Predator–prey size relationships in an African large-mammal food web

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Abstract

- Size relationships are central in structuring trophic linkages within food webs, leading to suggestions that the dietary niche of smaller carnivores is nested within that of larger species. However, past analyses have not taken into account the differing selection shown by carnivores for specific size ranges of prey, nor the extent to which the greater carcass mass of larger prey outweighs the greater numerical representation of smaller prey species in the predator diet. Furthermore, the top-down impact that predation has on prey abundance cannot be assessed simply in terms of the number of predator species involved.

- Records of found carcasses and cause of death assembled over 46 years in the Kruger National Park, South Africa, corrected for under-recording of smaller species, enabled a definitive assessment of size relationships between large mammalian carnivores and their ungulate prey. Five carnivore species were considered, including lion (Panthera leo), leopard (Panthera pardus), cheetah (Acinonyx jubatus), African wild dog (Lycaon pictus) and spotted hyena (Crocuta crocuta), and 22 herbivore prey species larger than 10 kg in adult body mass.

- These carnivores selectively favoured prey species approximately half to twice their mass, within a total prey size range from an order of magnitude below to an order of magnitude above the body mass of the predator. The three smallest carnivores, i.e. leopard, cheetah and wild dog, showed high similarity in prey species favoured. Despite overlap in prey size range, each carnivore showed a distinct dietary preference.

- Almost all mortality was through the agency of a predator for ungulate species up to the size of a giraffe (800–1200 kg). Ungulates larger than twice the mass of the predator contributed substantially to the dietary intake of lions, despite the low proportional mortality inflicted by predation on these species. Only for megaherbivores substantially exceeding 1000 kg in adult body mass did predation become a negligible cause of mortality.

- Hence, the relative size of predators and prey had a pervasive structuring influence on biomass fluxes within this large-mammal food web. Nevertheless, the large carnivore assemblage was dominated overwhelmingly

by the largest predator, which contributed the major share of animals killed across a wide size range.

Introduction

Size relationships have been recognized as central in structuring trophic linkages within food webs in both marine and terrestrial ecosystems (Cohen et al. 1993; Woodward et al. 2005). For predators, the upper size limit to the prey consumed is set by how successfully larger animals can be captured and subdued, while the lower size limit depends upon how frequently smaller dietary morsels can be found and eaten (Elton 1927). In contrast to the situation for most other predators, mammalian carnivores exceeding 20 kg in body mass commonly kill prey equal to or larger than their own body mass (Carbone et al. 1999). The expanding upper size limit to the prey species utilized has led to suggestions that the dietary range of larger carnivores is likely to be broader than that of smaller carnivores (Rosenzweig 1966; Gittleman 1985). Accordingly, it has been proposed that a nested dietary niche relationship exists (Sinclair, Mduma & Brashares 2003).

However, analyses based on the numerical representation of prey size classes may be misleading, because smaller animals are generally more abundant than larger ones (Damuth 1981). The relative dietary contribution to supporting the predator population depends not only on the frequency with which prey species differing in size are killed, but also on the carcass mass provided thereby for consumption by the predator. Furthermore, dietary niche relationships are represented more accurately by the relative preferences shown by predators for different prey species, controlling for differing relative abundance and hence encounter frequencies (Macarthur & Levins 1967; Pianka 1981).

Another complicating factor is that predators hunting as a group may be successful at subduing prey somewhat larger than could be killed by solitary predators of similar body size (Kruuk 1972; Schaller 1972). Moreover, for predators showing sexual size dimorphism males tend to capture somewhat larger prey than females of the same species (Radloff & du Toit 2004).

The top-down impact of predation on prey abundance depends not simply on the number of predator species to which each prey species is exposed (Sinclair et al. 2003), but rather on the magnitude of the aggregate change in mortality inflicted. Larger prey species must show a lower fundamental mortality rate than smaller species, to counterbalance their allometrically scaled maximum recruitment rate (White et al. 2007). Accordingly, a similar increase in annual adult mortality should have a greater effect on the population dynamics of larger prey species.

Few previous assessments of food web structure and dynamics have taken into account all these considerations, because the complexity of obtaining sufficient data on numerous species can easily become overwhelming. However, despite their rich species assemblage, African large-mammal predator–prey webs present a more tractable number of species, and greater potential to obtain adequate information on the linkages among them, than is the case for most other systems. Our analysis is

based on records of found carcasses, and predator responsible for the kill if predation was involved, collected in South Africa's Kruger National Park (henceforth Kruger) over 46 years, encompassing five mammalian carnivores larger than 10 kg in body mass, and 22 herbivore species spanning this size range.

The total database assembled between 1954 and 2000 amounted to 49 453 carcass records, of which 47 829 were ascribed to kills by a predator. Data from the first 12 years were summarized by Pienaar (1969). An analysis of the dynamics of the herbivore populations serving as prey (Ogutu & Owen-Smith 2003; Owen-Smith & Ogutu 2003), supported by estimates of stage-specific annual mortality (Owen-Smith & Mason 2005), enabled corrections to be made for under-recording of carcasses of smaller species. Additional adjustments were made to the census data indicating the relative availability of these prey species, also subject to under-recording of smaller species, in order to obtain relatively unbiased estimated of prey selection. For the purposes of this paper, we consider only the average patterns exhibited across the 19 500 km^2 extent of the protected area over the 46-year period spanned by the data. Over this time, the availability of most ungulate species showed no overall trend. In a subsequent analysis, changes in selection by predators in response to changing prey populations within this period, as well as to regional differences in prey availability, will be considered.

We expected to find that:
- The five predator species show distinct preferences for different size classes of prey, and that these preferences would be related to the body size of the predator, modified by the extent to which hunting takes place socially or solitarily.
- Each predator selects most strongly for the most abundant prey species within its preferred size range, taking into account also the habitat favoured for hunting. Specifically, coursing predators would tend to favour ungulate species occupying open habitats, and stalking predators the ungulate species found more commonly in thicker vegetation.
- The prey preference of the largest predator drops sharply only above a body mass of 1000 kg, i.e. within the megaherbivore size range defined by Owen-Smith (1988), contrary to findings by Sinclair et al. (2003) for Serengeti.
- Prey species larger than predator size make a greater dietary contribution than prey species smaller than the predator, because the greater carcass mass of the former outweighs the greater numerical predominance of the latter.
- The relative impact of predation on prey populations differs little among prey species smaller than 1000 kg, because the involvement of more predator species do not necessarily impose proportionately greater mortality.

Finally, we summarize these patterns by estimating the relative biomass fluxes linking the five carnivore species to different prey size ranges within the predator–prey web.

Methods

Database
The database consisted of the records of found carcasses reported by section rangers or other field staff in Kruger. These records were partitioned among three periods according to the form in which they were available. Those for the period 1954–65 were taken from Pienaar (1969). Records for the period 1966–85 were extracted from rangers' diary reports and entered subsequently into an electronic database, while those subsequent to 1986 were submitted electronically on computer sheets. Records for the most recent period were much less numerous than those for the earlier two periods, with those for 1986 missing (Table 1).

Table 1. Summary of the carcass records for Kruger Park spanning all causes of death by period; records for 1954–1966 from Pienaar (1969), remainder from unpublished South African National Parks files

Predator	Period				
	1954–66	1966–85	1987–2000	Combined	Proportion
Lion	12 217	11 655	2543	26 415	0.534
Leopard	5518	5629	1189	12 336	0.249
Cheetah	1092	1073	323	2488	0.050
Wild dog	2732	2541	248	5521	0.112
Spotted hyena	79	234	68	381	0.008
Jackal	60	158	14	232	0.005
Crocodile	197	117	7	321	0.006
Other predation	24	98	13	135	0.003
Other causes		1216	408	1624	0.059
Total	21 919	22 721	4813	49 453	

Cause of death was assessed from direct observation of the predator feeding on the carcass, tracks or other signs identifying the predator responsible, or other features of the carcass. The age class of the dead animal was noted as adult, subadult, young or juvenile, but with the basis for these subdivisions and their consistency unclear. The sex of the animal was also recorded where possible. Mortality incurred mainly by buffalo and kudu (scientific names of prey species appear in Appendix S2 in the Supplementary material) during periodic outbreaks of anthrax (Bengis et al. 2003) was evidently under-represented. The five carnivores responsible for 99% of the recorded predator kills, together with their body mass as represented by an adult female, are (in order of their contribution) lion (Panthera leo; 125 kg, Smuts, Robinson & Whyte 1980), leopard (P. pardus; 37 kg, Bailey 1993), African wild dog (Lycaon pictus; 25 kg, Gorman et al. 1998), cheetah (Acinonyx jubatus; 43 kg, Skinner & Smithers 1990), and spotted hyena (Crocuta crocuta; 70 kg, Skinner & Smithers 1990). However, kills by spotted hyenas are evidently hugely under-represented, as will be addressed below. Carnivores with too few records of ungulate kills for analysis included black-backed jackal (Canis mesomelas), caracal (Felis

caracasl), brown hyena (Hyaena brunnea), crocodile (Crocodylus niloticus), python (Python sebae) and martial eagle (Polemaetus bellicosus).

Adjustments to the Records
Juvenile ungulates were clearly under-represented in the carcass records, generally being consumed so completely as to leave no trace. Therefore, kills labelled 'juvenile' or 'young' were excluded, restricting the analysis to predation on adult or immature animals presumably over 1 year in age.

The bias against smaller prey species was corrected by relating the proportional representation of each ungulate species in the kill records (Appendix S1, Supplementary material) to the projected contribution by these species to the production of these carcasses (Appendix S2, Supplementary material), as follows. The annual carcass production was estimated as the product of population size and annual mortality rate for yearlings, subadults and adults at zero population growth (from Owen-Smith & Mason 2005; extrapolated to species of similar size). The population size estimate was based on the mean count total averaged across the three periods distinguished in the carcass records. Population totals for the period before 1966 were derived from the estimates provided by Pienaar (1963), plus the results of the first aerial count conducted in 1965. Those for the later periods were taken from aerial counts, repeated irregularly prior to 1977 and annually from then until 1996 (Viljoen & Retief 1994; Owen-Smith & Ogutu 2003). Population estimates for cryptic species not readily visible from the air were taken from Pienaar (1963), and adjusted using sighting frequencies relative to warthog from ground vehicle surveys of population structure undertaken annually between 1983 and 1996 (Mason 1990). The aerial count totals also needed to be corrected for undercount bias, dependent on body size, coat colour and habitat. The estimates of this bias reported in Mills & Biggs (1993) and Redfern et al. (2002) were extended to other species with similar characteristics (see Appendix S2, Supplementary material). Kills of bushpig (Potamochoerus larvatus), mountain reedbuck (Redunca fulvorufula), Lichtenstein's hartebeest (Alcelaphus lichtensteini), baboon (Papio ursinus), vervet monkey (Chlorocebus pygerythrus), porcupine (Hystrix africaeaustralis), aardvark (Orycteropus afer) and ostrich (Struthio camelus) were excluded from the analysis, because their population totals were either unknown or too low to estimate availability. These species combined contributed only 0·5% of the carcass records. Carnivore carcasses were excluded as generally not contributing to the food of the predator responsible for the kill.

A further correction needed to be applied for under-reporting of hyena kills, to allow for their contribution to the total prey mortality. Although spotted hyenas outnumber lions, the number of kills ascribed to hyenas amounted to less than 2% of those for lions. Even if half the food obtained by hyenas comes from scavenging rather than own kills (Henschel & Skinner 1990), this suggests that fewer than 5% of hyena kills were found relative to those of lions. This is probably because hyenas hunt only at night, with carcasses of smaller prey usually consumed completely, including bones, before dawn.

The conservative correction factors used to adjust the kill records are given in Appendix S1 in the Supplementary material. For lion, giraffe was assigned the baseline correction factor of 1·0 because it evidently produced the most readily found

carcasses. Kill records for other ungulate species were then adjusted upwards, based on the apparent extent of under-recording relative to the estimated production of carcasses. For cheetah and wild dog, which hunt mainly diurnally and kill mainly medium–small prey, plus leopard, which commonly drag prey into a tree where the carcass is readily visible, only kill records for the three smallest antelope species were adjusted upwards.

The adjusted kill records were then used to estimate the number of prey of each ungulate species killed by each of the five carnivore species annually, taking into account the estimated average predator population, daily meat requirement, prey composition, mean carcass mass and edible proportion (the latter taken from Viljoen 1993). Assumed mean predator totals for Kruger were 1800 lions, 2700 spotted hyenas, 700 leopards, 200 cheetahs and 300 wild dogs (Mills & Funston 2003; Funston & Ferreira unpublished). These totals appear consistent with the relative number of kills recorded for each carnivore, except for hyena (Table 1). Daily food consumption per adult female equivalent was estimated to be 5·8 kg/day for lions, 3·8 kg/day for hyenas, 2·2 kg/day for leopards, 2·1 kg/day for cheetahs and 3·5 kg/day for wild dogs (Mills & Biggs 1993). The annual kill rate per carnivore was adjusted until the projected daily food consumption amounted to 75% of the adult female requirement, thereby allowing for the proportion constituted by immature animals in the carnivore populations. This gave the following annual kill rates: lion, 15; leopard, 18; cheetah, 15; wild dog, 28. For hyena, a kill rate of nine animals per year was used, assuming that 60% of their annual diet was obtained by scavenging (based on Henschel & Skinner 1990).

Lastly, the projected total kills of each prey species annually, for all carnivores, was compared with the estimated annual number of deaths of each herbivore species, derived from population totals and mortality rates as described above. The scatter-plot of the ratio between projected predator kills and projected prey carcass production for each size class of prey appeared flat across most of the body mass range (Fig. 1), indicating that the correction factors adopted successfully counteracted the bias in finding carcasses related to herbivore size. For animals over 1000 kg in adult body mass, almost all the deaths were ascribed to causes other than predation (excluding juveniles). For small antelope, other carnivores besides the five species considered contributed additionally to mortality.
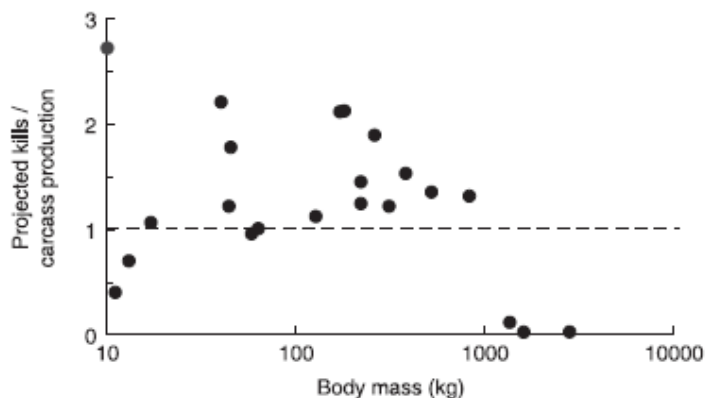
Fig. 1. Ratio of projected carnivore kills to projected annual carcass production plotted against body mass for each prey species.

Despite the defendable estimates used in making the adjustments, the mortality projected from carnivore numbers and kill rates exceeded the mortality loss projected from prey populations by approximately 50% on average across species. Some of the discrepancy results from the omission of juvenile prey from the analysis. Nevertheless, it seems that either carnivore abundance was somewhat lower in earlier times than the recent estimates used, or prey populations were substantially higher than those derived using the assumed undercount factors, or some combination of both. However, this discrepancy does not affect the interpretations drawn in the current paper, concerned with the relative size distributions of predators and prey.

Data Analysis and Interpretation

Prey body mass was assigned using the mean body mass of an adult female, listed in Appendix S2 in the Supplementary material (from Owen-Smith 1988). Prey size classes were assigned in the form of a doubling of the pivotal body mass, from 20 to 1250 kg, encompassing ranges between 33% below and 50% above the pivotal mass. Subsequent adjustments were made as follows. Nyala, the single species with a body mass around 80 kg, was shifted into the 40 kg category, while the smallest antelope species exhibited a mean body mass of approximately 15 kg rather than 20 kg. Elephant was included in the largest class, despite having a body mass approximately twice the pivotal mass.

The relative degree of selection for different prey species by each predator was derived by comparing the proportion in the prey killed with the proportion in the herbivore assemblage. Conventionally, 'preference' ratios calculated in this way are interpreted as indicating positive selection if they have a value greater than 1 (or zero on a log-transformed scale), and negative selection if they fall below this region of supposedly neutral selection. This interpretation is problematic, because the location of the neutral region depends on the set of prey species deemed to be available. For example, including the megaherbivores (i.e. elephant, rhino and hippo) among potential prey changes the preference ratios calculated for smaller prey species, in some cases altering whether the latter appear to be selected positively or negatively. Accordingly, the 'relative kill likelihood' was calculated by assigning the prey species showing the highest selection ratio for each predator a value of 1, and adjusting the selection ratios for other species relative to this maximum. This measure was interpreted as reflecting the reduced likelihood of other prey species being hunted and killed, relative to the most favoured species, assuming that encounters occurred randomly in relation to numerical prey abundance. Differences in encounters arising from clumping of prey in herds, the relative frequency with which a hunt is launched when each prey species is encountered, and the proportion of hunts that result in a kill, would be among the factors contributing towards the relative likelihood of a kill.

Results

Kill Size Distribution

In only 6% of the carcass records was death ascribed to a cause other than predation (Table 1). Only 13 carcasses of species exceeding 1000 kg in adult body mass were ascribed to predation (excluding predation on juveniles). These were mainly hippos, all presumed killed by lions apart from a hippo apparently killed by spotted hyenas. Ungulates weighing around 40 kg, comprising mainly impala, predominated numerically in the kills of all of the carnivores, even forming nearly 50% of kills by lions after the correction for under-recording (Fig. 2). Nevertheless, the proportional representation of this size category in lion kills was less than their relative abundance in the available prey, whereas the other four predators concentrated more strongly on impala and similar-sized prey than expected from the proportional representation of these species. Lions killed proportionally more prey in the size range 100–900 kg than the numerical availability of these species, while species larger than 100 kg were less well represented than their availability for cheetah, leopard and wild dog, but only those larger than 250 kg among spotted hyena kills.
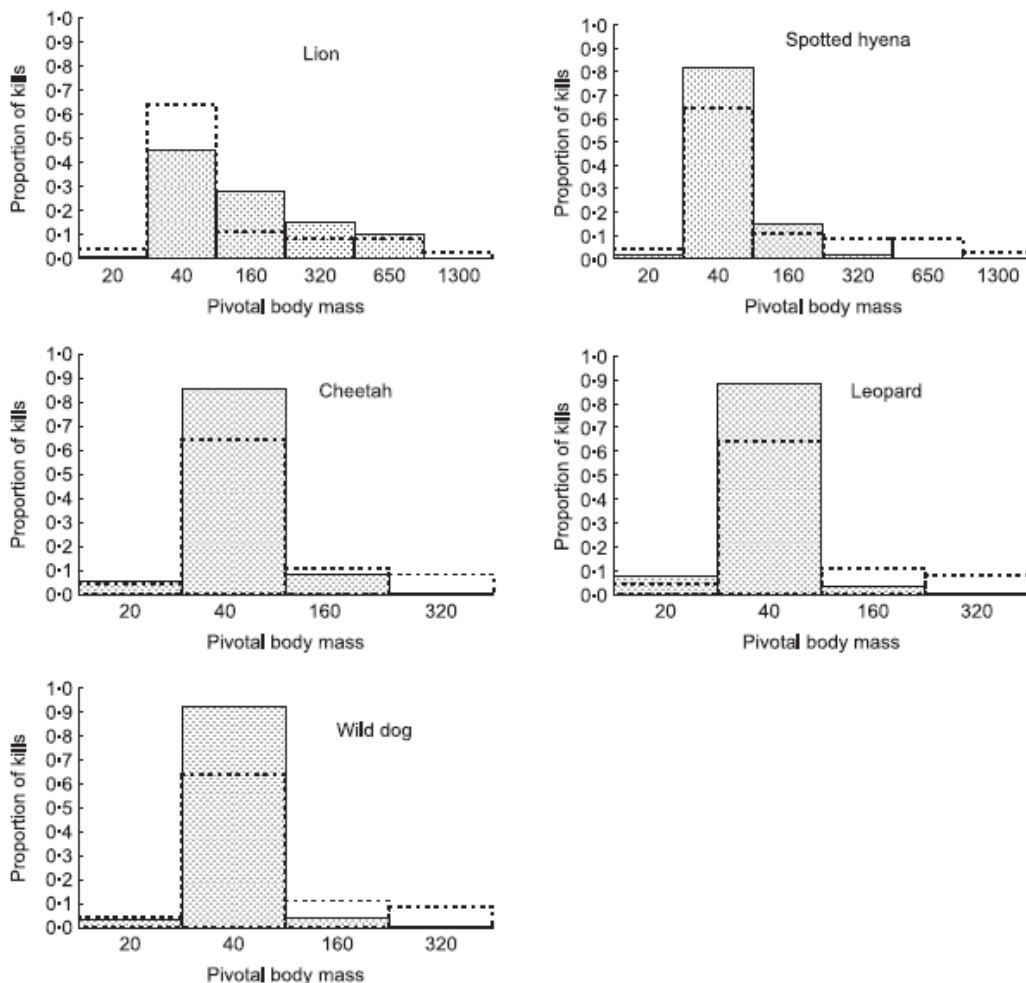
Fig. 2. Proportion of prey within different size ranges in the kill records for particular carnivore species (bars), compared with proportional availability (dotted lines).

Dietary Contribution

When converted to dietary intake on a mass basis, impala and similar-sized species constituted only 14% of the food consumed by lions, with the remainder spread fairly evenly across larger prey categories (Fig. 3). In contrast, impala-sized prey formed more than 50% of the diet of hyena, and 70–85% of the diet of the three smaller carnivores. Spotted hyena and cheetah obtained somewhat more of their food from ungulates weighing 100–250 kg than did leopard or wild dog.
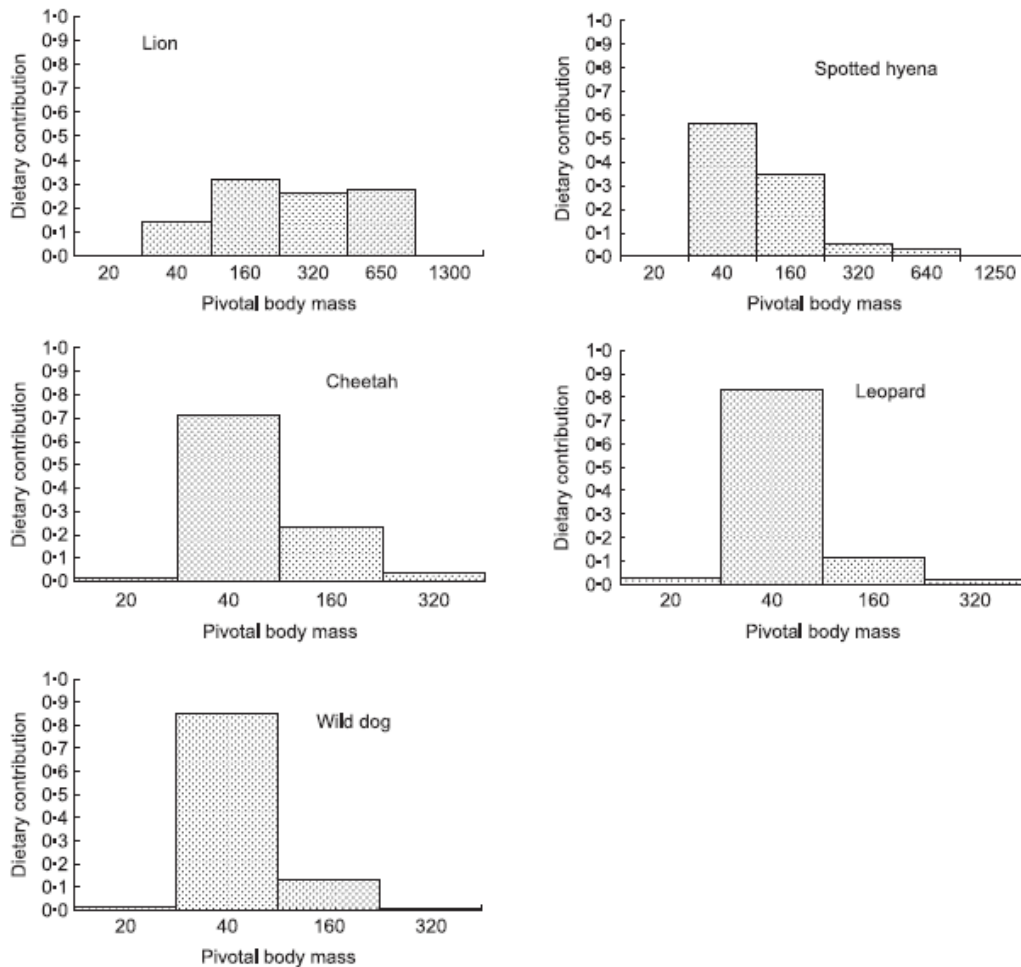
Fig. 3. Proportional dietary contributions by prey species within different size ranges for particular carnivore species.

Relative kill likelihood

Impala were much less likely to be killed by lions relative to their availability than larger ungulate species (Fig. 4). Wildebeest (body mass 220 kg) was the species most likely to be killed by lions, but waterbuck (body mass 180 kg), kudu (body mass 170 kg) and warthog (body mass 60 kg) showed an almost equal vulnerability to

forming prey. Relative kill likelihood by lions was only 60% for zebra (body mass 310 kg) and under 50% for buffalo (body mass 520 kg) and giraffe (body mass 825 kg), compared with wildebeest.
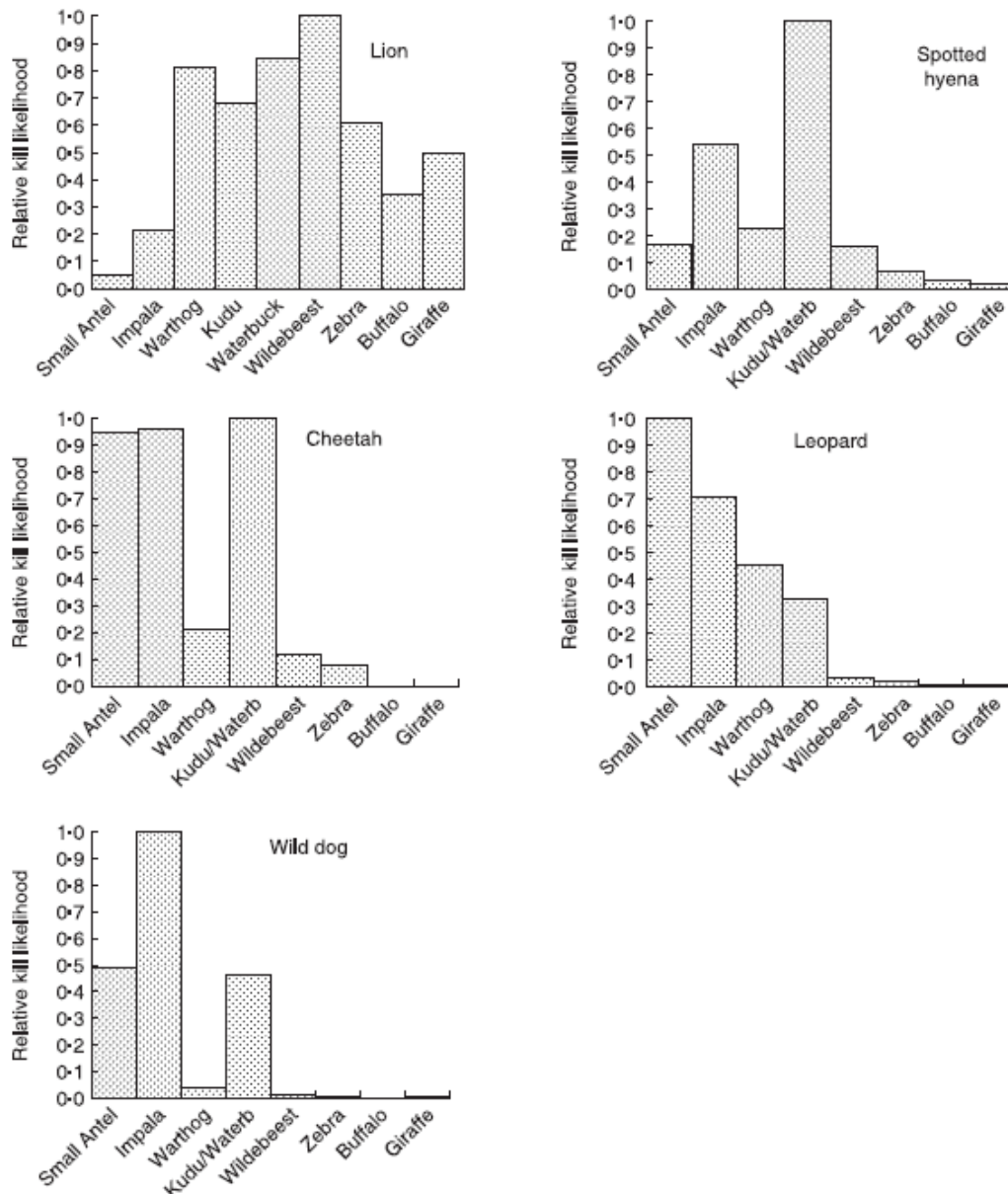

Fig. 4. Prey preferences expressed as relative kill likelihoods for some of the more common prey species, with the latter ranked in order of body size.

For spotted hyena, kudu plus waterbuck combined (because of the small sample of kills for each) were about twice as likely to be killed relative to encounters as impala, while wildebeest were much less likely to be killed (Fig. 4). Cheetah also showed a high likelihood of killing either kudu or waterbuck, as well as impala and small antelope species. For leopard, small antelope species were favoured most strongly, especially grey duiker and steenbok, with impala next most vulnerable. Bushbuck and

reedbuck, similar in size to impala, were also commonly killed. For wild dog, impala was clearly the most favoured prey species, but with kudu or waterbuck again featuring prominently among the medium–large ungulates. Notably, all three of the smaller carnivores were highly unlikely to kill wildebeest or larger species.

Prey selection compared with predator size

Because impala-sized animals formed the modal prey size for all of the predators, relative prey size selection was assessed in terms of the proportion of animals killed that were larger than impala (> 50 kg). There was a consistent increase in larger prey with increasing predator size (Fig. 5). However, the distinction among the four smaller carnivores was quite small, and the major difference lay in the proportion of prey larger than 50 kg killed by lions.
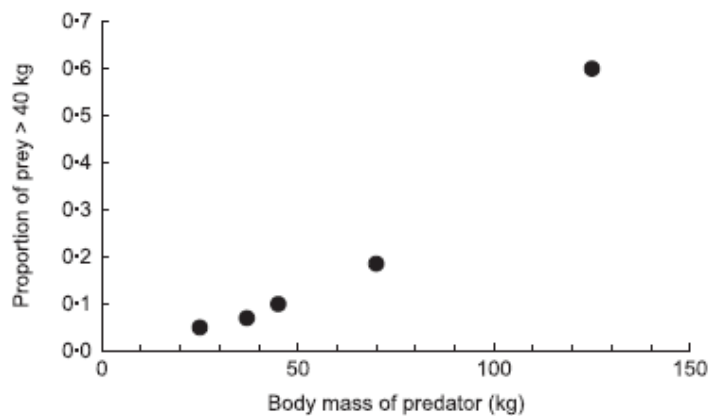

Fig. 5. Prey size selection indexed as the proportion of prey larger than impala (40 kg) killed relative to carnivore body mass (adult female).
 [Normal View]

Relative prey mortality imposed

For ungulate species from wildebeest size upwards, 90% or more of the predation incurred was ascribed to lion (Fig. 6). For kudu and waterbuck, projected kills ascribed to spotted hyena matched those by lion. Spotted hyena also accounted for 40% of the predation on impala, but with the other four carnivores also contributing substantially to impala mortality. Leopard was the major predator on small antelope, with hyena second in importance.
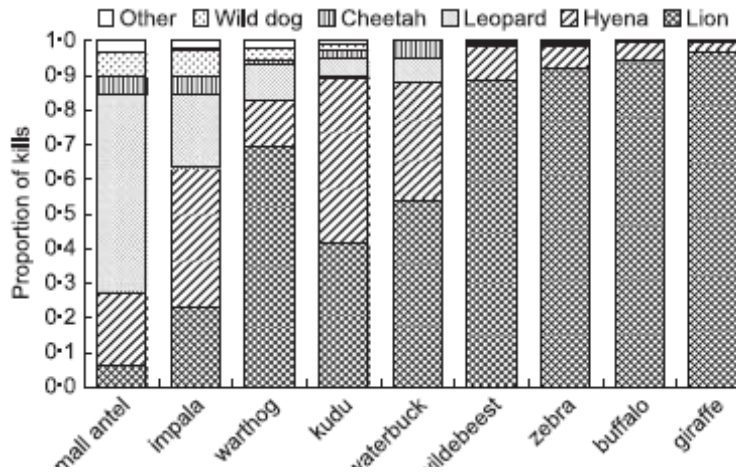
Fig. 6. Proportional contribution by different carnivores to mortality through predation incurred by some of the more common prey species.

Biomass structure and fluxes

Lion constituted approximately half the large carnivore biomass. Spotted hyena rivalled them in biomass but apparently obtained only approximately half their food through hunting. Hence, lion dominated by far the biomass fluxes through the large carnivore assemblage, and spread their consumption widely across herbivore size classes (Fig. 7). In contrast, predation by the remaining four carnivores was focused strongly on impala plus similar-sized ungulate species. Overall, about 65% of the prey biomass killed by carnivores was channelled through the lion population.
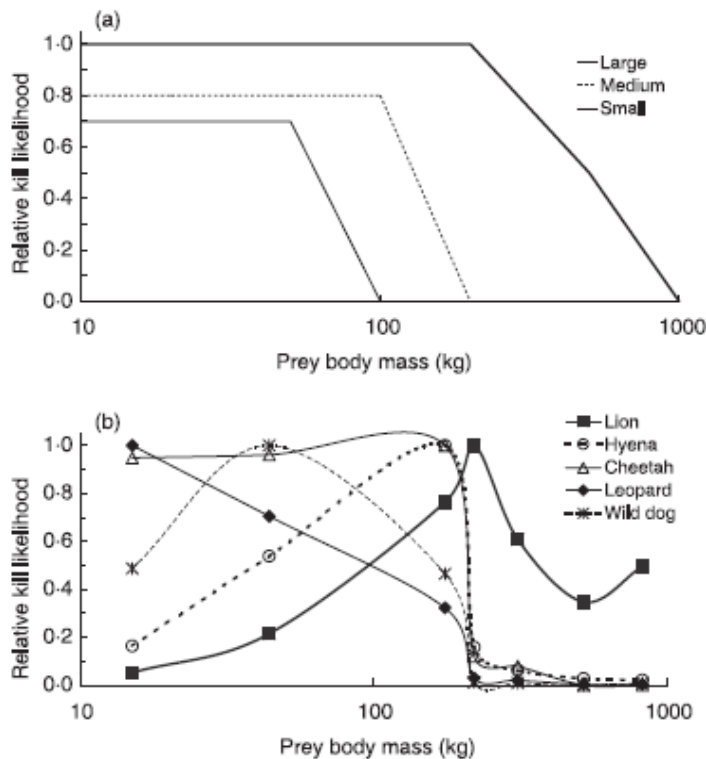
Fig. 7. (a) Schematic representation of the nested niche concept, with the dietary selection of smaller carnivores truncated at a lower prey size than those of larger carnivores. (b) Observed prey preferences of carnivores in Kruger (derived from estimated relative kill likelihoods) for prey species arrayed in order of their body size, excluding warthog as discrepant.

Discussion

Reliability of the carcass records

Our analysis involved several adjustments to suppress the bias against small prey in found carcasses and the under-representation of kills by spotted hyena. The estimate of the extent to which spotted hyena obtained their food by scavenging vs. predation was also based on a single study. Nevertheless, the prey proportions that we derived for lion corresponded closely with those recorded through direct observations of predation in the Mala Mala Private Game Reserve adjoining central Kruger (Radloff & du Toit 2004), as well as those observed by following lions through the night in the SE region of Kruger (Mills & Biggs 1993; Funston et al. 2001; Table 2). For leopard, cheetah and wild dog, direct observations in the latter two areas showed a higher proportion of small antelope killed than extrapolated from found carcasses. Nevertheless, the numerical predominance of impala in the kills made by these species was consistent.

Table 2. Comparative prey composition records from Kruger Park and adjoining wildlife reserves, expressed as proportion of recorded kills

Predator	Locality	Procedure	n	Proportion of kills (%)									Reference
				Small antelope	Bushbuck or reedbuck	Impala	Warthog	Kudu or waterbuck	Wildebeest	Zebra	Buffalo	Giraffe	
Lion	Kruger Park	Carcasses	23 829	0.2	0.8	20	2	20	20	16	14	5	This study
Lion	Kruger Park	Carcasses, adjusted		0.6	1	39	6	8	14	15	7	2.5	This study
Lion	Kruger, SE region	Observations	111	0	0	29	13	0	14	16	(4)	0	Mills & Biggs 1993
Lion	Malamala	Observations	2129	2	1	38	11	12	10	8	7.5	5	Radloff & du Toit 2004
Leopard	Kruger Park	Carcasses	10 275	8	8	76	2	2	0	0	0	0	This study
Leopard	Malamala	Observations	1452	24	9.5	48	6	3.5	< 1	< 1	0	0	Radloff & du Toit 2004
Leopard	Londolozi	Observations	63	14	0	28	15						Mills & Biggs 1993
Cheetah	Kruger Park	Carcasses	1914	5	8	77	1	7	0	0	0	0	This study
Cheetah	Malamala	Observations	321	21	3	65.5	2	3	1	0	0	0	Radloff & du Toit 2004
Cheetah	Kruger, SE region	Observations	61	13		44							Mills & Biggs 1993
Wild dog	Kruger Park	Carcasses	4509	3	4	88	0	4	0	0	0	0	This study
Wild dog	Malamala	Observations	179	22	5	67.5	0	3	0	0	0	0	Radloff & du Toit 2004
Wild dog	Kruger, SE region	Observations	52	12		54		12					Mills & Biggs 1993

Dietary contributions projected from the stomach contents of 257 lions killed in the central region of Kruger through 1974–8 were as follows: giraffe 43%, wildebeest 23%, zebra 15%, kudu plus waterbuck 6%, impala 5% and buffalo 4·5% (Smuts 1979). Corresponding projections from the carcass records for the southern half of Kruger over this period, corrected for under-recording bias, were giraffe 32%, zebra 21%, buffalo 20%, wildebeest 14%, kudu plus waterbuck 7% and impala 5%. This is quite close agreement, recognizing that wildebeest and giraffe are more abundant and buffalo relatively less represented in the central region than overall in the southern half of the park.

For spotted hyena, Smuts (1979) found that impala constituted 57·5% of the food consumed in central Kruger, followed by zebra (13%) and wildebeest (12%), compared with 52%, 5% and 5%, respectively, projected from the adjusted kill records for these hyenas across the whole park. Some of the stomach contents of hyenas would have come from scavenging on lion kills, accounting for the greater predominance of medium–large ungulates than estimated from kills ascribed to hyenas. The prevalence of impala indicates that much of the food of hyenas must have been obtained through hunting of this species in particular. While lions may obtain much of their food by scavenging from kills made by spotted hyenas in other parts of Africa (Kruuk 1972; Cooper, Holekamp & Smale 1999), this behaviour is seldom observed in Kruger (Funston et al. 2001).

Prey selection
The prey base for lion in Kruger extends over eight common species, but in total 15 prey species, 11 of which are shared little with other predators. Relatively little difference in kill likelihood was evident among prey species within the favoured size range of 60–250 kg, i.e. from half to twice the mass of a lioness, with the most abundant species in this size class (i.e. wildebeest) selected most strongly. The largest prey were constituted by adult male giraffe, weighing around 1200 kg, approximately 10 times the mass of the predator. Species under 20 kg in mass, i.e. 15% of predator body mass, contributed little to the prey base for lions, due probably to their agility. Studies elsewhere show buffalo to be numerically the predominant prey of lion in Chobe National Park in Botswana (Viljoen 1993), Kafue National Park in Zambia (Mitchell et al. 1965) and Lake Manyara National Park in Tanzania (Schaller 1972). Hayward & Kerley (2005) found that lion selected prey species preferentially within a mass range of 190–550 kg, but made no adjustment for the under-recording of smaller prey species. Over half of the giraffe and two-thirds of the buffalo killed by lion were adult animals in the Mala Mala Reserve adjoining Kruger (Radloff & du Toit 2004). A substantial fraction of the adult buffalo falling prey to lions are killed by male lions hunting independently of female prides (Funston et al. 1998, 2001; Radloff & du Toit 2004). In northern Botswana, lions hunting in groups of around 10 killed young elephants weighing up to 2500 kg in body mass, more than 10 times the mass of a male lion (Joubert 2006).

Three smaller carnivores concentrated on prey species below the size range favoured by lion, with a single antelope species about the same mass as these predators predominating, and seven additional ungulate species contributing. The upper size limit was constituted by species up to 200 kg in adult body mass, i.e. five to eight times predator mass. At the lower end, our analysis encompassed only ungulates

weighing 10 kg or more. However, leopard kills recorded in the Kruger database included scrub hare (Lepus saxatilis) and cane rat (Thryonomys swinderianus), as well as vervet monkey, all less than 15% of predator mass. In the Kalahari, prey species smaller than 10 kg constituted 10% of recorded kills of leopards (Mills 1990). Therefore, the prey size range appears to be no less broad for these smaller carnivores than for lion.

A carnivore shifting facultatively between predation and scavenging, i.e. spotted hyena, falls in the middle in body size. Spotted hyenas hunt infrequently in groups in Kruger (Henschel & Skinner 1990), which may explain why they rarely kill wildebeest or zebra weighing three to four times predator mass. Generally, hyenas tend to restrict their hunting to prey smaller than 150 kg (Kruuk 1972; Cooper 1990; Mills 1990).

Despite substantial overlap in the range of prey sizes killed, the dietary niches of the five carnivores tend to be distinct in terms of the prey size class preferentially selected (Fig. 7). The most favoured prey size appears to be one to two times carnivore body mass, with the two social predators (i.e. lion and wild dog) tending to select slightly larger prey relative to their size than the solitary hunting species (leopard and cheetah, although recognizing that male cheetah commonly hunt in coalitions; Mills, Broomhall & du Toit 2004). Leopard, cheetah and wild dog overlap strongly through sharing in common a high prey preference for impala, vastly the most abundant of the medium–small ungulates. However, leopards select most strongly for smaller antelope species inhabiting denser woody vegetation, notably bushbuck and duiker, which are killed relatively less frequently by cheetahs and wild dogs. Leopards also kill warthogs more commonly than do cheetahs or wild dogs, despite being smaller in size. Wild dog and cheetah, both cursorially hunting, mainly diurnal predators, seem similar in their prey selection despite differing in body size (Mills & Biggs 1993). Both species are limited in their distribution by aggressive interference competition from lions, rather than prey availability (Creel & Creel 1996; Mills & Funston 2003), and hence are more common in wooded rather than open habitats in Kruger (Mills & Gorman 1997; Mills, Broomhall & du Toit 2004). Their diurnal habitats seem related more to avoiding kleptoparasitism from spotted hyenas than to avoiding dietary competition with leopards (Carbone, du Toit & Gordon 1997).

Top-down limitation of prey populations
In Kruger, very few found carcasses of ungulates from giraffe size downwards lacked evidence of a predator kill, except during outbreaks of the disease anthrax (not represented in the database). Most deaths ascribed to causes besides predation were for elephants, rhinos and hippos, i.e. megaherbivores weighing over 1000 kg as adults. Nevertheless, the extent to which the mortality imposed by predation is additive cannot readily be assessed by the frequency with which carnivores seem responsible for a kill. Mortality may be predisposed by injuries, malnutrition or senescence, with predation merely advancing the time of death. The susceptibility of buffalo to predation appears strongly dependent on rainfall conditions and hence food sufficiency (Mills, Biggs & Whyte 1995; Funston & Mills 2006), although giraffe do not show this pattern (Owen-Smith, Mason & Ogutu 2005). Through killing prey rather than waiting for death from other causes, carnivores obtain pre-emptive access to the meat provided by the carcass.

The contention by Sinclair et al. (2003) that ungulates larger than 150 kg incur relatively less predation than smaller species, and hence are largely food-limited, is not supported by our findings from Kruger. The low proportion of the deaths of these very large ungulates ascribed to predation in the Serengeti (Sinclair et al. 2003) is probably an outcome of the huge numerical predominance of wildebeest and zebra, both highly favoured by lions, in this ecosystem. The ratio of predators to prey is vastly greater in Kruger than in Serengeti (Mills & Funston 2003). The reduced kill likelihood by lions for buffalo and giraffe in Kruger corresponds closely with the difference in the annual mortality that these large ungulates incur as adults relative to medium-sized species (Owen-Smith & Mason 2005). Hence, the diversity of carnivores preying on impala in Kruger had no greater impact on the abundance of impala than that of lions only on giraffe. Only among megaherbivores weighing substantially over 1000 kg as adults did predation fade out as a cause of adult mortality, making food limitation the sole factor controlling abundance.

Food web structure

The largest carnivore overwhelmingly dominates the large predator guild in Kruger (Fig. 8). Lions commandeer 65% of the biomass flux of prey killed, through constituting the greatest proportion of predator biomass, as well as by aggressively excluding and frequently killing other carnivores (Mills & Funston 2003). Ungulates larger than 250 kg contribute in aggregate more towards supporting the lion population than species within the favoured size range of 100–250 kg. Smaller carnivores kill mainly ungulates under 50 kg, although elsewhere spotted hyenas hunting in packs kill prey as large as adult oryx (Oryx gazella, 200 kg) and zebra (250 kg; Kruuk 1972; Mills 1984, 1990). In Kruger, these hyenas apparently rely to a greater extent on scavenging from lion kills (Henschel & Skinner 1990) than elsewhere (Kruuk 1972; Cooper et al. 1999). The relative rarity of cheetah and African wild dog in Kruger appears no different from the general pattern elsewhere in Africa, as a consequence of aggressive interference by larger carnivores (Mills & Funston 2003).
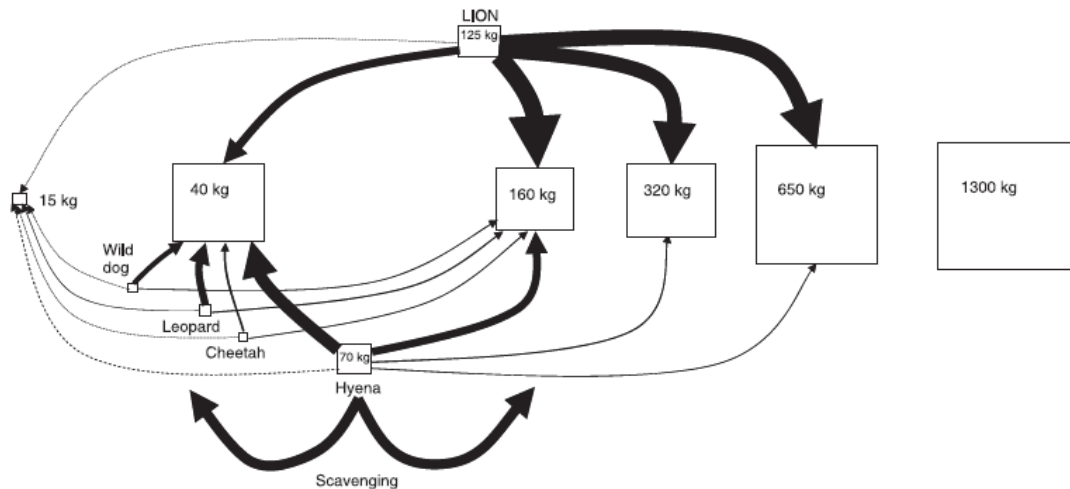

Fig. 8. Pictorial representation of biomass fluxes occurring within the predator–prey web. Boxes represent prey size classes, arranged relative to the log of the pivotal body

mass (indicated within each box) along the horizontal axis. The area of each box is proportional to the standing biomass of the species within this size class. Boxes representing carnivore species are likewise arranged relative to the log of adult body mass, with the area of each box proportional to carnivore biomass, amplified by a factor of 10 relative to prey biomass. The breadth of the lines connecting carnivore species to prey size classes is proportional to the biomass flux occurring through predation via this link. For spotted hyena, it was assumed that 40% of food was obtained through predation and 60% by scavenging.

Therefore, Damuth's (1981) claim that bioenergetic fluxes through populations are independent of body size applies neither to large herbivores (Owen-Smith 1988; du Toit & Owen-Smith 1989) nor to the large carnivores dependent on these herbivores as their food resource. The largest herbivores spread their consumption into the quality range favoured by smaller species, potentially restricting the abundance of the latter (Owen-Smith 2002). Similarly, through their substantial contribution to mortality incurred by impala, the staple prey species for other large carnivores, lions add exploitative competition to aggressive interference.

Our analysis for Kruger demonstrates the pervasive influence of body size in structuring the predator–prey component of the large-mammal food web. Despite overlap in the overall size range of prey killed among carnivores, relative body size strongly determines (a) relative kill success for particular size classes of prey species and (b) dietary dependency on different body size ranges of prey. Rather than niches being nested, each predator effectively exploits a broad size range of prey from an order of magnitude below to an order of magnitude above its own body mass, while preferring prey species equal to or somewhat larger than its own size. Only above a body mass of around 1000 kg do mammalian herbivores become generally free of predation, except on immature animals, and hence almost solely food-limited.

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