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Abstract: Successful conservation initiatives often lead to rapid increases in large carnivore densities to the extent that overpopulation occurs. Yet conservation managers have no way of knowing the carrying capacity of their reserves. Here we derived relationships between the preferred prey (species and weight range) of Africa's large predator guild and their population densities to predict their carrying capacity in ten South African conservation areas. Conservation managers intervened at several of these sites because of evidence of predator overpopulation and these provided independent tests of our predictions. Highly significant linear relationships were found between the biomass of the preferred prey species of lion, leopard, spotted hyaena and African wild dog, and the biomass of prey in the preferred weight range of cheetah. These relationships are more robust than previous work for lion, cheetah and leopard, and novel for spotted hyaena and African wild dog. These relationships predicted that several predators exceeded carrying capacity at four sites, two where managers expressed concerns about overpopulation due to a decline in wildlife abundance and two where carnivores were actively removed. The ability to predict the carrying capacity of large predators is fundamental to their conservation, particularly in small enclosed reserves. Every predator that preys on large, readily surveyed wildlife can have its carrying capacity predicted in this manner based on the abundance of its preferred prey. This will be beneficial for reintroduction attempts, threatened species management, overpopulation estimation, detecting poaching and in investigating intra-guild competition.

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Carrying capacity of large African predators: Predictions and tests

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ABSTRACT

Successful conservation initiatives often lead to rapid increases in large carnivore densities to the extent that overpopulation occurs. Yet conservation managers have no way of knowing the carrying capacity of their reserves. Here we derived relationships between the preferred prey (species and weight range) of Africa's large predator guild and their population densities to predict their carrying capacity in ten South African conservation areas. Conservation managers intervened at several of these sites because of evidence of predator overpopulation and these provided independent tests of our predictions. Highly significant linear relationships were found between the biomass of the preferred prey species of lion, leopard, spotted hyaena and African wild dog, and the biomass of prey in the preferred weight range of cheetah. These relationships are more robust than previous work for lion, cheetah and leopard, and novel for spotted hyaena and African wild dog. These relationships predicted that several predators exceeded carrying capacity at four sites, two where managers expressed concerns about overpopulation due to a decline in wildlife abundance and two where carnivores were actively removed. The ability to predict the carrying capacity of large predators is fundamental to their conservation, particularly in small enclosed reserves. Every predator that preys on large, readily surveyed wildlife can have its carrying capacity predicted in this manner based on the abundance of its preferred prey. This will be beneficial for reintroduction attempts, threatened species management, overpopulation estimation, detecting poaching and in investigating intra-guild competition.

1. Introduction

Reduction in distribution and abundance has led to almost 25% of extant Carnivoran species being threatened with extinction (Ginsberg, 2001). Their conservation ultimately depends upon the accurate assessment of their distribution and abundance to facilitate informed management decisions (Fuller and Sievert, 2001; Gros et al., 1996). In some places, conservation managers have started slowing these declines through translocations and reintroductions (Breitenmoser et al., 2001). Conservation areas where such translocations have occurred are often fenced and heavily managed, and these populations tend to increase rapidly in the absence of threatening processes (Smith, 2006). Managers of such sites are therefore faced with potential overabundance of translocated stock, without knowing the carrying capacity of these species, or the maximum number of individuals that a site can support without causing its deterioration. This is particularly

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important when such sites are relatively small, fenced and/or situated in hostile environments where movements of free-ranging animals will be necessarily curtailed.

Carnivore densities can vary over several orders of magnitude within species, but, in natural ecosystems, generally reflect the abundance of their prey (Bertram, 1975; Fuller and Sievert, 2001). Seminal work by van Orsdol et al. (1985) illustrated this relationship with lions (*Panthera leo*). Such relationships have subsequently been found in cheetah (*Acinonyx jubatus*) (Laurenson, 1995b) and leopard (*Panthera pardus*) (Stander et al., 1997). A relationship also exists between tigers (*Panthera tigris*) and their prey (Karanth et al., 2004) and such relationships have been used to predict the size of reintroduced Eurasian lynx (*Lynx lynx*) populations (Hetherington and Gorman, 2007). Similarly, the density of grey wolf (*Canis lupus*) is related to that of its prey, particularly moose (*Alces alces*) (Peterson et al., 1998, in Fuller and Sievert, 2001). Relationships between predator and prey density apply across the order Carnivora, where 10,000 kg of prey supports about 90 kg of a given carnivore species (Carbone and Gittleman, 2002).

In African savannas, predator–prey relationships are related to rainfall and vegetation productivity (East, 1984). While the initial research that identified the relationships between predator and prey density greatly improved our understanding of predator ecology, recent research on prey preferences allows us to investigate these relationships more intensively. For example, lion density was initially linked to the biomass of all available prey species (van Orsdol et al., 1985), while cheetah density was related to the biomass of prey weighing between 15 and 60 kg along with a negative relationship with lion density (Laurenson, 1995b). Leopard density exhibited a significant relationship with the biomass of prey weighing between 15 and 60 kg (Stander et al., 1997). These relationships are likely to be substantially improved by using the biomass of preferred prey species or preferred prey weight range of each predator (Table 1).

African wild dogs (*Lycaon pictus*) have never been a common species and there are probably basic ecological reasons for their scarcity (Creel and Creel, 1996), such as competitive limitation by lions and spotted hyaenas (*Crocuta crocuta*) (Creel and Creel, 1996) or cheetah (Hayward, unpubl. data). Yet there has been no study linking wild dog density with that of their available prey as was intimated by Fuller and Sievert (2001). The use of preferred prey species biomass or the biomass of prey in the wild dog's preferred weight range may yield such predictions (Table 1).

Although the Serengeti spotted hyaena population more than doubled during the corresponding increase in blue wildebeest (*Connochaetes taurinus*) abundance (Hofer and East, 1995), there has been no study to link hyaena density with that of their prey. Again strong relationships may be derived using the hyaena's preferred prey weight range, however given the high degree of dietary overlap with lions (Hayward, 2006), there may be a relationship between hyaena biomass and the biomass of large body mass prey that is preferred by lions (Hayward and Kerley, 2005).

No previous study has applied these predator–prey relationships to predicting predator carrying capacity, yet this is precisely the opportunity that the relationship between predator and prey density affords us (Fuller and Sievert, 2001). Here we used data from 22 reserves in eastern and southern Africa over different periods yielding 32 groups of population estimates to examine abundance relationships between predators and their prey using more detailed information on prey choice (Hayward, 2006; Hayward et al., 2006a; Hayward et al., 2006b; Hayward and Kerley, 2005; Hayward et al., 2006c). We then use our new regression equations and the information about prey choice to predict carnivore carrying capacity in ten sites in South Africa where reintroductions were planned

Table 1 – Preferred prey species and preferred prey body mass range of Africa's large predator guild

Predator species	Preferred prey species	Preferred prey body mass range (kg)	Reference
African wild dog	Kudu *Tragelaphus strepsiceros* Thomson's gazelle *Gazella thomsoni* Impala *Aepyceros melampus* Bushbuck *Tragelaphus scriptus*	16–32 and 120–140	Hayward et al. (2006c)
Cheetah	Blesbok *Damaliscus dorcas phillipsi* Impala Thomson's gazelle Grant's gazelle *G. granti* Springbok *Antidorcas marsupialis*	23–56	Hayward et al. (2006b)
Leopard	Impala Bushbuck Common duiker *Sylvicapra grimmia*	10–40	Hayward et al. (2006a)
Lion	Blue wildebeest *Connochaetes taurinus* Buffalo *Syncerus caffer* Gemsbok *Oryx gazelle* Giraffe *Giraffa camelopardalis* Plain's zebra *Equus burchellii*	190–550	Hayward and Kerley (2005)
Spotted hyaena	Nil, but high (69%) overlap of preferred prey of lions	56–182	Hayward (2006)

Preferred body mass range is based on 3/4 of adult female body mass.

or had occurred and where wildlife census data was available, but were not used in the derivation of our new relationships. These predictions were tested at sites where managers had expressed concern about carnivore overpopulation or had intervened due to declines in prey abundance. It is only with knowledge of predator carrying capacity that informed conservation management decisions can be made (Fuller and Sievert, 2001), such as predator reintroductions or removals, implementation of fertility control, or plans for park expansion.

2. Materials and methods

We reviewed the literature using electronic databases (Current Contents, Biological Abstracts, Web of Science), libraries and reference lists of other papers, and tabulated data on predator density and prey abundance at individual sites from the savanna ecosystems of southern and eastern Africa. This information was converted to biomass km^{-2} using 3/4 of adult female body mass (following Schaller (1972) to account for sub-adults and young preyed upon) estimates from Stuart and Stuart (2000) (see Appendix). Several studies were excluded because they were from extremely different habitat types, such as Afromontane forest (Sillero-Zubiri and Gottelli, 1992) and/or produced outlying results when plotted alongside other studies at that site at similar times (Dunham, 1992, 1994; Eloff, 1973; Kruger et al., 1999; Mills et al., 1978; Mizutani and Jewell, 1998). The methods used to gather these data varied among studies, however, like Creel and Creel (1996), we did not conduct post-hoc corrections to account for this as it was considered to be too subjective. If more than one density was recorded for an individual species in a decade, then either the mean of these was used or the estimate with the most accurate measure of prey abundance relating to it when obviously erroneous estimates were present.

Like other authors (Creel and Creel, 1996; Grange and Duncan, 2006), the majority of sites used were relatively unaffected by humans, however several have been fully or partially fenced (e.g. Hluhluwe-Umfolozi, Kruger), others have culls or hunting (e.g. Kruger, Selous) or pastoralism (Ngorongoro), and other populations were reintroduced (e.g. Hluhluwe). Where reintroduced populations were included, a sufficient time (>15 years) was left to allow the populations to attain carrying capacity.

We then regressed predator density against the biomass of significantly preferred prey and the biomass of prey within each predator's preferred weight range (see Introduction) using data presented in the Appendix and Table 1. These preferred prey species and weight ranges were calculated in previous studies on lion (Hayward and Kerley, 2005), leopard (Hayward et al., 2006a), cheetah (Hayward et al., 2006b), African wild dog (Hayward et al., 2006c) and spotted hyaena (Hayward, 2006). Given the high degree of dietary overlap between lions and hyaenas (Hayward, 2006), we also tested for relationships between hyaena density and that of the preferred prey of lions. We also regressed data presented in van Orsdol et al. (1985) on lion, in Stander et al. (1997) on leopard and Gros et al. (1996) on cheetah to derive predictive equations with which to compare those relationships derived from our work on prey preferences. We also used the equations calculated by Carbone and Gittleman (2002) to compare their predictive accuracy.

We then used these equations to predict the potential predator population density and size at ten sites where large predators have been or are being reintroduced using the wildlife census data presented in Tables 2 and 3. Essentially, these are our predictions of each sites' carrying capacity for each predator based on the available food resources in individual years.

The sites seeking estimates of carrying capacity for large predators were fenced reserves in South Africa's Eastern and Western Cape Provinces that ranged in size from 70 to 3410 km^2 (Tables 2 and 3). Addo Elephant National Park (Addo) is located 72 km north of Port Elizabeth in the Sub-tropical Thicket biome that supports dense thickets dominated by *Portulacaria afra* alongside grasslands derived from past agricultural practices (Vlok et al., 2003). Lions, spotted hyaenas and a leopard were reintroduced to the Main Camp section of Addo in 2003 and 2004 (Hayward et al., 2007a; Hayward et al., 2007b). There are plans to reintroduce lions into the Darlington and Nyathi sections of Addo (fully fenced and separate from Addo Main Camp) when wildlife densities attain sufficient levels to support a small population. The Greater Addo Elephant National Park (GAENP) includes these areas as part of the planning regime of a much larger reserve that will conserve thicket, savanna, grassland, fynbos, nama karoo and forest biomes (Boshoff et al., 2002). Shamwari Game Reserve is 40 km east of Addo and supports similar vegetation types to Addo (Vlok et al., 2003). Lion, cheetah, African wild dog and leopard have been reintroduced here since 2000, and the 2004 population estimates were 15 lion, 10 wild dog, two leopard and six cheetah (Hayward et al., 2007b). The Karoo National Park is 500 km north of Cape Town and is situated within the Nama Karoo biome and preparations are underway to reintroduce lion there. The Mountain Zebra National Park is 100 km north of Addo in the Nama Karoo biome. Cheetah were reintroduced there in 2007 (Hayward et al., 2007b). These sites support different vegetation communities however the habitat of large predators is dependent upon adequate prey (Hayward et al., 2007c; Karanth et al., 2004) and these sites support species diversity similar to sites throughout the rest of southern and eastern Africa.

We compared our predicted population estimates with those made for the proposed GAENP (Boshoff et al., 2002). These published population estimates were based on theoretical area requirements of each predator rather than available food resources and hence provide independent estimates.

Finally, we tested our predictions of large predator carrying capacity using sites where declines in prey species led to predator management. Eight lions were reintroduced to Madjuma Lion Reserve (15 km^2; 24°42′S; 27°58′E) in 1996 and immediately caused declines in blue wildebeest which ultimately led to the removal of the lions (Power, 2002). Lions were reintroduced to Phinda Resource Reserve in 1992 and managers removed 30 between 1996 and 1998 due to similar wildebeest declines (Hunter, 1998). By 1995 there were 13 lion and 21 cheetah (Hunter, 1998). Cheetah predictions were tested on Phinda also, although no cheetahs were removed by managers due to their high mortality rate, but there was a precipitous decline in common reedbuck *Redunca arundinum*

Table 2 – Wildlife densities (# km^{-2}) at prediction sites

Site	Mass (kg)	Shamwari					Karoo			Mountain Zebra			Addo			Nyathi	Darlington	GAENP
Years		2000	2001	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	2004	2004	
Habitat		Thicket, transformed grasslands					Nama karoo			Nama karoo			Thicket, grasslands			Thicket	Nama karoo	Thicket, grassland, fynbos, savanna, forest, nama karoo
Area (km^2)		187.46					700			185			134			70	90	3410
Baboon	12						0.02	0.03	0.02	0.03	0.02	0.04						1.58
Blesbok	53	1.88	1.68	1.84	1.65	0.94			0.01	1.49	1.22	1.40				0.11	0.29	
Buffalo	432	0.16	0.18	0.18	0.28	0.27	0	0	0.01	0.23	0.42	0.45	2.46	2.83	2.65	0.04	0.01	0.29
Bushbuck	46	4.85	4.85	5.33	5.33	4.96							0.34	0.74	0.77	0.44		3.12
Bushpig	46	1.67	1.67	1.44	1.44	1.33								0.30	0.37			1.25
Duiker, blue	3				0.43	0.35												9.58
Duiker, common	16	4.81	4.81	4.93	4.93	4.53	0.02	0.03	0.02	0.03	0.05	0.06	0.48	0.53	0.41	0.19	0.08	6.25
Eland	345	0.61	0.56	0.59	0.66	0.37	0.40	0.19	0.25	1.07	1.04	1.13	1.36	1.43	0.79	1.24		0.12
Elephant	1600	0.23	0.26	0.28	0.26	0.28							2.54	2.79	2.54	0.90		0.14
Gemsbok	158	0.29	0.33	0.36	0.46	0.31	0.69	0.83	0.92							0.21	0.71	
Giraffe	550	0.82	0.96	0.85	0.96	0.13												
Grysbok	7	0.49	0.49	0.43	0.49	0.27												7.52
Hartebeest	95	0.75	0.74	0.69	0.84	0.60	0.71	0.77	0.87	1.27	1.35	1.52	1.36	1.86	2.15	2.43	0.11	0.39
Hippopotamus	750	0.75	0.85	0.96	0.11	0.82												0.02
Impala	30	2.49	3.72	4.75	5.21	3.50												
Klipspringer	10						0.39	0.41	0.39	0.08	0.07	0.14						1.43
Kob	45	0.19	0.18	0.15	0.19													
Kudu	135	4.85	4.27	4.81	5.26	4.81	0.54	0.64	0.50	0.91	0.78	1.03	4.57	8.44	5.27	0.54	0.74	0.92
Nyala	47	0.64	0.13	0.18	0.23	0.33												
Oribi	14																	0.36
Ostrich	70	0.29	0.22	0.69	0.20	0.64	0.35	0.27	0.34	0.56	0.52	0.65	1.43	1.54	1.95	0.60	0.20	
Reedbuck, bohor	32																	0.65
Reedbuck, common	32		0.21	0.16	0.21													0.07
Reedbuck, mountain	23	1.47	1.63	1.87	1.87	1.73	0.06	0.07	0.06	2.41	1.47	3.78						0.57
Rhinoceros, black	800	0.59	0.69	0.75	0.85	0.96	0.01	0.01	0				0.75	0.75	0.52			0.34
Rhinoceros, white	1400	0.75	0.75	0.85	0.11	0.11												
Sable	180															0.01		
Springbok	26	1.63	1.48	1.44	1.79	0.74	3.31	2.54	1.19	4.76	4.76	6.34				0.36	5.90	0.79
Steenbok	8						0.04	0.06	0.04	0.10	0.12	0.04		0.15	0.75	0.01	0.23	4.16
Vervet monkey	3.5									0.02	0.02	0.01						26.08
Warthog	45	0.13	0.35	0.30	0.98	1.23							0.79	2.22	2.22	0.03		0.63
Waterbuck	188	0.33	0.35	0.35	0.38	0.33										0.03		
Wildebeest, blue	135	0.93	0.57	0.78	0.68	0.29				1.64	1.63	1.99					0.68	0.01
Zebra, plains	175	0.33	0.45	0.62	0.74	0.63	0.05	0.04	0.06	0.30	0.31	0.15	0.15	0.22	0.27	0.43		0.53
Zebra, mountain	179			0.37	0.37		0.51	0.54	0.49	1.90	1.61	1.62					0.08	0.30

Shamwari data comes from distance estimates of walked transects (J.O'Brien, pers. comm.), Greater Addo Elephant National Park (GAENP) come from predictions of future populations sizes by Boshoff et al. (2002) and remaining data from South African National Parks aerial census data (G. Castley, unpubl. data). These data can be converted to biomass (kg km^{-2}) by multiplying by 3/4 of the adult female body mass of each species (mass) based on body masses given in Stuart and Stuart (2000) for mammals and Schaller (1972) for ostrich. All sites are fenced.

Table 3 – Wildlife densities (# km^{-2}) at test sites

Site Years	Madjuma 1997	Madjuma 1998	Phinda 1995	Pilanesberg 1997
Habitat Area (km^2)	Savanna 15		Savanna 170	Savanna 70
Baboon				
Blesbok				0.11
Buffalo				0.04
Bushbuck				0.44
Bushpig				
Duiker, blue				
Duiker, common				0.19
Eland				1.24
Elephant				0.90
Gemsbok				0.21
Giraffe			0.39	
Grysbok				
Hartebeest	5.33	2.33		2.43
Hippopotamus				
Impala	5.00	5.73	11.36	
Klipspringer				
Kob				
Kudu	2.13	0.53	1.48	0.54
Nyala			12.49	
Oribi				
Ostrich				0.60
Reedbuck, bohor				
Reedbuck, common			0.46	
Reedbuck, mountain				
Rhinoceros, black				
Rhinoceros, white				
Sable				0.01
Springbok				0.36
Steenbok				0.01
Vervet monkey				
Warthog	3.47	1.73	5.12	0.03
Waterbuck				0.03
Wildebeest, blue	1.67	8.53	3.69	
Zebra, plains	0.33	5.73	3.12	0.43
Zebra, mountain				

Madjuma data comes from Power (2002), Phinda from Hunter (1998), and Pilanesberg data from van Dyk and Slotow (2003). Where stated these density estimates were derived from aerial censuses. These data can be converted to biomass (kg km^{-2}) by multiplying by 3/4 of the adult female body mass of each species from body masses given in Table 2. All sites are fenced.

(Hunter, 1998). Lion were reintroduced to Pilanesberg National Park in 1993 (van Dyk and Slotow, 2003) and exceeded 50 individuals in 1998 (Tampling and du Toit, 2005). Four years later, excessive lion predation had led to declines in the blue wildebeest population of 45%, eland by 76%, waterbuck by 67% and kudu by 65% (Tampling and du Toit, 2005). We compared our estimates of lion carrying capacity with the number of lions in Pilanesberg and related these to the timing of the prey population declines.

3. Results

The population density of each large African predator was significantly related to the biomass of significantly preferred prey and/or the biomass of prey in their preferred weight range (Table 4). The relationships that explained the greatest amount of variance in the data for each predator were biomass of preferred prey of lion ($r^2 = 0.626$), leopard ($r^2 = 0.833$), spotted hyaena ($r^2 = 0.487$) and wild dog ($r^2 = 0.523$), and preferred weight range for cheetah ($r^2 = 0.519$; Table 4). We consider these our best methods of predicting the population size and carrying capacity of each predator. We quote these results hereafter, although both preferred weight range and preferred prey biomass provide very similar predictions (Pearson's $R > 0.95$, $p < 0.001$; Table 4).

Previously published relationships between lion density and lean season prey biomass (van Orsdol et al., 1985) explained a greater proportion of the variance ($r^2 = 0.722$), although the smaller sample size used meant these relationships were not as significant (Table 4). Previously published leopard and cheetah relationships (Gros et al., 1996; Stander et al., 1997) exhibited a similar response (Table 4).

Solving the equations that best explained the variance in the data for each predator (Table 4) using the prey density for reintroduction (Table 2) and test sites (Table 3), we predicted the density and number of predators at seven sites over several years (Table 5). Addo Main Camp, Madjuma, Phinda and Pilanesberg had the greatest carrying capacity for lion, while the Karoo National Park, the Nyathi and Darlington sections of Addo and the entire GAENP were predicted to have the lowest lion density (Table 5). Shamwari has also seen a slight decline in lion carrying capacity since 2003 due to a reduction in available preferred prey (Table 5). Spotted hyaena carrying capacity predictions exhibited similar results to that of lions (Table 5).

The predictions based on the relationships identified by van Orsdol et al. (1985) for lions were two to three times higher than our predictions derived from a larger sample size and there was little difference between lean or mean season biomass predictions (Table 5). The predictions of leopard carrying capacity based on the Stander et al. (1997) relationships were also generally two to three times higher than our predictions (Table 5). Similarly, the predictions of cheetah carrying capacity based on Gros et al.'s (1996) relationships were similar to ours for small populations but became excessive at larger predicted population sizes (Table 5).

The predictions of carrying capacity based on the predator–prey relationships identified by Carbone and Gittleman (2002) yielded similar results to ours for lion (Tables 5 and 6). The predictions for spotted hyaena, leopard, cheetah and African wild dog were far greater than our predictions however (Tables 5 and 6).

Thirteen lions at Phinda in 1995 were four below our predicted carrying capacity, however the 21 cheetahs exceeded our predictions by 14 and we consider the intervention by managers there as a supporting test for our predictions (Table 5). We predicted a carrying capacity of two lions for the 15 km^2 Madjuma Game Reserve, but four times this number were reintroduced and the wildebeest population declined precipitously – providing another independent test of our predictions

Table 4 – Relationships between predator density (log_{10}; x-axis) and the various measures of prey biomass (log_{10}; y-axis) derived from data presented in the Appendix

Species	Preferred prey species	Preferred prey weight range	Previously published relationships	Source of previously published relationships
African wild dog	$y = -2.780 + 0.470x$; $r^2 = 0.523$; $P = 0.012$; $n = 10$	$y = -3.012 + 0.494x$; $r^2 = 0.465$; $P = 0.021$; $n = 10$		
Cheetah	$y = -2.543 + 0.369x$; $r^2 = 0.397$; $P = 0.051$; $n = 9$	$y = -2.641 + 0.411x$; $r^2 = 0.519$; $P = 0.019$; $n = 9$	$y = 0.021 + 0.002x$; $r^2 = 0.616$; $P = 0.007$; $n = 10$ (cheetah biomass)	Derived from Gros et al. (1996); relationships based on untransformed data
Leopard	$y = -2.248 + 0.405x$; $r^2 = 0.833$; $P < 0.001$; $n = 11$	$y = -2.455 + 0.456x$; $r^2 = 0.775$; $P < 0.001$; $n = 11$	$y = 0.0027 + 0.0020x$; $r^2 = 0.720$; $P = 0.002$; $n = 11$	Derived from Stander et al. (1997); data not log transformed
Lion	$y = -2.158 + 0.377x$; $r^2 = 0.626$; $P < 0.001$; $n = 23$	$y = -1.363 + 0.152x$; $r^2 = 0.271$; $P = 0.009$; $n = 23$	$y = 0.0870 + 0.0001x$; $r^2 = 0.480$; $P = 0.009$; $n = 11$ (mean prey biomass)	Derived from van Orsdol et al. (1985); data not log transformed
			$y = 0.0828 + 0.0002x$; $r^2 = 0.722$; $P < 0.001$; $n = 11$ (lean season biomass)	
Spotted hyaena	No preferred prey species	$y = -2.195 + 0.467x$; $r^2 = 0.487$; $P = 0.001$; $n = 17$		
Spotted hyaena against lion prey preferences	$y = -1.959 + 0.349x$; $r^2 = 0.462$; $P < 0.001$; $n = 17$	$y = -1.386 + 0.230x$; $r^2 = 0.257$; $P = 0.032$; $n = 17$		

(Fig. 1). We predicted a carrying capacity of 50 lions in Pilanesberg in 1997 based on the available prey (Table 5). This was exceeded in 1998–1999 and, soon after, declines in several prey species occurred (Tampling and du Toit, 2005). We also consider this as an independent test of our predictions.

Our predictions for the GAENP far exceeded the population sizes estimated by Boshoff et al. (2002). They predicted the expanded park would support 58 lion, 55 spotted hyaena, 36 leopard, 50 wild dog and six cheetah, however only our prediction for wild dog population size approximates theirs (Table 5).

4. Discussion and conclusion

The relationship between predator density and the biomass of its prey is not new, but our use of a far broader suite of sites to elucidate this relationship, our use of predator specific prey preference parameters and our estimation and testing of large predator carrying capacity are novel. The relationships we describe between predator density and either the biomass of significantly preferred prey or the biomass of prey in the predator's preferred weight range is highly significant in almost all cases (Table 4). The larger sample size we used, which included diverse habitat types (excepting Afromontane forest; Table 1), compared to previous studies (Gros et al., 1996; Stander et al., 1997; van Orsdol et al., 1985), meant that our relationships explained less of the variance in the data for lion and cheetah than those earlier, smaller studies, however we believe our relationships offer more robust predictive power across a range of sites. The greater explanatory power of the relationship we calculated for leopard (Table 4) is probably due to our use of a more accurate preferred weight range of 10–40 kg (Hayward et al., 2006a), rather than the 15–60 kg previously used.

Although the basis of these relationships is sound (Fuller and Sievert, 2001), like previous analyses, only leopard, and perhaps that of lion, is good enough for unrestrained support. Fuller and Sievert (2001) have identified numerous factors that confound these relationships including the difficulty in censusing carnivores, variations in methodology, appropriate definitions of food density, interspecific competition and intra-guild predation, genetics and disease. Nonetheless, more than half the variation in the predator density data is explained by the density of their preferred prey for all predators except spotted hyaena.

Our relationships appear more conservative than those previously identified (Table 4), possibly because we used a larger sample size and/or because we looked at preferred prey in our calculations. These previous relationships provided estimates at least twice the size of ours, and often more (Table 5). Given the potential dire consequences of overpopulation of large predators (Hunter, 1998; Power, 2002), particularly when confined to small reserves, we recommend using our more conservative relationships in determining the carrying capacity of large predators at a site.

The relationship we found between wild dog density and prey in their preferred weight range conflicts with results from Kruger where wild dog density was lowest in areas of high preferred prey density (Mills and Gorman, 1997). It seems likely that at a local or habitat scale wild dogs avoid areas of high prey and competitor density, in the same way cheetahs seek competition refuge (Durant, 1998). At the landscape scale however, wild dog density increases with prey density (Table 4).

Carbone and Gittleman (2002) based their relationship between predator density and prey biomass on the body mass of the predator. These results were similar to ours for lion, but were far higher than ours for leopard, spotted hyaena, and the competitively inferior wild dog and cheetah (Tables 4 and 5). The depressive influence of these larger predators in eastern Africa on cheetah and wild dog densities are well known (Creel and Creel, 1996; Creel et al., 2004; Laurenson,

Table 5 – Predicted density and population size (in parentheses) of each large predator estimated by each different method

Site	Shamwari					Karoo			Mountain Zebra			Addo						Madjuma		Phinda	Pilanesberg
Year/predictive method	2000	2001	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	Nyathi	Darlington	GAENP	1997	1998	1995	1997
Wild dog prey	0.036 (7)	0.038 (7)	0.041 (8)	0.042 (8)	0.040 (7)	0.012 (9)	0.013 (9)	0.012 (8)	0.016 (3)	0.015 (3)	0.017 (3)	0.034 (5)	0.046 (6)	0.037 (5)	0.013 (1)	0.014 (1)	0.020 (68)	0.029 (0)	0.022 (0)	0.032 (5)	0.022 (11)
Wild dog weight	0.029 (5)	0.029 (6)	0.032 (6)	0.033 (6)	0.030 (6)	0.012 (8)	0.012 (8)	0.009 (7)	0.021 (4)	0.021 (4)	0.024 (4)	0.024 (3)	0.032 (4)	0.025 (3)	0.009 (1)	0.017 (1)	0.017 (58)	0.040 (1)	0.035 (1)	0.030 (5)	0.021 (11)
Cheetah prey	0.021 (4)	0.022 (4)	0.023 (4)	0.023 (4)	0.019 (4)	0.015 (10)	0.013 (9)	0.010 (7)	0.020 (4)	0.020 (4)	0.022 (4)				0.008 (1)	0.019 (2)	0.009 (25)	0.018 (0)	0.019 (0)	0.025 (4)	0.017 (8)
Cheetah weight	0.027 (5)	0.028 (5)	0.030 (6)	0.031 (6)	0.028 (5)	0.015 (10)	0.013 (9)	0.010 (7)	0.023 (4)	0.021 (4)	0.025 (5)	0.010 (1)	0.016 (2)	0.016 (2)	0.009 (1)	0.019 (2)	0.020 (70)	0.024 (0)	0.022 (0)	0.042 (7)	0.019 (9)
Leopard prey	0.052 (10)	0.055 (10)	0.060 (11)	0.061 (11)	0.056 (11)	0.004 (3)	0.004 (3)	0.004 (3)	0.004 (1)	0.005 (1)	0.006 (1)	0.017 (2)	0.021 (3)	0.021 (3)	0.016 (1)	0.006 (1)	0.045 (155)	0.043 (1)	0.045 (1)	0.060 (10)	0.038 (19)
Leopard weight	0.046 (9)	0.048 (9)	0.053 (10)	0.055 (10)	0.049 (9)	0.027 (19)	0.025 (17)	0.018 (12)	0.032 (6)	0.032 (6)	0.036 (7)	0.012 (2)	0.015 (2)	0.015 (2)	0.014 (1)	0.035 (3)	0.042 (143)	0.034 (1)	0.037 (1)	0.050 (9)	0.031 (15)
Lion prey	0.063 (12)	0.062 (12)	0.066 (12)	0.069 (13)	0.058 (11)	0.042 (29)	0.045 (31)	0.047 (33)	0.065 (12)	0.070 (13)	0.072 (13)	0.096 (13)	0.102 (14)	0.100 (13)	0.043 (3)	0.052 (5)	0.053 (181)	0.109 (2)	0.126 (2)	0.102 (17)	0.101 (51)
Lion weight	0.107 (20)	0.107 (20)	0.107 (20)	0.109 (20)	0.102 (19)	0.092 (64)	0.082 (57)	0.086 (60)	0.111 (20)	0.113 (21)	0.114 (21)	0.132 (18)	0.134 (18)	0.131 (18)	0.110 (8)	0.055 (5)	0 (na)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
Hyaena weight	0.150 (28)	0.150 (28)	0.160 (30)	0.166 (31)	0.153 (29)	0.102 (71)	0.106 (75)	0.107 (75)	0.153 (28)	0.147 (27)	0.154 (29)	0.148 (20)	0.192 (26)	0.168 (23)	0.112 (8)	0.097 (9)	0.093 (316)	0.237 (4)	0.244 (4)	0.177 (30)	0.172 (86)
Hyaena – lion prey[a]	0.083 (16)	0.082 (15)	0.088 (16)	0.091 (17)	0.078 (15)	0.057 (40)	0.061 (43)	0.064 (45)	0.086 (16)	0.092 (17)	0.094 (17)	0.123 (17)	0.131 (18)	0.128 (17)	0.059 (4)	0.070 (6)	0.071 (201)	0.139 (2)	0.158 (2)	0.130 (22)	0.129 (65)
Lion[b]	0.122 (23)	0.123 (23)	0.128 (24)	0.132 (25)	0.123 (23)	0.098 (69)	0.097 (68)	0.097 (68)	0.117 (22)	0.116 (21)	0.121 (22)	0.132 (18)	0.148 (20)	0.136 (18)	0.104 (7)	0.097 (9)	0.111 (378)	0.134 (2)	0.136 (2)	0.135 (23)	0.135 (67)
Lion[c]	0.129 (24)	0.130 (24)	0.137 (26)	0.142 (27)	0.130 (24)	0.097 (68)	0.097 (67)	0.096 (67)	0.122 (23)	0.121 (22)	0.127 (23)	0.142 (19)	0.163 (22)	0.147 (20)	0.105 (7)	0.095 (9)	0.114 (389)	0.145 (2)	0.147 (2)	0.145 (25)	0.146 (73)
Leopard[d]	0.105 (20)	0.112 (21)	0.130 (24)	0.140 (26)	0.112 (21)	0.041 (29)	0.037 (26)	0.030 (21)	0.076 (14)	0.068 (13)	0.091 (17)	0.031 (4)	0.047 (6)	0.047 (6)	0.028 (2)	0.056 (5)	0.064 (218)	0.084 (1)	0.073 (1)	0.256 (44)	0.055 (28)
Cheetah[e]	0.028 (5)	0.030 (6)	0.037 (7)	0.040 (7)	0.030 (6)	0.007 (5)	0.006 (4)	0.003 (2)	0.019 (3)	0.016 (3)	0.023 (4)	0.003 (0)	0.009 (1)	0.009 (1)	0.003 (0)	0.012 (1)	0.015 (1481)	0.021 (0)	0.017 (0)	0.079 (49)	0.012 (6)

We have not presented estimates of variability due to space constraints. The similarity of predicted population sizes at the same site during periods of different prey availabilities reflects this. *Prey* refers to predictions based on the biomass of significantly preferred prey species; and *weight* refers to the biomass of prey within the preferred weight range of a predator. Prey biomass was calculated by multiplying the prey densities in Table 1 by published body mass estimates (3/4 of adult female body mass) from Table 2.

a Refers to relationships between spotted hyaena density and the preferred prey of lions (see Section 2 for explanation).

b Refers to the predictions based on van Orsdol et al. (1985) relationship between lion density and mean prey biomass.

c Refers to their relationship with lean season prey biomass.

d Refers to the relationship of leopard density and prey biomass by Stander et al. (1997).

e Refers to the relationship between cheetah biomass and prey biomass (Gros et al., 1996).

1995a,b; Laurenson et al., 1995). The differences in predicted carrying capacity between our two methods may be because metabolic relationships were used to estimate population density without consideration of the competitively inhibitive influence of large predators.

Test sites support our estimates of carrying capacity. Madjuma Game Reserve occupies only 15 km^2 but housed eight lion before precipitous declines in blue wildebeest (Fig. 1) led to the removal of lions in 2001 (Power, 2002). Our analysis suggests this population size was four times that which the reserve could support (Table 5).

The rapidly expanding lion population in Phinda was 13 in 1995 (three years after reintroduction), however managers recognised that this was approaching carrying capacity with the blue wildebeest population plummeting, and subsequently removed 30 lion (Hunter, 1998). Our estimate of carrying capacity for lion in Phinda in 1995 was 17 individuals (Table 5).

There were 21 cheetah in Phinda in 1995 and the common reedbuck population was declining sharply, however no cheetah were removed due to a high cheetah mortality rate caused by lion predation (Hunter, 1998). Our results suggest that this decline in reedbuck abundance was due to overabundance of cheetah in the reserve as common reedbuck are within the preferred weight range of cheetah prey (Hayward et al., 2006b).

Within a year of Pilanesberg's lion population exceeding our estimate of carrying capacity (51), blue wildebeest, eland (*Tragelaphus oryx*), waterbuck (*Kobus ellipsiprymnus*) and kudu (*Tragelaphus strepsiceros*) populations began to decline dramatically without any evidence of disease (Tampling and du Toit, 2005). The lion population increased to 59 in 2001, by which time the blue wildebeest population had declined by 45%, eland by 76%, waterbuck by 67% and kudu by 65% , apparently due to excessive predation by lions (Tampling and du Toit, 2005). Each of these species are significantly preferred prey or are within the preferred prey weight range of lions (Hayward and Kerley, 2005) and hence would be expected to be heavily preyed upon during lion overpopulation.

The most recent estimate of lion population size in Shamwari was 15, while we predicted a carrying capacity in 2004 of only 11 lion (Table 5). Independent to this research, Shamwari managers became concerned at the size of their lion population, such that they have contracepted one lioness and sold another, when a sub-adult male coalition at dispersing age escaped from the reserve (Hayward et al., 2007b). Further evidence that this population may be beyond carrying capacity is the recent decline in the number of lions Shamwari can support (Table 5) suggesting hyper-predation is occurring.

Our predictions of the potential population size of large predators in the GAENP differ substantially from those of Boshoff et al. (2002). This is undoubtedly because they based their estimates of predator density on space use, rather than resource use. There is no justification for this as predator space use reflects the availability of food resources which vary greatly between sites (van Orsdol et al., 1985). Conversely, they based their estimates of prey density on food availability in each habitat unit which is justified. Consequently, their prey estimates are likely to be accurate and, given that we used these in our estimates of predator population size, our

Table 6 – Predicted population densities and size (in parentheses) of large predators in each reserve based on Carbone and Gittleman's (2002) equation $y = (94.54x - 1.03) \times \left(\frac{z}{10000}\right)$, where x is the predator's body mass (lion = 142 kg, leopard = 46.5 kg, cheetah = 50 kg, wild dog = 25 kg and spotted hyaena = 58.6 kg from Stuart and Stuart (2000) and z = prey biomass; R^2 = 0.86, n = 24) with the prey biomass based on the prey densities presented in Table 1

Site	Shamwari					Karoo			Mountain Zebra			Addo						Madjuma		Phinda	Pilanesberg
Year/species	2000	2001	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	Nyathi	Darlington	GAENP	1997	1998	1995	1997
African wild dog	0.666 (125)	0.684 (128)	0.773 (145)	0.852 (160)	0.682 (128)	0.448 (147)	0.410 (135)	0.402 (132)	0.520 (104)	0.509 (102)	0.584 (117)	0.845 (113)	1.149 (154)	0.922 (123)	0.161 (16)	0.080 (8)	0.451 (1538)	0.892 (13)	0.927 (14)	0.896 (152)	0.903 (452)
Cheetah	0.326 (61)	0.335 (63)	0.379 (71)	0.417 (78)	0.334 (63)	0.219 (72)	0.201 (66)	0.197 (65)	0.255 (51)	0.249 (50)	0.286 (57)	0.414 (55)	0.563 (75)	0.451 (60)	0.079 (8)	0.039 (4)	0.221 (753)	0.437 (7)	0.489 (7)	0.439 (75)	0.442 (221)
Leopard	0.352 (66)	0.361 (68)	0.408 (76)	0.450 (84)	0.360 (67)	0.236 (78)	0.217 (71)	0.212 (70)	0.274 (55)	0.269 (54)	0.308 (62)	0.446 (60)	0.606 (81)	0.486 (65)	0.085 (9)	0.042 (4)	0.238 (812)	0.471 (7)	0.489 (7)	0.473 (80)	0.477 (238)
Lion	0.111 (21)	0.114 (21)	0.129 (24)	0.142 (27)	0.114 (21)	0.075 (25)	0.069 (22)	0.067 (22)	0.087 (17)	0.085 (17)	0.098 (20)	0.141 (19)	0.192 (26)	0.154 (21)	0.027 (3)	0.013 (1)	0.075 (257)	0.149 (2)	0.155 (2)	0.150 (25)	0.151 (75)
Spotted hyaena	0.277 (52)	0.284 (53)	0.332 (60)	0.354 (66)	0.283 (53)	0.186 (61)	0.171 (56)	0.167 (55)	0.216 (43)	0.212 (42)	0.243 (49)	0.351 (47)	0.478 (64)	0.383 (51)	0.067 (7)	0.033 (3)	0.188 (640)	0.371 (6)	0.385 (6)	0.373 (63)	0.376 (188)

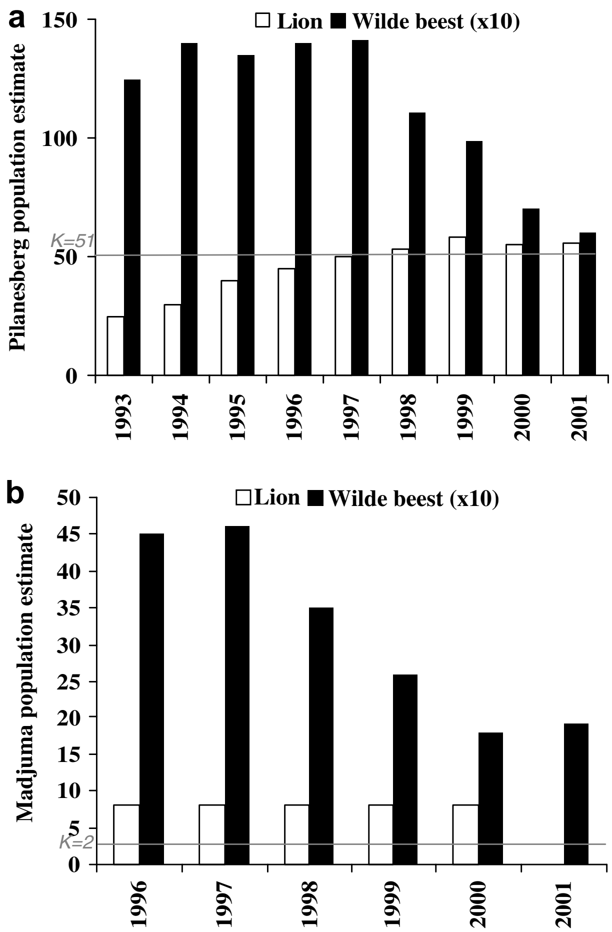

Fig. 1 – Comparison between the predicted carrying capacity of lion at (a) Pilanesberg and (b) Madjuma and the response of blue wildebeest – a preferred prey species. The predicted carrying capacity (*K*) for both is shown as a grey line. There was a negative correlation between lion and wildebeest population sizes at Pilanesberg (Spearman's $r = -0.653$; $N = 9$; $P = 0.057$), but no relationship existed at Madjuma because the lion population was contracepted. Long-term prey abundance data for Phinda were not available so the test of cheetah carrying capacity was not presented graphically here.

estimates of predator density are likely to be more realistic than theirs for GAENP.

Our carrying capacity predictions for proposed reintroduction sites have also received support from management. Although concessionary contracts require predators (lion) to be reintroduced to Nyathi and Darlington sections of Addo, park managers are refusing to do so until wildlife densities attain sufficient levels (L. Moolman, pers. comm.). Our data suggest these sites are currently only able to support very low predator populations (Table 5) particularly given the potential for stochastic forces to drive small, enclosed populations extinct (Caughley and Gunn, 1996). An alternative option might be to use Carbone and Gittleman's (2002) predictions, for subordinate, threatened species, such as African wild dog or cheetah, to create larger, self-sustaining populations of these species in the absence of competitively dominant predators, although given the excessively high predictions we do not recommend this.

Our predictions of carrying capacity for each large predator also make ecological sense. We predicted the highest density of lion at small, enclosed reserves that are often stocked at artificially high levels sustained by heavy management regimes, such as Madjuma, Phinda and Addo (Table 5). The lowest densities predicted for lion were for newly restocked areas where the founder prey population base is still growing, such as Nyathi and Darlington, or in arid areas that naturally support low wildlife densities, such as the Karoo (Table 5). Furthermore, the predictions for spotted hyaena mimic those of lion reflecting the degree of competition between these two top predators and the non-specific nature of hyaena predation (Hayward, 2006).

The highest predicted densities of African wild dogs were at the smaller, enclosed reserves, but also at sites with high densities of common duiker, bushbuck and kudu, such as Shamwari. Low densities were predicted for the restocking sites and arid areas (Table 5).

The highest densities of cheetah were predicted for Phinda and Shamwari. Phinda supports high density of impala (*Aepyceros melampus*), reedbuck and nyala (*Tragelaphus angusi*) – all within the cheetahs preferred prey weight range (Hayward et al., 2006b). The Eastern Cape lacks many of the cheetah's preferred prey species, but Shamwari has compensated for this by introducing species that did not originally occur there, notably blesbok *Damaliscus dorcas phillipsi*, in order to provide sufficient food. South African National Parks (Addo, GAENP, Karoo, Mountain Zebra) have policies against introducing extralimital species and hence these have the lowest predicted carrying capacity for cheetahs. The predicted density of leopard reflected sites with high densities of bushbuck and duiker, such as Phinda and Shamwari (Table 5).

Although the prediction and test sites used here are all fenced, and therefore geographically closed, and within South Africa, these methods are applicable well beyond such sites. These methods estimate predator density based on the preferred prey density and this relationship applies to fenced or unfenced reserves throughout Africa as it was derived from a combination of such sites. Furthermore, while fenced reserves are common in southern Africa, throughout the world conservation areas are increasingly becoming islands of natural habitat in a sea of disturbed environments (Andren, 1994; Saunders et al., 1991), and the cause of such isolation has little effect on the results described here.

The creation of geographic closure via fencing offers scientific benefits by allowing tests of predictions of carrying capacity. It will be much more difficult to define the area a carrying capacity estimate applies to in unfenced sites without other hostile elements that create a 'metaphorical' fence. Predictions of large carrying capacities at sites surrounded by such hostile elements should not be viewed as conservation security given the conflict with humans on reserve boundaries is the biggest extinction threat to large carnivores in conservation areas (Woodroffe and Ginsberg, 1998). Given wide ranging species, such as cheetahs and African wild dogs, are most at risk of such extinction causes (Woodroffe and Ginsberg, 1998), recent evidence of the importance of fencing for successful wild dog reintroduction (Gusset et al., in press) suggests consideration should be given to securely separating humans and large predators.

This is the first time the carrying capacity of large predators has been predicted and successfully tested, and the equations in Table 4 should become a valuable tool for conservation managers. Using our methods and equations, the carrying capacity of Africa's large predators can be estimated for any site where prey densities are known as we have accurately tested them in desert, savannah and thicket biomes that comprise the majority of the habitats where Africa's large predator guild occurs. It is likely that similar results are possible for all other generalist predators that have been sufficiently studied. For example, efforts to secure the endangered Florida panther (*Puma concolor coryi*) have focused on landscape and habitat issues to increase the population (Kautz et al., 2006), however prey availability is the fundamental habitat requirement of large predators (Hayward et al., 2007; Karanth et al., 2004) and so determining landscape level area requirements based on preferred prey carrying capacity in each habitat may be a better option. Alternatively, this technique can be used to improve the accuracy of population viability analyses by including a prediction of carrying capacity (Brook et al., 1997). Calculating predator carrying capacity at a site annually after wildlife censuses can determine whether management actions are necessary to enhance available food resources or limit the number of predators, as well as determine the potential for an area to support minimally viable populations. By targeting preferred prey species or weight ranges in expensive wildlife censuses, the costs of conservation management actions aimed at top order predators may also be reduced.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.06.018.

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