Kill rates and food consumption

The movement pattern of leopards provided cues that we used to find kills. We searched for kills within areas where the leopards had been active for several consecutive hours (during the 24-hr intensive tracking sessions – Fig. 1), or for at least two consecutive days (during the daily tracking periods). Radio fixes were usually obtained between 9 am and 5 pm during the daily radio tracking. When a radio fix was positioned less than ca 500 m from the location of the previous day, we tracked the leopard in intervals of ca 1 hour during the rest of the day. This procedure was followed to make sure that we obtained fixes while the leopard was feeding at the kill. We were careful not to disturb the leopards while they were feeding to avoid that kills were abandoned. In order to estimate the biomass consumed from each kill, we multiplied the proportion consumed by the live weight of the kill (LW). We assumed that the percentage of wastage from completely consumed kills in this study was comparable with estimates by Stander *et al.* (1997): LW < 5 kg = 0%, LW 5–25 kg = 5% and LW > 25 kg = 30%. Live weights of prey were obtained from Schaller (1967), Ali and Ripley (1978), Dinerstein (1980), Fleagle (1988) and Karanth and Sunquist (1995). Deviations from the maximum amount consumed were estimated visually. In three cases, when the sex and age of chitals were un-

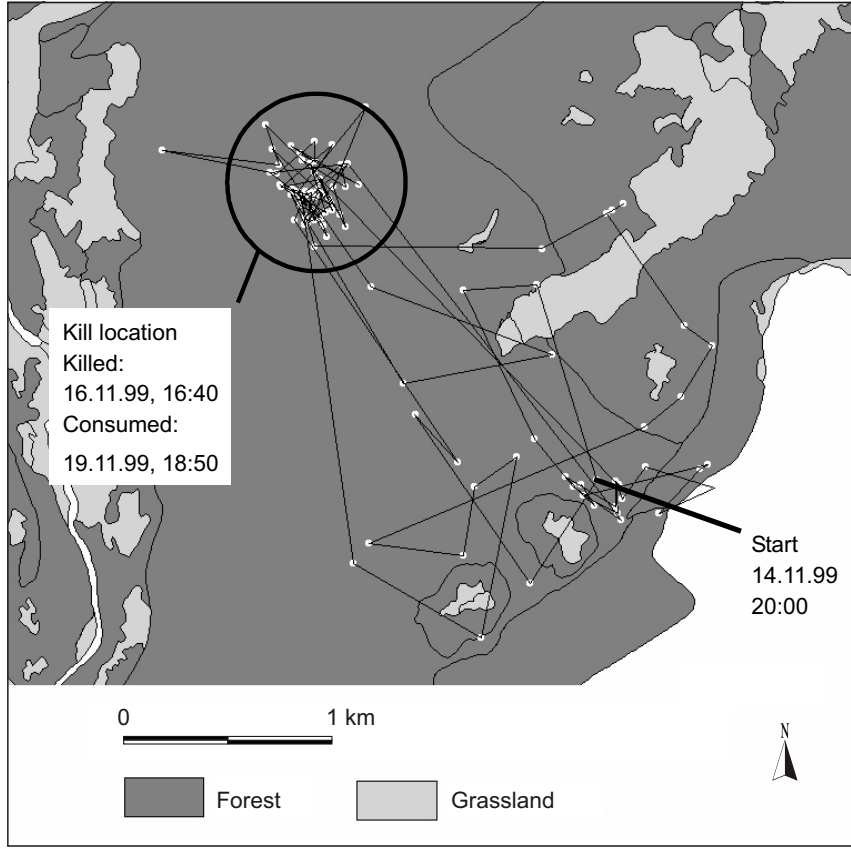


Fig. 1. Movement pattern of a radio-collared female leopard with cubs in Bardia National Park, Nepal, during 5 days of intensive tracking. White dots represent the location of the leopard every hour. The circle indicates a cluster of fixes where one kill – an adult male chital – was found later.

known, we assigned weights to these animals by averaging the weights of 13 other chitals of known sex and age.

We estimated the daily average biomass consumed by the leopards during the 24-hour intensive tracking sessions by using Equation 1:

$$FC = \frac{\sum_{i=1}^n LW_i TC_i \frac{t_i}{T_i}}{Nh} \quad \text{Equation 1}$$

where FC – daily food consumption, LW – live weight of the kill, TC – total proportion of the kill consumed, t – time spent by the leopard on the kill during the intensive tracking session, T – total amount of time spent on the kill before, during and after the intensive tracking session and Nh – total number of days of intensive tracking (19 days). Formulas from Thompson (1992) were used for calculating kill rates and daily food consumption for the daily radio tracking periods (eq. 2), and variances for the estimates from both tracking schemes (eq. 3):

$$\beta = \frac{\sum_{i=1}^n y_i}{\sum_{i=1}^n x_i} \quad \text{Equation 2}$$

where β – kill rate (kills per day) or food consumption (kg per day), i – the sampling period 1 to n , n – total number of sampling periods, x_i – the number of days in sampling interval i to estimate total number of kills (Y) where y_i = the number of kills in sampling interval i (or kg of prey killed in sampling period i).

$$Var(\beta) = 1 - \frac{x}{X} \frac{\sum_{i=1}^n (y_i - \beta x_i)^2}{\bar{x}^2 n(n-1)} \quad \text{Equation 3}$$

where x – total number of days sampled and X – the number of days between the start and the end of each of the two main sampling periods ($X = 237$). The finite population correction $(1 - x/X)$ was excluded from the estimates based on 24-h tracking.

Results

24 hour intensive tracking

During the 13 days of intensive tracking of F1 we found 3 chital, 1 peacock *Pavo cristatus* and 1 paddy bird *Padda oryzivora* (Table 1). M1 killed 2 adult male chital and 1 domestic dog during 4 days of intensive tracking. No kills were recorded during the 2 days of intensive tracking of M2. All edible biomass was consumed from the kills made by F1, while two of the kills of M1 were only partially eaten. We estimated that the three leopards consumed 89.2 kg of meat during the 19 days of intensive tracking, rendering an average (\pm SE) daily consumption of 4.7 ± 0.3 kg of meat during this period for all the leopards. The males consumed 4.3 ± 1.1 kg/day and the female consumed 4.9 ± 0.4 kg/day. In three instances, the leopards fed on kills that had been made before the tracking sessions started. Hence, since only five of the eight prey items were killed during the tracking periods, the sample size was too limited for estimating kill rates.

Daily tracking

We found 25 kills during the 180 days that F1 was tracked daily. Among these, there were 14

chital (6 adult males, 4 adult females, 1 yearling, 2 fawns, 3 of unknown sex and age), 1 Indian muntjac, 4 primates (2 rhesus macaques *Macaca mulatta* and 2 common langurs *Semnopithecus entellus*), and 6 birds (4 peafowl, 1 unidentified raptor and 1 paddy bird). The utilizable body mass of all but 3 kills was consumed entirely.

There was a significant and positive relationship between the live weight of the kills (LW) and the number of days spent at the kill site (T) ($F = 16.30$, $df = 18$, $p = 0.001$). However, a stronger relationship was observed between the total amount of meat consumed from the kills (MC) and T ($F = 29.96$, $df = 18$, $p < 0.001$; Fig. 2). The age of cubs (CA) did not predict T ($F = 0.26$, $df = 18$, $p = 0.616$), LW ($F = 3.474$, $df = 18$, $p = 0.080$) or MC ($F = 2.97$, $df = 18$, $p = 0.103$). However, we found a significant relationship between daily consumption rate while feeding at kills (MC/T) and CA (4.84 , $df = 18$, $p = 0.042$), indicating that kills were consumed faster when the age of the cubs increased (Fig. 3).

The daily straight-line movement distances during periods of confirmed kills averaged 194 ± 43 m (SE), and 1128 ± 100 m between kills. The difference in ln-transformed movement distances was significant (t -test: $t = -7.77$, $df = 117$, $p < 0.001$). By examining the distribution of the radio fixes of F1, we identified 9 peri-

Table 1. Estimated amount of biomass consumed from kills made during 19 days of hourly intensive tracking of 3 radio marked leopards (Female F1, Males M1 and M2) in Bardia National Park, Nepal. Live weights (LW, kg) of prey were derived from ^aSchaller (1967), ^bAli and Ripley (1978), ^cown observations or ^dby averaging the weights of 13 chitals of known sex and age that were killed by a female leopard in our study area. The columns of total biomass consumed refer to the total consumption during the periods before, during and after the intensive tracking sessions. P – the consumed proportion of the kill, CW – weight of the consumed mass, Ad – adult, M – male.

Predator	Prey			Biomass consumed during tracking			Biomass consumed in total		
	Species	Age/Sex	LW	P	CW	Days	P	CW	Days
F1	Chital	Ad/M	64 ^a	0.53	33.6	3	0.70	44.8	4
F1	Chital	Ad/M	64	0.23	14.9	1	0.70	44.8	3
F1	Peafowl	Ad/M	5 ^b	0.95	4.8	1	0.95	4.8	1
F1	Paddy- bird	?	0.4 ^c	1.00	0.4	1	1.00	0.4	1
F1	Chital	?	57.5 ^d	0.18	10.1	1	0.70	40.3	4
M1	Chital	Ad/M	64	0.00	0.0	1	0.00	0.0	0
M1	Chital	Ad/M	64	0.25	16.0	1	0.25	16.0	1
M1	Dog	?	20 ^c	0.48	9.5	1	0.95	19.0	2
Sum	89.2			170.0					

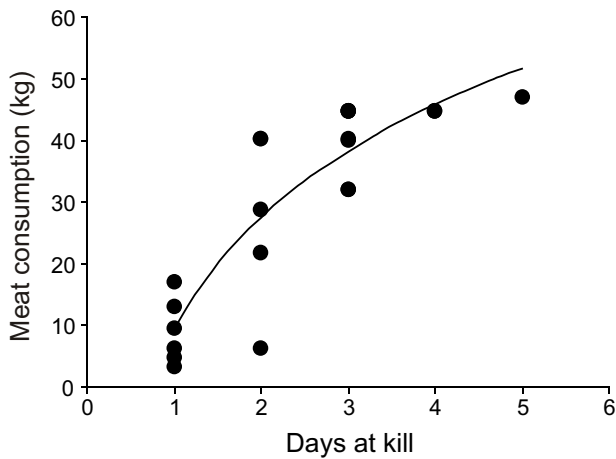


Fig. 2. Prey consumption of a leopard family group (2 cubs) in Bardia National Park, Nepal: the relationships between the length of feeding periods (no. of days from a prey was killed until it was abandoned) and the total amount of meat consumed from the kill.

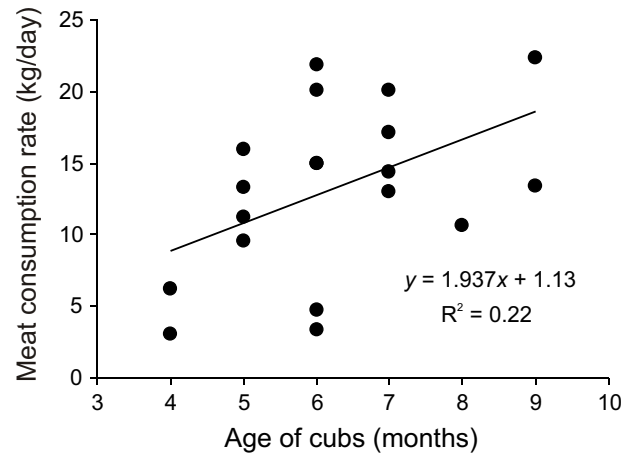


Fig. 3. Prey consumption rates of a leopard family group (2 cubs) in Bardia National Park, Nepal: the relationships between the age of the cubs (months) and the rate of meat consumption while feeding at kills (kg/days).

ods with markedly short daily movements (131 ± 20 m), indicating that kills had been consumed that we were unable to locate. In order to approximate the weights and species categories (ungulates and other prey) of the suspected kills, we analyzed the relationships between the total amounts of meat consumed from the confirmed kills (MC), the number of days spent at the kill site (T) and the age of the leopard's cubs (CA). The best Generalized Linear Model predicting MC included only one term, T (Table 2). MC did not increase linearly with T. Instead, it increased abruptly in the interval 1 day to 3 days, and tended to level out when more than 3 days had been spent at the kill. Accordingly, a

logarithmic model of the relationship between MC and T performed better than the linear model ($\Delta\text{AICc} = 7.05$, Fig. 2), and the following formula was used to approximate the amount of meat consumed during periods of suspected kills (MS): $\text{MS} = 26.3\ln(\text{T}) + 9.4$.

The predicted amounts consumed from six of the suspected kills were 9.4 kg, and ranged between 27 and 52 kg in the three remaining kills. Hence, a minimum of 3 suspected kills were ungulates, as these were the only available prey species weighing more than 27 kg. Since nearly all confirmed ungulate kills were completely consumed, we assumed that the six suspected kills with consumption < 10 kg were not ungu-

Table 2. Prey consumption of a female leopard with cubs in Bardia National Park, Nepal: Generalized Linear Models of how the age of cubs (CA) and number of days spent feeding on kills (T) predicted the total amount of meat consumed from the kills. * - $p < 0.05$, ** - $p < 0.001$. AICc - Akaike Information Criterion corrected for small samples. W - Akaike weight.

Model	Parameters	AICc	ΔAICc	W
M1	T* - CA + T:CA	142.32	3.23	0.14
M2	T** + CA	141.75	2.66	0.18
M3	T**	139.09	0.00	0.68

Table 3. Kill rates and food consumption rates (\pm SE) of a radio collared female leopard with cubs in Bardia National Park, Nepal. “Confirmed kills” were found by searching in clusters of radio fixes after the leopard had left the location. “Suspected kills” were assumed to have occurred at times when daily movement distances were markedly shorter (131 ± 20 m (SE)) than the average movement distance (1128 ± 100 m).

	Ungulates		All kills	
	Confirmed	Confirmed + Suspected	Confirmed	Confirmed + Suspected
Kill rate (days/kills \pm SE)	12.9 \pm 1.0	10.6 \pm 0.7	7.8 \pm 0.6	5.6 \pm 0.4
Consumption rate (kg/day \pm SE)	2.7 \pm 0.2	3.4 \pm 0.2	3.0 \pm 0.2	4.0 \pm 0.3

lates. The estimated kill rate of ungulates by F1 based only on confirmed kills was 1 per 12.9 ± 1.0 days (Table 3). Including suspected kills produced an estimate of 1 per 10.6 ± 0.7 days. Including all kill categories, the kill rates were 1 per 7.8 ± 0.6 days and 1 per 5.6 ± 0.4 days among confirmed kills and confirmed + suspected kills, respectively. The female F1 consumed up to 4.0 ± 0.9 kg of meat daily (Table 3).

Discussion

Results differ markedly among studies of leopard kill rates and food consumption (Table 4). Concerning daily food consumption, the estimates reported by Stander *et al.* (1997) are relatively low, whereas our estimates and those from Bailey (1993) are higher. The estimates of kill rates show an opposite pattern; Stander *et al.* (1997) and Bothma and le Riche (1986) presented higher kill rates than reported in Bailey (1993) and in our study.

Evaluating the different methods is a reasonable starting point when explaining these differences. We showed that the amount of time the leopards spent at the kill sites was positively related to the sizes of the kills. Furthermore, the predicted sizes of suspected kills were generally smaller than the confirmed kills. These findings imply that the probability of finding kills was positively related to their size, and that our kill rate estimate that included all kills, both large and small, may have been somewhat lower than the actual kill rate. On the other hand, the esti-

mated rates of killing ungulates should be more accurate. Among the methods applied in our study, we consider the daily radio tracking with inclusion of suspected kills to have provided the most appropriate data for comparisons with other studies. This method produced the largest kill sample and, thus, more precise estimates of food consumption than the 24h intensive tracking method. Furthermore, including suspected kills in the estimates reduced what we believe was the most pronounced bias in the food consumption data, ie underestimation. Among the other studies, Bailey (1993) used a method somewhat similar to ours, ie it was based on daily radio tracking and the inclusion of suspected kills. Stander *et al.* (1997) and Bothma and le Riche (1986) may have avoided underestimation by following the daily track routes of leopards, which probably ensured that a very large fraction of kills were discovered, regardless of size. Accordingly, underestimation of small prey in our study and in Bailey (1993) may be a factor that partially explains the difference in kill rate estimates among the studies.

Differences in prey availability among the study areas may be another factor explaining the different kill rate estimates. In Stander *et al.* (1997), the two most frequently killed prey species, steenbok *Raphicerus campestris* (13% of kills) and duiker *Sylvicapra grimmia* (32.8% of kills) occurred in a total density below 0.5 individuals per km². To our knowledge, no estimates of prey density are available from the study area of Bothma and le Riche (1986). However, the fact that the sizes of leopard home ranges in that

Table 4. Estimated kill rates and food consumption rates of leopards reported from this study and previous studies.

Reference	Habitat and location	Kill rates (days/kills \pm SE)			Consumption rates (kg/day \pm SE)			Remarks
		Male	Single female	Female with cubs	Male	Single female	Female with cubs	
This study	Subtropical forest, Nepal			5.6 \pm 0.4	4.3 \pm 1.1		4.0 \pm 0.3	Kill rate: Daily radio-tracking of 1 female, 25 confirmed and 9 suspected kills. Consumption rates: 6 days of 24h tracking of 2 males and 180 days of daily tracking of 1 female
Stander <i>et al.</i> (1997)	Semi-arid savannah Namibia	4.6	5.1–5.6	3.9–4.4	3.1–3.3	1.6 \pm 0.5	2.6 \pm 0.5	Daily follows of spoor. 131 kills
Bothma and le Riche (1986)	Semi-arid savannah South Africa	3.3		1.5		3.5	4.9	Kill rates: Daily follows of spoor. 24 kills. Consumption rates: 1 male (sample size not reported) and 2 females (followed for 14 days)
Bailey (1993)	Woodland savannah South Africa	7.2	7.5			4.4–4.7		Kill rates: Daily radio-tracking. 95 kills, including confirmed and suspected kills. Consumption rates: Daily tracking of 2 males for 40 days each

area were the largest ever recorded in the world (Bothma *et al.* 1997) is an indication of low prey density (Gittleman and Harvey 1982). In contrast, Bailey (1993) reported a relatively high prey density and, in our study area, the density of the most common prey species, chital, exceeded 50 individuals per km² (Odden 2008). As a consequence of the high prey densities, the leopards may have been more selective towards larger prey sizes, implying that fewer kills were needed to fulfill the energetic demands.

Interestingly, the highest estimates of daily food consumption (this study and Bailey 1993) stem from the two study areas with the lowest estimates of kill rates and the smallest average leopard home ranges (Bothma and le Riche 1986, Bailey 1993, Bothma *et al.* 1997, Stander *et al.* 1997, Odden and Wegge 2005). These findings conflict with the conclusion of Gittleman

and Harvey (1982), that food consumption should be higher where range sizes are large due to a positive correlation between range size and metabolic needs. The results may be better explained by Wilson's (1975) principle of stringency, ie that time-energy budgets are evolved so as to fit periods of low food abundance, or large food requirements (eg rearing of offspring or reproductive activities). According to Jeschke (2007), the principle of stringency implicates that carnivores are often released from time-energy constraints in areas where food abundance is high. The contrasting consumption rates among the leopard studies may therefore reflect differences in time-energy constraints due to the pronounced difference in prey availability. In other words, relatively high consumption rates may be possible when prey density is high.

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