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How much does a spotted hyaena eat? Perspective from the Namib Desert

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Summary

The amount of food consumed by a clan of spotted hyaenas in the Namib desert was determined gravimetrically for 19 nights and the amount consumed by each individual was calculated according to its feeding time budget. At large, fleshy ungulate carcasses, each adult clan member ate about 8·7kg nightly, except for the bottom-ranking male, who obtained only half that amount per night. Skin and bone remains were consumed at a slower rate of 2kg/hyaena/night. Medium-sized ungulates were devoured rapidly so that each hyaena obtained more during such feeding nights than at large carcasses. Over a 29 day period, a hyaena clan consumed five cacasses at a rate of 4·0kg/hyaena/day, which compared well with previous estimates of average daily consumption in large social carnivores studied elsewhere. Annually, sixteen Namib hyaenas ate some 4·8% of the ungulate biomass, removing, in terms of numbers 14·3% of the gemsbok and 2·2% of the mountain zebra. This depletion did not appear to limit these populations.

Résumé

La quantité de nourriture ingérée par un groupe d'hyènes tachetées dans le désert de Namib a été déterminée par gravimétrie pendant 19 nuits et la quantité consommée par chaque individu a été estimée en fonction du laps de temps passé à se nourrir. Lorsqu'il s'agit de grandes carcasses entières d'ongulés, chaque membre adulte du groupe mange environ 8·7kg chaque nuit sauf le mâle de rang inférieur qui ne reçoit que la moitié de cette quantité par nuit. La peau et les os restants sont consommés à un rythme plus faible, à raison de 2kg/hyène/nuit. Les ongulés de taille moyenne sont dévorés rapidement de sorte que chaque hyène reçoit plus lorsque le repas est ainsi composé que lorsqu'il s'agit de grandes carcasses. Sur une période de 29 jours, un groupe d'hyènes a consommé cinq carcasses, à raison moyenne de 4kg/hyène/24h, ce qui s'accorde bien avec les estimations antérieures de consommation journalière moyenne, réalisées ailleurs lors d'études sur les grands carnivores sociaux. Chaque année, seize hyènes du Namib mangeaient quelque 4·8% de la biomasse en ongulés, prélèvement qui correspond à 14·3% des oryx et 2·2% des zèbres des montagnes. Cette réduction ne semble pas devoir limiter ces populations.

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Introduction

A quantitative estimate of food consumption by carnivores is valuable to assess the predator's relationships with prey populations in natural ecosystems and to indicate how available food is partitioned among a predator population. A previous estimate of the average daily food consumption of spotted hyaenas, *Crocuta crocuta* (Erxleben), was made by Kruuk (1972), who used the observed killing rate and carcass utilization of a hyaena clan to estimate that each hyaena ate 2kg/day. In contrast, daily energy use, determined from radio isotope (sodium) turnover rates of spotted hyaenas in South Africa by Green, Anderson & Whateley (1984), gave an estimated food consumption of 3·8kg/hyaena/day.

In a study encompassing the social and spatial organization, feeding behaviour and bone accumulation habits of hyaenas in the central Namib Desert (Henschel, Tilson & von Blottnitz, 1979; Tilson, von Blottnitz & Henschel, 1980; Tilson & Hamilton, 1984; Tilson & Henschel, 1986), food intake at carcasses was measured gravimetrically. Furthermore, the known differential rates of carcass disposal over a one-month period were used to evaluate the impact of the spotted hyaena population on ungulate populations in the region. This known consumption over a one month period was compared with a subjective classification of meals as large or small in order to test its validity. The latter method should be useful for future computations of food consumption in studies of hyaenas where it is impossible to determine this gravimetrically.

Methods

The 3080km^2 study area contained sixteen spotted hyaenas (twelve adults) occurring in three clans at Natab, Nareb and Zebra Pan, along a 115km section of the Kuiseb River within the Namib–Naukluft Park, South West Africa/Namibia. The most important prey species were 625 gemsbok (*Oryx gazella*, Linnaeus), which were dispersed throughout the study area, and 980 mountain zebra (*Equus zebra hartmannae*, Matschie), which were concentrated in the Zebra Pan region (Tilson *et al.*, 1980), and small scattered herds of springbok (*Antidorcas marsupialis*, Zimmerman).

Observations of individually identified spotted hyaenas consuming food were conducted during 67 nights between December 1977 and June 1978 at three provisioned goat carcasses and at fifteen gemsbok and mountain zebra carcasses, which were located by us soon after they had been killed. During the first few nights following the death of a gemsbok or mountain zebra, all feeding activities were observed directly at the carcass and dislodged fragments were accounted for. We weighed carcasses on a platform balance before and after the hyaenas had fed on 19 such nights to determine their weight loss.

Total feeding time was determined by recording the number of minutes each individual fed (Tilson & Hamilton, 1984). Adults were assumed to feed at equal rates and 6–12 month old cubs at half the average adult feeding rate. The quantity consumed by an individual during a night was calculated by multiplying the ratio of individual feeding time to total feeding time by the weight loss of the carcass.

Table 1. Gravimetric estimate of quantity (kg) consumed per night by individual hyaenas feeding to satiation on different prey carcasses. Hyaenas A, B, C and D of each clan are listed in descending rank order.

			Quantity consumed (kg)							Feeding
			Females		Males		Juveniles			time
Carcass	Night	Clan	A	B	C	D	E	F	Total	(min)
Gemsbok	1	Natab	10·4	10·0	7·7		3·5	3·5	35·0	459
	2		4·7	12·1	12·0	7·2			36·0	304
	3		2·9	4·9	7·2	3·9	2·1	2·1	23·0	417
Gemsbok	1	Natab	14·4	12·4	10·5		9·9	9·9	57·0	702
	2		7·8	9·2	10·2		3·7	5·1	36·0	384
	3		8·2	2·1	5·6		2·9	4·2	23·0	328
Gemsbok	1	Natab	9·7			2·4	1·7	2·2	16·0	215
	2		10·8	8·4		3·8	5·3	5·7	34·0	461
	3		6·8	6·7		3·3	3·5	4·8	25·0	572
Zebra*	1	Zebra	5·8						5·8	41
	2	Pan	7·4						7·4	52
	3		14·5	14·5					29·0	204
	4		7·6	9·1					16·7	117
	5		5·3	6·8					12·1	85
	6		13·4	8·3					21·7	222
	7		12·0	3·7					15·7	208
Goat	1	Natab	13·2	16·8					30·0	75
Goat	1	Natab	9·9	9·9	15·2				35·0	53
Goat	1	Natab	15·2	8·0		1·6	5·0	6·2	36·0	271

*Data obtained from unhabituated individuals have been excluded.

Results

Consumption of large fleshy carcasses

A large carcass, such as a gemsbok ($\pm$150kg), or mountain zebra ($\pm$250kg), was more than a small hyaena group of three to five individuals could consume in a night. An orderly feeding progression prevailed: a dominant female and her cubs fed first, followed by other females and males. Each adult usually fed alone according to the priority granted by its relative social status (Tilson & Hamilton, 1984). As a result of this feeding pattern, all but the bottom-ranking clan members present at a large fleshy carcass usually ate to satiation.

We calculated (Table 1) that the consumption by the two dominant females of the Natab clan and a high-ranking male was similar ($P > 0{\cdot}1$; $t_{34} = 0{\cdot}64$); each consumed an average of 8·7kg (s.e. = 0·6; range = 2·1–14·4kg) of meat per night. This amount probably represents the natural satiation level of an adult in the absence of disruptive competition. By contrast, a low-ranking male, who was often excluded from feeding (Tilson & Hamilton, 1984), consumed significantly less per night ($\bar{x}h = 4{\cdot}1$kg; s.e. = 1·3; $t_4 = 7{\cdot}74$; $P < 0{\cdot}05$).

Consumption of remains

When the bulk of a large carcass had been consumed, the remainder was dismantled by the hyaenas and carried away for individual consumption elsewhere, often in the vicinity of dens (Henschel *et al.*, 1979). It was difficult to account for all food remains at this stage, thus precluding precise determination of food intake. For three gemsbok carcasses, the known amount still available per adult hyaena at the beginning of the fourth night of feeding was $5{\cdot}9 \pm 0{\cdot}1$kg. In two nights each hyaena that fed for longer than an hour was estimated to consume two-thirds of this. Remaining bones dried-up and were abandoned. The quantity consumed in such meals ($n = 14$) thus amounted to 2kg/hyaena/night. In subsequent computations, such meals of skin and bone, which were classified as small, were assumed to be equivalent to 2kg.

Consumption of small fleshy carcasses

A small carcass, such as a goat ($\pm$33kg), which is about the same size as a springbok, was consumed entirely within 1–3h. Not only was the feeding rate four times faster than on gemsbok carcasses (Tilson & Hamilton, 1984), but each hyaena ate significantly more ($\bar{x}h = 12{\cdot}6$kg; s.e. $= 1{\cdot}3$; $t_6 = 5{\cdot}42$; $P < 0{\cdot}05$) than the quantity (8·7kg) usually consumed at large carcasses. Instead of leaving a fraction of the goat carcass uneaten for later consumption, scramble competition over the remains continued until nothing remained, at which stage each hyaena had consumed 8–17kg (Table 1).

Monthly food intake

On one occasion we observed three adult hyaenas and two cubs consuming 130kg of an adult gemsbok during five nights. Observations were incomplete during the ten nights that followed, but we found no evidence that the hyaenas fed in that period. During the following 14 nights, these hyaenas consumed one adult and two yearling gemsbok and a provisioned goat, totalling 330kg. Because the first 15 nights represented a period of minimum consumption (2·2kg/hyaena/night) and the subsequent 14 days a period of maximum carcass availability (5·9kg/hyaena/day), we estimated that the total consumption of 460kg in 29 days, or 4·0kg/hyaena/day, represented the mean consumption rate of food.

For comparison, the number of large (9kg) and small (2kg) meals eaten in the same period were counted. The 42 large and 31 small meals were estimated to be equivalent to 440kg, which was only 4% less than the value obtained by direct means. This supports the validity of the latter method.

Annual food requirements

Assuming that the minimum, mean and maximum consumption estimates were representative for the hyaena population in the study area, annual food requirements would amount to an average of 19·4 (range: 11·1–28·3) tonnes of food, or 4·8% (2·8–7·0%) of the total ungulate biomass (404 tonnes). We calculated the expected killing rate of ungulates based on a determination of diet by scat analysis (Tilson *et al.*, 1980). According to this, twelve adult hyaenas and four cubs annually removed ninety (51–131) or 14·3% (8·2–21·0%) of the gemsbok, twenty-two (12–32) or 2·2% (1·3–3·2%) of the mountain zebra, about three springbok and goats and about three ostrich (Table 2). Since at least 10% of the gemsbok carcasses were calves and 20% of the zebra carcasses were foals (Tilson *et al.*, 1980), the figures slightly underestimated the number of ungulates removed.

Table 2. Annual consumption by three Namib hyaena clans estimated by the method outlined by Kruuk (1972).

Species	Mass (kg) consumed	Diet (%)	Weight (kg) of 100 prey items	No. of prey items min	No. of prey items mean	No. of prey items max
(a) **Natab Clan** (4 adults, 2 cubs)						
Gemsbok	150	93·1	13,965	25·6	44·8	65·6
Springbok	40	2·8	112	0·8	1·3	2·0
Goat	35	2·8	98	0·8	1·3	2·0
Ostrich	130	1·4	182	0·4	0·7	1·0
Total mass consumed (kg)	min = 3954 kg	mean = 691 7kg	max = 10,110 kg			
(b) **Nareb Clan** (3 adults)						
Gemsbok	150	82·2	12,330	12·9	22·5	32·9
Zebra	250	9·9	2475	1·6	2·7	4·0
Springbok	40	0·6	24	0·1	0·2	0·2
Klipspringer	11	1·5	16	0·2	0·4	0·6
Steenbok	10	0·4	4	0·1	0·1	0·2
Goat	35	0·2	7	0·0	0·1	0·1
Hyaena	60	0·6	36	0·1	0·2	0·2
Ostrich	130	1·9	247	0·3	0·5	0·8
Total mass consumed (kg)	min = 2372 kg	mean = 4150 kg	max = 6066 kg			
(c) **Zebra Pan Clan** (5 adults, 2 cubs)						
Gemsbok	150	50·0	7500	12·8	22·4	32·7
Zebra	250	42·1	10,525	10·8	18·9	18·9
Ostrich	130	3·9	507	1·0	1·7	2·6
Total mass consumed (kg)	min = 4745 kg	mean = 8300 kg	max = 12,133 kg			

Discussion

At a large fleshy ungulate carcass in the Namib, an adult hyaena normally ate a large meal of 9kg, except a low-ranking male, which obtained less. Henschel (1987) has suggested that the high feeding priority of females, often at the expense of unrelated immigrant males, favours mature females and their cubs in obtaining more of the high-protein food required for growth or reproduction. When feeding on carcasses persists for longer than half an hour, each Namib hyaena usually got a small meal of about 2kg. By counting the number of large and small meals consumed and multiplying by 9kg and 2kg (respectively), one can estimate the quantity of food eaten over a given period in studies where this is not possible by any other means.

Spotted hyaenas make efficient use of a food abundance, yet are capable of enduring periods of over a week without food. At a large carcass, a hyaena can eat substantial meals for a number of nights in succession until all meat is finished. Matthews (1939) found that few culled hyaenas in East Africa had undigested food in their stomachs. He concluded that a hyaena keeps food in its stomach for just a

Table 3. Body mass, consumption estimates and ecological parameters determined for adult spotted hyaenas from the Namib compared to the Kruger National Park (Henschel, 1986) and Ngorongoro (Kruuk, 1972).

	Namib	Kruger Park	Ngorongoro
Body mass (kg)	±65	65	52
Clan size	6	11	61
Territory size (km^2)	570	130	35
Ungulate carcasses killed vs. scavenged (%)	>50	18	84
Ungulate density (number/km^2)	0·6	11·0	95·0
Daily activity period (h)	—	6·6	3·8
Daily distance moved (km)	—	20·1	10·1
Consumption (kg/hyaena/day)	4·0	3·8	2·0
Consumption (g/kg/day)	61·5	58·5	38·5

short time before it passes to the small intestines or regurgitates indigestible parts. This would enable a hyaena to eat again soon after its last meal. The maximum feeding capacity recorded for hyaenas from southern Africa, where adults weigh about 65kg (Whateley, 1980; Smithers, 1983; Henschel, 1986), exceeds 25% of their body mass. Bearder (1977) measured one hyaena eating 18kg in one night, an observation supported by the maximum of 17kg measured for a Namib hyaena. The ability to cope with extended periods of feast or famine probably imparts a great advantage to a hunter and scavenger whose available food supply is capricious.

The estimate of mean food consumption of 4·0kg/hyaena/day in the present study is similar to the 3·8kg/hyaena/day estimated independently by Green *et al.* (1984) and Henschel (1986) in South Africa. In contrast, Kruuk (1972) estimated that East African hyaenas consumed about 1·5–2·0kg/hyaena/day. The four consumption estimates were obtained by different methods, which could have influenced the results. Kruuk (1972) counted all kills observed in the territory of a Ngorongoro clan in 38 days and estimated the degree of utilization by hyaenas. Green *et al.* (1984) measured sodium and water turnover rates of three individuals, but did not test the validity of converting these data to quantitative values. In the Namib Desert, we determined the weight loss of carcasses to calculate the amount consumed by a clan over a 29 day period. We also calibrated a subjective visual classification of the size of meals consumed by feeding individuals using gravimetric means. The latter method was applied by Henschel (1986) in the Kruger National Park for 115 meals observed to be consumed during fifty-five continuous observation periods of 24h each.

Other possible reasons for differences in findings between southern Africa and East Africa could be:

(a) Hyaenas from different regions differ in clan size, territory size, ungulate density, daily activity periods, daily distances moved and food quality, which are related to the degree to which hyaenas kill or scavenge (Table 3). These factors may contribute to differences in daily energy expenditure. This suggests that generalizations of hyaena food requirements may not be possible and may have to be determined independently for each area.

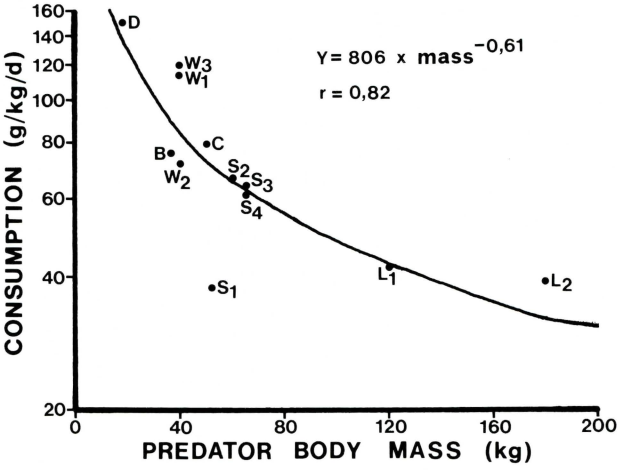

Fig. 1. Logarithmic estimated mean daily consumption by large carnivores relative to their body mass. Species codes are: D = African wild dog (*Lycaon pictus*); W = wolf (*Canis lupus*); B = brown hyaena (*Hyaena brunnea*); C = cheetah (*Acinonyx jubatus*); S = spotted hyaena (*Crocuta crocuta*); L = lion (*Panthera leo*). Data sources are: D = Estes & Goddard, 1967; W1 = Mech, 1970; W2 = Fritts & Mech, 1981; W3 = Peterson *et al.*, 1984; B = Mills, 1977; C = Schaller, 1972; S1 = Kruuk, 1972; S2 = Green *et al.*, 1984; S3 = present study; S4 = Henschel, 1986; L1 and L2 = Schaller, 1972.

(b) Adults in East Africa are 20% smaller than those in southern Africa, but their estimated average daily food consumption was 50% less (Table 3). In comparison with other species, Kruuk's (1972) estimate was less than expected for a social carnivore of that size, whereas the southern African estimates compared better with expected values (Fig. 1). It is possible that Kruuk (1972) had underestimated the number of carcasses killed by the Ngorongoro clan, or overestimated the number of individuals that benefitted from observed kills.

The general shape of the curve on Fig. 1 resembles the expected relationship of metabolic rate to mass of mammals (Gordon, 1977), but, to date, no field study of large social carnivores has related quantity eaten to energy content of food of a particular quality and to an individual's energetic requirements. The need to do this is emphasized by very different results obtained in various studies of wolves (Fig. 1). Peterson, Woolington & Bailey (1984) attributed this to differences in prey vulnerability, which would suggest that above the energy required for subsistence, consumption may also depend on the availability of food.

Although the question of whether predators limit prey populations requires data on recruitment rates of the prey species, these were not available for the Namib during our study period. However, in an area situated 200km away, Joubert (1971) found that although typically each mature zebra female foaled each year, only 21% of the population were foals. He concluded that the 12% loss was probably due to predation by hyaenas, lions and leopards. In our study area, hyaenas were the sole predators of zebra, removing some 2–3% of the population annually.

In fifty-nine fortnightly ground surveys of gemsbok conducted in our study area between July 1978 and December 1980 immediately after our study period, von Blottnitz (unpubl.) sighted a mean of 128 gemsbok, but did not always classify them by age. He found that during peak breeding months of August to December, calves represented 13–17% of gemsbok counted at Natab, 9–24% at Zebrapan and 10–21% south of the Nareb region. As these are minimum figures, the actual birth rate of gemsbok was probably somewhat higher. These data suggest that recruitment should have more than offset the 14% (8–21%) loss of gemsbok, which was removed by spotted hyaenas annually.

The density of the spotted hyaena population was limited by factors other than food, namely the availability of water and shelter along a linear oasis through the desert (Tilson & Henschel, 1986). Our findings indicate that it was unlikely that these predators limited the size of prey populations in the Namib. This conclusion agrees with previous authors (Kruuk, 1972; Bearder, 1977; Mills, 1984; Henschel, 1986) that there is no evidence that spotted hyaenas depress prey populations in any region where this question has been investigated.

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