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Large predators and their prey in a southern African savanna: a predator's size determines its prey size range

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Summary

1. A long-term (13-year) data set, based on > 4000 kills, was used to test whether a sympatric group of large predators adheres to the theoretical predictions that (1) mean prey body size and (2) prey diversity increase as functions of predator body size.
2. All kills observed by safari guides are documented routinely in Mala Mala Private Game Reserve, South Africa. We analysed these records for lion (*Panthera leo*, Linnaeus), leopard (*Panthera pardus*, Linnaeus), cheetah (*Acinonyx jubatus*, Schreber) and African wild dog (*Lycaon pictus*, Temminck). Males and females of the sexually dimorphic felid species were treated as functionally distinct predator types. Prey types were classified by species, sex and age class.
3. Prey profiles were compared among predator types in terms of richness and evenness to consider how both the range of prey types used and the dominance of particular prey types within each range may be influenced by predator size. No significant size-dependent relationships were found, so factors separate from or additional to body size must explain variation in prey diversity across sympatric predators.
4. A statistically strong relationship was found between mean prey mass and predator mass ($r^2 = 0{\cdot}86$, $P = 0{\cdot}002$), although pairwise comparisons showed that most predators killed similar prey despite wide differences in predator size. Also, minimum prey mass was independent of predator mass while maximum prey mass was strongly dependent on predator mass ($r^2 = 0{\cdot}71$, $P = 0{\cdot}017$). The ecological significance is that larger predators do not specialize on larger prey, but exploit a wider range of prey sizes.

Key-words: allometry, coexistence, diet breadth, guild relations, large carnivores.

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Introduction

Relationships between predator and prey body sizes have been examined frequently in meta-analytical studies of coexistence within predator guilds, from which two generalizations have emerged: an increase in predator size is associated with increases in (1) mean prey size (Rosenzweig 1966; Gittleman 1985; Vézina 1985; Carbone *et al.* 1999) and (2) prey diversity (Schoener 1969; Wilson 1975; Gittleman 1985; Cohen *et al.* 1993). For terrestrial vertebrate predators, Vézina (1985) argued further that within the overall relationship between predator and prey sizes there are separate relationships for insectivores, piscivores and carnivores ('carnivores' in this case being consumers of primarily vertebrate prey other than fish). Vézina's analysis indicated that carnivores have the highest prey/predator mass ratio, with the larger carnivores taking disproportionately larger prey than the smaller ones.

Meta-analysis is used commonly for developing and testing general principles in ecology, although the practice is fraught with various statistical problems of bias and non-independence (Gates 2002). Furthermore, in the case of predator–prey relations there is a general paucity of data on complete prey profiles, which has restricted some meta-analyses (e.g. Carbone *et al.* 1999) to only the most common prey used by each predator. It is thus important to test generalizations such as those cited above on primary data sets comprising complete prey profiles in which the frequencies of all prey types and size classes are represented. To make inferences on resource partitioning also requires that free-living sympatric predators be studied in the same area, in the same way, over the same period. To date the few published studies of this type have provided little or no

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support for the generalizations arising from meta-analyses. Using field observations and experimental manipulations Dickman (1988), for example, showed that the smaller predators in an insectivorous mammal guild took the smaller prey but then switched to larger prey when the larger predators were removed. Consequently prey selection could depend more on competition among predator guild members than on any inherent relationship between predator and prey sizes.

A confounding factor in predator–prey studies that include a wide size-range of mammalian predators is high variability in the diets of the smaller species, which can switch between insectivory, omnivory and carnivory. It now appears that a striking transition in prey selection occurs at a predator mass of about 21·5 kg, with those species below the threshold taking prey of < 45% predator mass and those above taking prey of > 45% predator mass (Carbone *et al*. 1999). Also, all canid and felid species above the threshold prey purely on vertebrates, while those below may feed omnivorously or prey on both invertebrates and vertebrates. This new finding implies that large carnivores (> 21·5 kg) constitute a distinct functional group from which predator–prey size relationships should emerge more clearly than from carnivore assemblages that are distributed across both sides of the body mass threshold (e.g. Ray & Sunquist 2001). Nevertheless, the few examples of such studies to date have also been inconclusive. In India, analyses of scats and kill records confirmed that the largest predator (the tiger, *Panthera tigris* Linnaeus) did kill the largest prey, but then pack-hunting dholes (*Cuon alpinus* Pallas) commonly killed larger prey than leopards, which are solitary but heavier than dholes (Karanth & Sunquist 1995). In North America, Pierce, Bleich & Bowyer (2000) found that despite substantial differences in body size and contrary to predictions on size-related prey partitioning, coexisting mountain lions (*Puma concolor* Linnaeus) and coyotes (*Canis latrans* Say) both preyed on young and adult mule deer (*Odocoileus hemionus* Rafinesque).

Being comparatively species-rich, the African savanna large carnivore guild has been the subject of various reviews of interspecific interactions among predators and between predators and their prey (e.g. Kruuk & Turner 1967; Pienaar 1969; Schaller 1972; Mills 1984; Frame 1986; Mills & Biggs 1993). In all cases, however, the requirements of meta-analysis (see Gates 2002) could not be met, mainly because of methodological, spatial and temporal differences between autecological studies. In this paper we present analyses based on a unique set of primary data collected by photographic safari guides over a continuous 13-year period in South Africa, covering kill records for lion, leopard, cheetah and African wild dog. Because these records were collected concurrently for all four species in the same area and in the same way over a long period, we are confident in using this uniquely large data set (> 4000 kills) to test whether prey size and prey diversity do both vary as functions of predator body size.

Methods

STUDY AREA

All kill records were collected between 1988 and 2000 in Mala Mala Private Game Reserve (midpoint: 31°35′ E, 24°51′ S) in the lowveld of the Limpopo Province, South Africa. Mala Mala is one of several private game reserves that for > 50 year have been collectively managed as a conservancy (570 km^2) within which indigenous animals have free movement across property boundaries. In 1993 the game fence along the 29 km boundary between Mala Mala and Kruger National Park was removed, bringing Mala Mala into a conservancy covering some 20 000 km^2.

The vegetation in Mala Mala is mainly mixed *Combretum*/*Terminalia* woodland as described by Gertenbach (1983) for Kruger, with narrow strips of riparian woodland along the main watercourses. The Sand River provides perennial surface water and numerous tributaries dissect the undulating landscape, which includes scattered granite-topped inselbergs (*koppies*). Annual rainfall is about 600 mm, falling mainly between September and April (Gertenbach 1980), and in the study period the reserve experienced its driest and wettest years in recorded history (since 1908) with 237 mm in 1991/92 and 1126 mm in 1999/2000.

There are about five prides of lions with all or parts of their territories on Mala Mala and it is estimated that > 20 different leopards are encountered monthly, of which 10 known individuals are resident in Mala Mala. Cheetahs and wild dogs range widely across Mala Mala, adjacent private reserves and Kruger, and wild dogs regularly den in Mala Mala, as do spotted hyenas *Crocuta crocuta* (Erxleben).

DATA COLLECTION

Mala Mala has operated as an exclusive destination for photographic safaris since 1964 and detailed reports on wildlife sightings have been kept since 1988. There are usually about eight game-viewing vehicles (range 1–15) active in Mala Mala on any one day, operating out of three separate lodges, taking clients on dawn and dusk game drives (about 06.00–09.30 h and 16.00–20.00 h, respectively). An experienced ranger conducts each game drive and is accompanied by a tracker, with rangers maintaining constant radio contact with each other. Rangers follow a road network and coordinate their movements to maximize encounters with 'charismatic' species, with large predators being particularly sought after. For each large predator sighting the location is reported by radio together with the sex and age class (juvenile, subadult, adult) of each individual and the general activity of the individual or group when it was encountered. When predators are found feeding on prey or witnessed making a kill, the species, sex and age class of the prey are also reported as completely as possible. All these details are transcribed

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into a written report every evening as part of the daily routine.

DATA ANALYSIS

A database was built from the original game drive reports for the period January 1988–December 2000. Large felids exhibit marked sexual size-dimorphism and the males and females tend to segregate when hunting, so the sexes were treated as separate predator types for lions, leopards and cheetahs. Wild dogs hunt in mixed packs and the sexes are of similar size, so they were considered as one predator type. Kills attributed to felid females were all kills where a female was present, including those made by single females, groups of females accompanied by their offspring and occasionally (e.g. with lions) by adult males. Kills attributed to males were those made by individuals or coalitions where no females were present. Spotted hyenas were excluded from this analysis because, due to their scavenging behaviour (Henschel & Skinner 1990), it was considered too difficult to determine whether or not a kill being fed on by hyenas could be attributed to hyena predation.

Because of the wide variation in body size across sex and age classes among bigger prey species, the following prey types were defined for ungulates and primates: juvenile (male and female), subadult male, subadult female, adult male, adult female, 'unknown' (not sexed or aged). For the various other smaller prey species that were not aged and sexed, and for which intraspecific size variation is comparatively small, the prey type was simply the species. Two data sets were then compiled to describe the prey profiles of each predator type: one defined by prey type, the other by species only for all prey. Species recorded as having been killed but rarely consumed (e.g. other predators, such as spotted hyenas) were not considered as prey and were omitted.

ANALYSIS OF PREDATOR–PREY BODY MASS RELATIONSHIPS

Body mass values for predator types (Table 1) were taken from published records made as closely as possible to the study area. The lion (Smuts, Robinson & Whyte 1980), leopard (Bailey 1993) and wild dog (Gorman *et al*. 1998) masses are all from the central or southern parts of the neighbouring Kruger. The cheetah masses are from animals originating in Namibia but released into Kruger in 1969 (Labuschagne 1979). Three male cheetahs shot in the Mala Mala area some time before 1951 compare well with the Namibian data (mean values of 52·6 kg and 53·9 kg, respectively; Roberts 1951).

For mammalian prey types, values of adult male and female body mass (Appendix I) were taken from

Table 1. Mean adult mass (kg) of predator types and typical body mass (kg) of their respective ungulate and primate prey, after adjusting for differences between age and sex classes within each prey species (see Methods for calculations and Appendix I for scientific names)

	Predator type (and body mass)						
Prey species	Lion male (188)[a]	Lion female (124)[a]	Leopard male (61·3)[b]	Leopard female (37·3)[b]	Cheetah male (53·9)[c]	Cheetah female (43·0)[c]	Wild dog (25·2)[d]
Ungulates							
African buffalo	426	446	165				
Bushbuck		41·9	34·3	30·7		34·2	50·0
Bushpig		44·4*					
Common duiker		15·2	13·3	14·0	16·2	13·9	14·6
Giraffe	880	668	303				
Hippopotamus	1013*						
Impala	35·4	31·8	35·5	30·9	32·6	28·8	30·8
Klipspringer				9·9*			
Kudu	193	165	100	88·9	110	57·8	108
Nyala	46·4*	100	61·8	43·4		34·3	46·4*
Reedbuck			36·3			28·6*	
Steenbok	11·3	10·2	10·1	10·4	8·47*	10·7	10·4
Tsessebe		127	95·3*				
Warthog	56·5	55·6	36·9	20·4	42·4*	20·4	
Waterbuck	210	193	63·0	63·0	63·0		135*
White rhinoceros		1055					
Wildebeest	145*	162	63·6	63·6	63·6	63·6	
Zebra	197	175	112				
Primates							
Chacma baboon	11·6*	13·0	7·08	11·6*			
Vervet monkey		5·51	4·09	4·76			

[a]Smuts *et al*. 1980; [b]Bailey 1993; [c]Labuschagne 1979; [d]Gorman *et al*. 1998. *Unit mass for that prey species, as age and sex were not recorded.

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Skinner & Smithers (1990) and Owen-Smith (1988). In the absence of growth curves for all prey species, subadult mass was approximated by multiplying adult male or female mass by 0·7; values for juveniles were approximated by multiplying mean adult mass by 0·3 (based on impala, from Fairall 1983). The proportional representation of each prey type in the kill records for each predator type (Appendix II), combined with the body mass estimates for each prey type, allowed the calculation of the typical mass of ungulate and primate prey species killed by each specific predator type (Table 1). In prey profiles where certain primate and ungulate species had no age or sex information, the unit mass of that species was used (3/4 adult female body mass; Owen-Smith 1988). Unit mass was used in the same way for all mammalian prey species that were not ungulates or primates. Adult mass was used for birds (Maclean 1984) and reptiles (Jacobsen 1989).

ANALYSES OF PREDATOR BODY MASS–PREY DIVERSITY RELATIONSHIPS

Measures of diversity, or heterogeneity, have two components: richness and evenness (Krebs 1999). For the prey profile of any particular predator, richness represents the number of different prey types, while evenness represents the extent to which preferred or common prey types dominate numerically over all the others. We measured both from the prey profiles of each predator type. In this case birds (except ostriches, *Struthio camelus* Linnaeus) were lumped together as one prey type, as were reptiles. Richness is affected directly by sample size and there were large variations in sample size between the prey profiles of the various predator types. The rarefaction method (Krebs 1999) was thus used to determine the expected number of prey types or prey species present in a random sample of kills that was smaller than the original. Reducing the prey profiles of all predator types to the same standard number of kill records in this way allowed for meaningful comparisons of prey richness among predator types. A standardized sample size has to be large enough to reveal any real differences in prey richness between predator types, but small enough to incorporate as many predator types as possible. To determine this, cumulative curves were plotted to see how the number of prey types increased as the number of randomly drawn kill records increased. On the basis of these curves cheetah males were excluded from the analysis, as that sample size was too small ($n = 41$). A sample of $n = 140$ (the size of the lion male prey sample) was set as the standardized sample for the rarefaction calculations that were then performed for all the other predator types. Although none of the curves reached a clear asymptote in prey types within 140 kills, they had differentiated by this point and 140 kills constituted the largest sample possible without losing the largest predator type (lion males). To run the rarefaction calculations using prey types, the kill records for which sex and age were 'unknown' for a particular prey species were allocated to sex and age classes by using the proportions in the kills for which this information had been recorded (values in brackets, Appendix II). For example, if juveniles accounted for 35% of the sexed and aged impalas killed by wild dogs, then 35% of the 'unknown' impalas killed by wild dogs were also considered to be juveniles. A separate rarefaction calculation was performed using prey species only, for which no adjustments to the original data were required.

Camargo's index (Camargo 1993; Krebs 1999) was used to compare evenness among prey profiles. This index, which ranges from $E' = 0$ (no evenness) to $E' = 1$ (complete evenness), is independent of species richness (Smith & Wilson 1996) and so no standardization of sample sizes was required. E' was calculated for prey profiles described in terms of both prey species and prey type.

ANALYSIS OF PREY SIMILARITY IN RELATION TO PREDATOR SIZE SIMILARITY

Similarity (overlap) in each of the 21 possible pairwise comparisons of the seven prey profiles was quantified using Morisita's index of similarity (Krebs 1999), using the same prey data as for the rarefaction calculations. In addition all ungulate and primate prey for which no age and sex data were available (0·42% of the total sample, Appendix II) were made adult females arbitrarily for standardized comparisons. Predator size similarity was quantified for each of the 21 possible pairs of predator types by calculating the mass of the smaller predator of the pair as a proportion of the larger one.

Results

From the percentage frequency of occurrence in kill records (see Appendices I and II for species names and kill data) impala emerged as the most common prey species for cheetahs (males 70·7%, females 64·6%), wild dogs (67%), leopards (males 47·1%, females 48%) and female lions (40%). Warthog was the second most common prey species taken by female lions (11%), male leopards (11%) and male cheetahs (7%), while duiker came second for female leopards (20%) and wild dogs (16·2%). After impala the next most common prey species taken by female cheetahs were steenbok (11·8%) and duiker (11·4%). Male lions were found to concentrate on much bigger prey, most frequently killing buffalo (45%) and giraffe (19·3%). The modal prey type was juvenile impala for all predator types except male leopard (mode = adult female impala) and male lion (mode = adult male buffalo). The median prey type for wild dog, female cheetah and female leopard was adult duiker; for male cheetah it was adult female impala, for male leopard it was adult female bushbuck, for female lion it was subadult male warthog and for male lion it was juvenile giraffe. From frequency distributions of prey size classes, with prey size expressed as a proportion of predator size (Fig. 1), it can be seen that the prey

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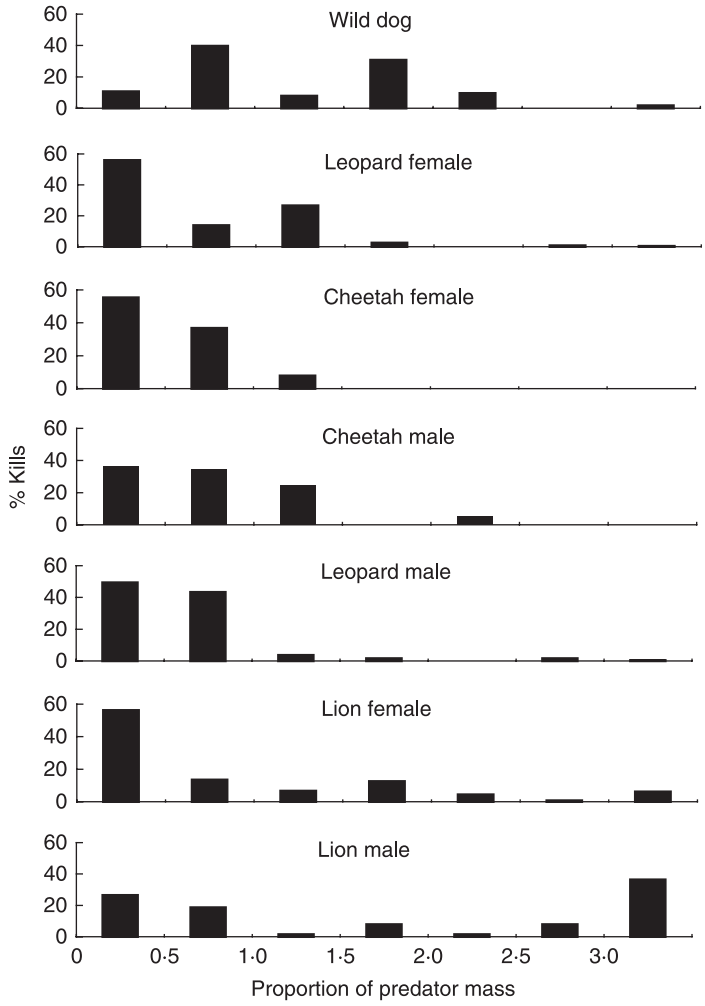

Fig. 1. Size frequency distributions showing the prey profile of each predator type, where prey size classes are expressed in relation to the predator's mass (e.g. the size class 1·0–1·5 includes all prey that are equal to, or up to 1·5 times heavier than, the mass of the predator). Predator types are arranged top to bottom from smallest (wild dog) to largest (lion male).

Table 2. Descriptive statistics for the body mass data (kg) of prey killed by each predator type, as determined from their kill records (n = number of kill records per predator type). Predator types are listed from top to bottom in order of increasing body mass (see Table 1)

Predator type	n	Mean prey body mass	SE	95% confidence interval of mean	Range of prey mass		Prey : predator body mass ratio
					Minimum	Maximum	
Wild dog	179	29·8	1·28	27·3–32·4	3	157	1·2 : 1
Leopard female	962	25·2	0·48	24·2–26·1	0·05	157	0·7 : 1
Cheetah female	280	25·0	0·60	23·8–26·2	3	63·6	0·6 : 1
Cheetah male	41	38.9	3.12	32.6–45·2	8.47	110	0.7 : 1
Leopard male	490	34.2	1.12	32.0–36·4	0.07	303	0.6 : 1
Lion female	1989	126	3.51	120–133	0.67	1540	1.0 : 1
Lion male	140	399	24.5	351–448	5.39	1192	2.1 : 1

profiles of most predator types are skewed towards a high representation of prey that is smaller than the predator. Interesting exceptions are wild dogs, which are highly cooperative pack hunters, and male lions, for which a distinctly platykurtic prey distribution demonstrates a tendency to kill prey from an exceptionally wide range of size classes.

PREY SIZE IN RELATION TO PREDATOR SIZE

From analysing the frequencies of occurrence of prey types within the prey profile of each predator type, it emerged that among the large felids the males typically took heavier prey than the females (Table 2). Male lions, the heaviest of the seven predator types, killed on

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average the heaviest prey (399 kg). Female lions utilized the largest range of body masses (1539 kg), although this was because of one incident when they managed to kill a sick white rhino bull. After omitting that, there was little difference between the prey body mass ranges used by male and female lions (1186 kg and 1191 kg, respectively). Female cheetahs were shown to be specialists for relatively small prey (mean mass = 25·0 kg; range = 60·6 kg). The ranks of mean predator and prey masses were correlated significantly (r_s = 0·831, $P < 0·05$) and the logarithms of both mean and maximum prey mass were both correlated significantly with the logarithm of predator mass, while no relationship was found with minimum prey mass (Fig. 2). The largest predators achieved the highest prey/predator body mass ratios (Table 2), although there was no clear overall relationship between prey/predator body mass ratio and predator body size. Pack-hunting wild dogs, for example, were able to kill prey that was disproportionately large for an individual wild dog's size.

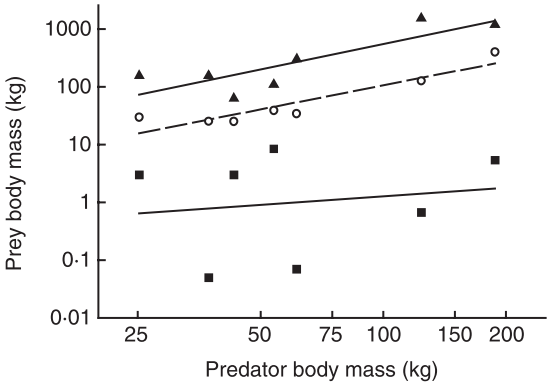

Fig. 2. Predator–prey body mass relationships. Maximum (triangles), mean (circles) and minimum (squares) prey body mass is plotted against predator body mass on logarithmic axes. Regressions: $Y_{mean} = 1·39X - 0·74$ ($r^2 = 0·86$, $P = 0·002$); $Y_{max} = 1·46X - 0·17$ ($r^2 = 0·71$, $P = 0·017$); $Y_{min} = 0·49X - 0·88$ ($r^2 = 0·03$, $P = 0·72$); where Y_{mean}, Y_{max} and Y_{min} are mean (dashed), maximum (solid, top), and minimum (solid, bottom) values of $\log_{10}$ (prey body mass) and X is $\log_{10}$ (predator body mass).

PREY DIVERSITY IN RELATION TO PREDATOR SIZE

By calculating for each predator type the number of prey types and prey species expected in a standardized sample of 140 kill records (Table 3), it was shown that lions and leopards are highly opportunistic predators in comparison with cheetahs and wild dogs. Weak relationships were found between predator body size and prey richness but these were not statistically significant, whether prey richness was expressed in terms of prey types ($r^2 = 0·41$, $P = 0·167$) or prey species ($r^2 = 0·37$, $P = 0·198$). There was no pattern to be found in comparisons of evenness across prey profiles (Table 3). Male lions selected the most evenly among both prey species ($E' = 0·31$) and prey types ($E' = 0·45$), while leopard females had the most uneven prey profiles in terms of prey species ($E' = 0·24$) but lion females were most uneven in terms of prey types ($E' = 0·33$). There was no statistically significant relationship between prey evenness and predator body mass.

PREY SIMILARITY BETWEEN PREDATORS OF SIMILAR SIZE

Across all pairwise comparisons there was an overall tendency for predators with low similarity in size to have low similarity in prey profiles, although this was because male lions (Fig. 3, data-points clustered in lower left) have low size-similarity with most other predator types (size overlap < 0·4 in all comparisons except with female lions) and have equally dissimilar prey profiles (Morisita's index < 0·4 in all comparisons). More significantly, in 15 of the 21 possible pairwise comparisons, the similarity in prey was consistently high (Morisita's index > 0·67) despite the similarity in body mass varying widely (range in proportional overlap = 0·199 – 0·879; Fig. 3).

Discussion

When kill data are collected through a combination of direct observations and opportunistic finds, as in Mala

Table 3. Richness and evenness of the prey profile of each predator type. In each case richness is the number of prey types or species expected in a standardized prey profile (using $n = 140$ kills), as determined by the rarefaction method. Evenness, a measure of how evenly the different prey types or species contribute to the prey profile of each predator type, is indicated by Camargo's index E′ (ranging from 0 to 1; 1 = completely even). The original sample sizes from which the calculations were made are shown in Table 1. Predator types are listed from top to bottom in order of increasing body mass

	Richness		Evenness (E′)	
Predator type	Prey types	Prey species	Prey types	Prey species
Wild dog	17·4	7·55	0·41	0·30
Leopard female	26·8	12·2	0·37	0·24
Cheetah female	19·0	8·74	0·40	0·28
Leopard male	32·5	17·5	0·43	0·26
Lion female	37·1	13·9	0·33	0·26
Lion male	27·0	14·0	0·45	0·31

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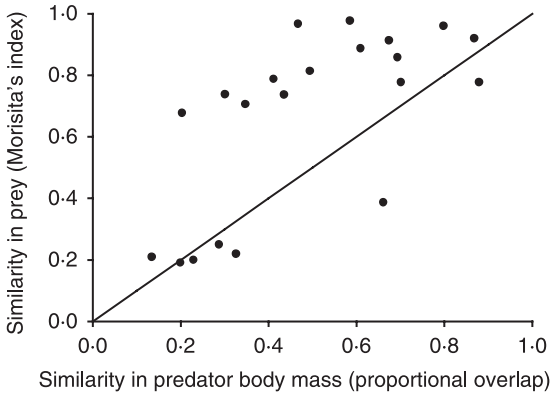

Fig. 3. Similarity in prey profiles compared with similarity in body mass for all possible pairs of predator types ($n = 21$). The diagonal line of perfect fit shows where data points would be expected to lie if predators of different size partitioned their prey resources by consistently selecting prey according to an optimal predator : prey size ratio.

Mala, there is always a concern that the smaller prey items will be under-represented because they are consumed quickly and are relatively inconspicuous to observers. This bias appears to have been minimized in the Mala Mala data, however, due perhaps to the high observer effort resulting from the intensive and frequent coverage of the reserve by game-viewing vehicles. Taking impala as an example (the most common prey species), of 1362 sexed and aged kills made by the four predator species in Mala Mala the juveniles and subadults made up 61·4%. In the adjacent Kruger National Park where impala 'lambs' and adults were directly observed being killed by the same four predator species, lambs represented 43·1% of all the 116 impala kills (Mills & Biggs 1993). The lower value from Kruger could be due to sampling error, or perhaps the lamb/adult transition was categorized differently in Kruger from the subadult/adult transition in Mala Mala. Nevertheless, the comparison indicates that it is unlikely that the smaller prey types were significantly under-represented in the Mala Mala data. Furthermore, any influences on prey selection imposed by seasonal variation within years, and rainfall-related cyclic variation across years, were dampened over the long and continuous study period (13 years). The large number of different individuals (from several generations) of each predator type that contributed to this data set also reduced the probability of bias caused by idiosyncrasies of individual predators ('habit killers'; see Kruuk & Turner 1967).

PREY SIZE IN RELATION TO PREDATOR SIZE

The significant positive relationship found in the Mala Mala data between predator and prey body mass is consistent with predictions of the global-scale meta-analyses of Vézina (1985), Gittleman (1985) and Carbone *et al*. (1999). Further support is provided by the larger male felids in Mala Mala taking consistently larger prey than their female conspecifics. For all seven predator types, mean prey body mass was > 45% of predator body mass as predicted for large predators by Carbone *et al*.'s (1999) meta-analysis. The prey/predator body mass ratio in Mala Mala was highest (2·1) for the largest predator type (lion males), as predicted by Vézina (1985), but the next largest ratio (1·2) was for wild dogs, which are the lightest of the predator types. The pack-hunting behaviour of wild dogs (Reich 1981) enables them to catch larger prey than if they hunted alone (which all the other predators in our analysis do, at least some of the time) and Cohen *et al*. (1993) suggested that aggregated mass rather than individual mass should be used for group hunters. With the mean pack size of 8·8 dogs in the Kruger–Mala Mala region (Mills & Gorman 1997) this would represent a 'predator' of about 220 kg and a prey/predator body mass ratio of 0·13, which is miniscule compared to those of all the other predator types (Table 2). However, in the absence of kleptoparasitism from other guild members wild dogs would be expected to kill larger prey (Lamprecht 1978; Carbone, du Toit & Gordon 1997) and wild dog packs are indeed capable of pulling down adult zebras, for example (Malcolm & Van Lawick 1975; Creel & Creel 2002). Hence the anomalous prey/predator mass ratio for wild dogs in Mala Mala is perhaps enforced by interspecific interactions within the large predator guild. A similar anomaly applies to female cheetahs in Mala Mala, where the body mass range (60 kg) and the mean body mass (25 kg) of their prey are both very low in relation to predator body mass (43 kg). This could also be enforced by a high kleptoparasite challenge, and indeed McVittie (1979) found that cheetahs in areas where potential kleptoparasites were rare or absent in Namibia killed larger prey than their counterparts existing within an intact large carnivore guild in East Africa.

The Mala Mala data show that all predator types kill small prey (< 10 kg), so prey size range is entirely dependent on maximum prey size, which increases significantly with predator body mass (Fig. 2). This confirms the findings of both Cohen *et al*. (1993) and Gittleman (1985) that increased predator size is associated with increased variation in prey size.

PREY DIVERSITY IN RELATION TO PREDATOR SIZE

Previous analyses of relationships between predator body mass and prey diversity have all quantified diversity in terms of prey size classes, and the Mala Mala data support these relationships (see above). It does not follow, however, that similar trends will be found if prey diversity is measured in taxonomic terms. Using prey species as well as prey types, and dealing with diversity in terms of richness and evenness, we found no relationship between predator body size and prey diversity. Furthermore, since there was no consistent size-related trend among predator types in terms of the evenness (Table 3) or kurtosis (Fig. 1) of their prey frequency distributions, we could compare prey diversity simply in terms of prey richness, but still no size-dependent

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relationship was found to apply across predator types. Clearly, large predators discriminate between potential prey types on the basis of functional characteristics such as size, defensive ability, escape behaviour, body condition, group structure, habitat affinity, etc. We suggest that the complexity of these interacting factors, compounded by the opportunistic behaviour of large predators, will confound attempts to analyse prey diversity in any terms other than body size.

IMPLICATIONS FOR PREDATOR GUILD STRUCTURE

The Mala Mala data confirm that mean prey size increases as a function of predator body size in the African savanna large predator guild. This does not imply, however, that larger predators specialize on larger prey and thereby promote resource partitioning within the guild, as studies on other predator guilds have suggested (Rosenzweig 1966; Gittleman 1985; Karanth & Sunquist 1995, 2000). For this hypothesis to hold would require that similarity in predator size is associated with similarity in prey, but we found that most predator types took similar prey despite wide dissimilarities in predator size (Fig. 3). Furthermore, the positive relationship between mean prey mass and predator mass in Mala Mala was significant only because maximum prey mass increased with predator mass while minimum prey mass remained virtually constant. This indicates that the larger predators benefit from increased dietary options in a manner analogous to that of the larger members of herbivore guilds in African savannas (du Toit & Owen-Smith 1989). Additional size advantages accrue to the larger predators (e.g. lions) in being able to displace smaller guild members from favoured habitats and prey types through interference competition (see also Mills & Biggs 1993; Mills & Gorman 1997). We suggest, therefore, that for large predators in African savannas the ecological significance of the relationship between predator and prey sizes should be interpreted as larger predators having wider predatory options rather than as different-sized predators specializing on different-sized prey. If the larger members of the guild were removed the next members in size would be expected to respond by increasing their prey size range. Unlike the large predator guilds of tropical forests, among which prey size specialization appears to be important for coexistence (Karanth & Sunquist 1995, 2000; Hart, Katembo & Punga 1996; but see Ray & Sunquist 2001), our findings demonstrate wide dietary overlap among syntopic large predators and emphasize the significance of interspecific competition in structuring the large predator guild in African savannas (see also Mills & Biggs 1993; Durant 1998; Creel & Creel 2002).

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Appendix I

Prey species and their respective body mass values (kg) as used to determine the body mass of each prey type. Figures in brackets represent best estimates. References: 1, Skinner & Smithers (1990); 2, Owen-Smith (1988); 3, Maclean (1984); 4, Jacobsen (1989)

Species		Body mass				
Common names	Scientific names	Adult male	Adult female	Adult	Chick	Ref.
Ungulates						
African buffalo	*Syncerus caffer* (Sparrman)	590	513			1
Bushbuck	*Tragelaphus scriptus* (Pallas)	50·0	37·0			2
Bushpig	*Potamochoerus porcus* (Linnaeus)		59·2			1
Common duiker	*Sylvicapra grimmii* (Linnaeus)	16·2	16·2			1
Giraffe	*Giraffa camelopardalis* (Linnaeus)	1192	828			1
Hippopotamus	*Hippopotamus amphibius* (Linnaeus)		1350			2
Impala	*Aepyceros melampus* (Lichtenstein)	54·4	40·9			1
Klipspringer	*Oreotragus oreotragus* (Zimmermann)		13·2			1
Kudu	*Tragelaphus strepsiceros* (Pallas)	228	157			1
Nyala	*Tragelaphus angasi* (Gray)	108	61·8			1
Reedbuck	*Redunca arundinum* (Boddaert)	51·8	38·2			1
Steenbok	*Raphicerus campestris* (Thunberg)	10·9	11·3			1
Tsessebe	*Damaliscus lunatus* (Burchell)	127	127			2
Warthog	*Phacochoerus aethiopicus* (Pallas)	79·6	56·5			1
Waterbuck	*Kobus ellipsiprymnus* (Ogilby)	240	180			2
White Rhino	*Ceratotherium simum* (Burchell)	2200	1600			2
Wildebeest	*Connochaetes taurinus* (Burchell)	231	193			2
Zebra	*Equus burchelli* (Gray)	313	302			1
Primates						
Chacma baboon	*Papio ursinus* (Kerr)	31·8	15·4			1
Vervet monkey	*Cercopithecus aethiops* (Linnaeus)	5·51	4·09			1
Rodents						
Cape porcupine	*Hystrix africaeaustralis* (Peters)		12·6			1
Greater canerat	*Tryonomys swinderianus* (Temminck)		3·81			1
Tree squirrel	*Paraxerus cepapi* (A. Smith)		0·20			1
Mouse				(0·07)		1
Other mammals						
Aardvark	*Orycteropus afer* (Pallas)		51·4			1
Pangolin	*Manis temminckii* (Smuts)		7·2			1
Scrubhare	*Lepus saxatilis* (F. Cuvier)		4·0			1
Birds						
Gymnogene	*Polyboroides typus* (Smith)				(0·05)	3
Ostrich	*Struthio camelus* (Linnaeus)			68·7		3
Francolin	*Francolinus* spp.			(0·5)		3
Korhaan	*Eupodotis* spp.			(0·67)		3
Woodland kingfisher	*Halcyon senegalensis* (Linnaeus)			0·07		3
Reptiles						
Large plated lizard	*Gerrhosaurus validus* (A. Smith)			0·32		4
Rock monitor	*Varanus albigularis* (Daudin)			1·05		4
Tortoise	*Geochelone pardalis* (Bell)/*Kinixys belliana spekii* (Gray)				(3·00)	4

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Appendix II

The number and percentage occurrence of each prey type in the diet of each predator type during the 13-year study period. The total number and percentage of kills within each mammalian prey species (and within birds and reptiles) are indicated in bold type. Wherever possible a breakdown of sex and age is provided within a species with: u/k = unknown, M = male, F = female, A = adult, S/A = sub-adult, J = juvenile. The adjusted numbers, as used in the diversity analysis, are provided in brackets (see Methods for details)

Prey types			Occurrence in diet of each predator type													
			Lion male		Lion female		Leopard male		Leopard female		Cheetah male		Cheetah female		Wild dog	
Species	Sex	Age	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Ungulates																
African Buffalo			**63**	**45·0**	**95**	**4·78**	**1**	**0·20**								
Buffalo	u/k	u/k	8	5·71	21	1·06										
Buffalo		J	18 (21)	12·9	16 (21)	0·80	1	0								
Buffalo	M	A	24 (28)	17·1	21 (27)	1·06										
Buffalo	M	S/A	2	1·43	4 (5)	0·20										
Buffalo	F	A	10 (11)	7·14	29 (37)	1·46										
Buffalo	F	S/A	1	0·71	4 (5)	0·20										
Bushbuck					**24**	**1·21**	**51**	**10·41**	**86**	**8·94**			**9**	**3·21**	**9**	**5·03**
Bushbuck	u/k	u/k			8	0·40	17	3·47	26	2·70			5	1·79	7	3·91
Bushbuck		J			1 (2)	0·05	9 (13)	1·84	20 (29)	2·08						
Bushbuck	M	A			8 (12)	0·40	13 (20)	2·65	12 (17)	1·25					2 (9)	1·12
Bushbuck	M	S/A			1	0·05			4 (6)	0·42						
Bushbuck	F	A			6 (9)	0·30	8 (12)	1·63	20 (29)	2·08			3 (7)	1·07		
Bushbuck	F	S/A					4 (6)	0·82	4 (6)	0·42			1 (2)	0·36		
Bushpig					**1**	**0·05**										
Common duiker					**17**	**0·85**	**43**	**8·78**	**194**	**20·17**	**2**	**4·88**	**32**	**11·43**	**29**	**16·20**
Duiker	u/k	u/k			6	0·30	14	2·86	84	8·73			6	2·14	12	6·70
Duiker		J			1 (2)	0·05	4 (6)	0·82	16 (28)	1·66			4 (5)	1·43	2 (3)	1·12
Duiker	M	A			4 (6)	0·20	7 (10)	1·43	29 (51)	3·01	1	2·44	7 (8)	2·50	3 (5)	1·68
Duiker	M	S/A					3 (5)	0·61	6 (11)	0·62						
Duiker	F	A			6 (9)	0·30	10 (15)	2·04	52 (92)	5·41	1	2·44	12 (15)	4·29	11 (19)	6·15
Duiker	F	S/A					5 (7)	1·02	7 (12)	0·73			3 (4)	1·07	1 (2)	0·56
Giraffe			**27**	**19·29**	**86**	**4·32**	**1**	**0·20**								
Giraffe	u/k	u/k	4	2·86	30	1·51										
Giraffe		J	4 (5)	2·86	24 (37)	1·21	1	0·20								
Giraffe	M	A	9 (11)	6·43	14 (21)	0·70										
Giraffe	M	S/A	2	1·43	1 (2)	0·05										

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Appendix II *Continued*

Prey types			Occurrence in diet of each predator type													
			Lion male		Lion female		Leopard male		Leopard female		Cheetah male		Cheetah female		Wild dog	
Species	Sex	Age	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Giraffe	F	A	8 (9)	5·71	11 (17)	0·55										
Giraffe	F	S/A	6 (9)	0·30												
Hippopotamus			**1**	**0·71**												
Impala			**19**	**13·57**	**796**	**40·02**	**231**	**47·14**	**462**	**48·02**	**29**	**70·73**	**181**	**64·64**	**121**	**67·60**
Impala	u/k	u/k	5	3·57	255	12·8	51	10·4	91	9·46	4	9·76	28	10·0	43	24·0
Impala		J	4 (5)	2·86	160 (235)	8·04	37 (47)	7·55	136 (169)	14·1	10 (12)	24·4	65 (77)	23·2	30 (47)	16·8
Impala	M	A	4 (5)	2·86	61 (90)	3·07	28 (36)	5·71	44 (55)	4·57	5 (6)	12·2	10 (12)	3·57	10 (15)	5·59
Impala	M	S/A			94 (138)	4·73	31 (40)	6·33	49 (61)	5·09	3	7·32	18 (21)	6·43	4 (6)	2·23
Impala	F	A	4 (6)	2·86	127 (187)	6·39	61 (78)	12·4	97 (121)	10·1	7 (8)	17·1	43 (51)	15·4	25 (39)	14·0
Impala	F	S/A	2 (3)	1·43	99 (146)	4·98	23 (30)	4·69	45 (56)	4·68			17 (20)	6·07	9 (14)	5·03
Klipspringer									**1**	**0·10**						
Kudu			**2**	**1·43**	**185**	**9·30**	**17**	**3·47**	**25**	**2·60**	**2**	**4·88**	**7**	**2·50**	**4**	**2·23**
Kudu	u/k	u/k			43	2·16	4	0·82	7	0·73	1	2·44			2	1·12
Kudu		J			17 (22)	0·85	7 (9)	1·43	10 (14)	1·04			7	2·50	1 (2)	0·56
Kudu	M	A	1	0·71	53 (69)	2·66										
Kudu	M	S/A			13 (17)	0·65										
Kudu	F	A	1	0·71	37 (48)	1·86	5 (7)	1·02	3 (4)	0·31					1 (2)	0·56
Kudu	F	S/A			22 (29)	1·11	1	0·20	5 (7)	0·52	1 (2)	2·44				
Nyala			**1**	**0·71**	**12**	**0·60**	**1**	**0·20**	**4**	**0·42**			**3**	**1·07**	**1**	**0·56**
Nyala	u/k	u/k	1	0·71	1	0·05							1	0·36	1	0·56
Nyala		J							1	0·10			1	0·36		
Nyala	M	A			9 (10)	0·45										
Nyala	M	S/A			1	0·05										
Nyala	F	A			1	0·05	1	0·20	1	0·10						
Nyala	F	S/A							2	0·21			1 (2)	0·36		
Reedbuck							**1**	**0·20**					**1**	**0·36**		
Reedbuck	u/k	u/k											1	0·36		
Reedbuck	M	S/A					1	0·20								
Steenbok			**2**	**1·43**	**23**	**1·16**	**9**	**1·84**	**57**	**5·93**	**1**	**2·44**	**33**	**11·79**	**11**	**6·15**
Steenbok	u/k	u/k	1	0·71	11	0·55	6	1·22	13	1·35	1	2·44	11	3·93	7	3·91
Steenbok		J			1 (2)	0·05			4 (5)	0·42			1 (2)	0·36		
Steenbok	M	A			4 (8)	0·20			14 (18)	1·46			7 (11)	2·50	1 (3)	0·56
Steenbok	M	S/A			1 (2)	0·05	1 (3)	0·20								
Steenbok	F	A	1 (2)	0·71	6 (11)	0·30	2 (6)	0·41	25 (32)	2·60			13 (19)	4·64	2 (5)	1·12
Steenbok	F	S/A							1	0·10			1	0·36	1 (3)	0·56

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Appendix II *Continued*

Prey types			Occurrence in diet of each predator type													
			Lion male		Lion female		Leopard male		Leopard female		Cheetah male		Cheetah female		Wild dog	
Species	Sex	Age	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Tsessebe					**2**	**0·10**	**1**	**0·20**								
Tsessebe	u/k	u/k			1	0·05	1	0·20								
Tsessebe	F	A			1 (2)	0·05										
Warthog			**8**	**5·71**	**224**	**11·26**	**56**	**11·43**	**35**	**3·64**	**3**	**7·32**	**3**	**1·07**		
Warthog	u/k	u/k	7	5·00	107	5·38	22	4·49	13	1·35	3	7·32				
Warthog		J			23 (44)	1·16	21 (35)	4·29	22 (35)	2·29			3	1·07		
Warthog	M	A			34 (65)	1·71	4 (7)	0·82								
Warthog	M	S/A			6 (11)	0·30	3 (5)	0·61								
Warthog	F	A	1 (8)	0·71	51 (98)	2·56	6 (9)	1·22								
Warthog	F	S/A			3 (6)	0·15										
Waterbuck			**2**	**1·43**	**61**	**3·07**	**3**	**0·61**	**8**	**0·83**	**1**	**2·44**			**1**	**0·56**
Waterbuck	u/k	u/k			16	0·80			1	0·10					1	0·56
Waterbuck		J			4 (5)	0·20	3	0·61	7 (8)	0·73	1	2·44				
Waterbuck	M	A	1	0·71	22 (30)	1·11										
Waterbuck	M	S/A			7 (10)	0·35										
Waterbuck	F	A	1	0·71	9 (12)	0·45										
Waterbuck	F	S/A			3 (4)	0·15										
White rhinoceros					**3**	**0·15**										
White rhinoceros	u/k	u/k			1	0·05										
White rhinoceros	M	S/A			1 (2)	0·05										
White rhinoceros		J			1	0·05										
Wildebeest			**3**	**2·14**	**217**	**10·91**	**7**	**1·43**	**1**	**0·10**	**2**	**4·88**	**1**	**0·36**		
Wildebeest	u/k	u/k	3	2·14	88	4·42	1	0·20								
Wildebeest		J			36 (60)	1·81	6 (7)	1·22	1	0·10	2	4·88	1	0·36		
Wildebeest	M	A			32 (54)	1·61										
Wildebeest	M	S/A			3 (5)	0·15										
Wildebeest	F	A			51 (86)	2·56										
Wildebeest	F	S/A			7 (12)	0·35										
Zebra			**9**	**6·43**	**167**	**8·40**	**7**	**1·43**								
Zebra	u/k	u/k	7	5·00	100	5·03	1	0·20								
Zebra		J	1 (4)	0·71	39 (97)	1·96	5 (6)	1·02								
Zebra	M	A			4 (10)	0·20										
Zebra	F	A	1 (5)	0·71	20 (50)	1·01										
Zebra	F	S/A			4 (10)	0·20	1	0·20								

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Appendix II *Continued*

Prey types			Occurrence in diet of each predator type													
Species	Sex	Age	Lion male No.	%	Lion female No.	%	Leopard male No.	%	Leopard female No.	%	Cheetah male No.	%	Cheetah female No.	%	Wild dog No.	%
Primates																
Chacma baboon			**1**	**0·71**	**49**	**2·46**	**10**	**2·04**	**4**	**0·42**						
Baboon	u/k	u/k	1	0·71	36	1·81	9	1·84	4	0·42						
Baboon		J			4 (15)	0·20	1 (10)	0·20								
Baboon	M	S/A			1 (4)	0·05										
Baboon	F	A			7 (26)	0·35										
Baboon	F	S/A			1 (4)	0·05										
Vervet monkey					**2**	**0·10**	**5**	**1·02**	**25**	**2·60**						
Monkey	u/k	u/k			1	0·05	4	0·82	19	1·98						
Monkey	M	A			1 (2)	0·05			3 (13)	0·31						
Monkey	M	S/A							1 (4)	0·10						
Monkey	F	A					1 (5)	0·20	2 (8)	0·21						
Rodents																
Cape porcupine			**1**	**0·71**	**6**	**0·30**	**3**	**0·61**	**1**	**0·10**						
Greater canerat							**12**	**2·45**	**15**	**1·56**						
Tree squirrel							**2**	**0·41**	**3**	**0·31**						
Mouse							**2**	**0·41**								
Other mammals																
Aardvark					**3**	**0·15**	**2**	**0·41**								
Pangolin			**1**	**0·71**												
Scrub hare					**12**	**0·60**	**11**	**2·24**	**32**	**3·33**			**10**	**3·57**	**3**	**1·68**
Birds					**2**	**0·10**	**8**	**1·63**	**8**	**0·83**	**1**	**2·44**				
Gymnogene	chick								1	0·10						
Francolin							8	1·63	5	0·52						
Korhaan					1	0·05			1	0·10						
Ostritch					1	0·05					1	2·44				
Woodland kingfisher									1	0·10						
Reptiles					**2**	**0·10**	**6**	**1·22**	**1**	**0·10**						
Large plated lizard									1	0·10						
Rock monitor							4	0·82								
Tortoise					2	0·10	2	0·41								
Total			140	100	1989	100	490	100	962	100	41	100	280	100	179	100