

Testing Predictions of the Prey of Lion (*Panthera leo*) Derived from Modelled Prey Preferences

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71 ABSTRACT Apex predators are often threatened with extinction, and reintroduction is one method conservation managers are using to secure their persistence. Yet the ability to predict what these predators will eat upon reintroduction is lacking. Here we test predictions of the diet of the lion (*Panthera leo*), derived from dietary electivity index and optimality theory, using independent data collected from reintroduced and resident populations. We solved the Jacobs' index preference equation for each prey species of the lion using values calculated by Hayward and Kerley (2005) and prey abundance data from 4 reintroduction sites and 1 resident lion population over several years. We then compared these estimates with actual kill data gathered from each site and time period, using the log-likelihood ratio and linear regression. The model precisely predicted the observed number of kills in 9 of the 13 tests. There was a highly significant linear relationship between the number of lion kills predicted to occur at a site and the number observed for all but one site (mean $r^2 = 0.612$; $\beta = 1.03$). Predicting predator diet will allow conservation managers to stop responding and start planning in advance for reintroductions and environmental variation. Furthermore, ensuring that sufficient food resources are available is likely to increase the success of reintroduction projects. In addition, managers responsible for threatened prey species will be able to predict the vulnerability of these species to predation in the event of predator reintroductions or changes in abundance. These methods are applicable to virtually all large predators that have been sufficiently studied. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):000–000; 2007)

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Large predators are frequently threatened with extinction (Ginsberg 2001), yet conservation managers are beginning to slow and even reverse these declines through translocation and reintroduction programs (Kleiman 1989). Historically, the success of large carnivore reintroductions has been poor (Breitenmoser et al. 2001) and one reason for this may be a lack of suitable prey at reintroduction sites.

Recent reviews of the prey preferences of large African predators have revealed that each species has a limited range of optimal prey species (Hayward and Kerley 2005; Hayward 2006; Hayward et al. 2006a, 2006b, 2006c). If these prey species are not present at a site in sufficient numbers then the predator may be unlikely to persist.

For example, wildlife managers at South Africa's Madjuma Game Reserve thought the high impala (*Aepyceros melampus*) density would be sufficient to sustain the reintroduced lion (*Panthera leo*) population without detrimentally affecting other prey species. Within 2 years, however, the blue wildebeest (*Connochaetes taurinus*) population declined drastically leading to the removal of the lions (Power 2002). This could have been averted if managers had sufficient knowledge of lion prey preferences, which would have illustrated that blue wildebeest are significantly preferred and impala significantly avoided by lion (Hayward and Kerley 2005), and were able to predict lion diet based on the number of prey available.

Similarly, the cheetah (*Acinonyx jubatus*) reintroduction to South Africa's Suikerbosrand Nature Reserve failed within 2 years when precipitous declines in common reedbuck (*Redunca arundinum*) numbers led to their removal (Pettifer 1981a, b). A more detailed knowledge of cheetah prey preferences (Hayward et al. 2006b) would have identified this problem prior to the reintroduction, allowing conservation managers to plan ways to avert the failed attempt. Predation by the newly reintroduced cheetahs in the Phinda Game Reserve led to similar declines in common reedbuck (Hunter 1998) that would have rendered the reintroduction a failure were it not for the high cheetah mortality rate. Clearly then, an ability to predict the diet of reintroduced predators will improve the success rate of such reintroductions.

Threatened prey species have also been placed at risk through inadequate knowledge of predator prey preferences. The vulnerable roan antelope (*Hippotragus equines*) almost declined to extinction in Kruger National Park after aerial censuses revealed man-made waterholes had opened up habitat for zebra (*Equus burchelli*) and blue wildebeest from which they had previously been excluded (Harrington et al. 1999). Lions followed these 2 species into the area and ended up preying upon the roan also, thereby driving its decline (Harrington et al. 1999). Blue wildebeest and zebra are both significantly preferred prey species of lion (Hayward and Kerley 2005). The roan is within the lion's optimal prey weight range but generally escapes preferential predation through its inherent rarity which makes it too

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energetically expensive for lions to search extensively for them to preferentially prey upon them (Hayward and Kerley 2005). When waterholes opened up the roan's habitat to competitors, it lost the protection of relative rarity and became heavily preyed upon (Harrington et al. 1999). Detailed research was required to determine that predation caused the roan decline, rather than competition with water-dependent herbivores, however, an ability to predict the response of predators to changes in prey relative abundance may have made this research unnecessary.

Knowledge of predator diet is crucial for their management, yet without substantial field work, wildlife managers currently have little idea of the specifics of predator-prey interactions at their sites. The lion illustrates the importance wildlife managers place on ascertaining the diet of large predators, and there are at least 42 published accounts of its diet from throughout its distribution (see review by Hayward and Kerley 2005). These studies, however, are only snapshots of an ever-changing continuum that arises through variations in predator and or prey population sizes. The ability to predict what a large predator will prey upon is likely to improve the success of conservation initiatives and improve management of conservation estate.

The large number of published dietary studies makes the lion ideally suited to having predictions made about its diet. No previous model has been created to predict the species specific diet of a large predator. Here, we used preference indices calculated for almost all recorded lion prey species (Hayward and Kerley 2005) to predict the diet of lions in situations of varying predator and prey abundances from sites that were not used in the initial prey preferences study (Hayward and Kerley 2005). We subsequently tested the precision of these predictions with actual predation data collected at each of these sites.

STUDY AREA

Our test data came from Zimbabwe's Wankie (now Hwange) National Park (Wankie) and reintroduced lion populations in South Africa's Addo Elephant National Park (Addo), Shamwari Game Reserve (Shamwari), Madikwe Game Reserve (Madikwe), and the Greater Makalali Conservancy (Makalali). The data from Wankie came from published work from the early 1970s on the extant lion population totalling approximately 500 individuals (19°00'S; 26°30'E; Wilson 1975). This data was less rigorously collected as those at other sites, however, they serve to illustrate the robust nature of this technique.

Addo (33°30'S, 25°45'E) was located in South Africa's Eastern Cape Province, 80 km north of Port Elizabeth. Six lions (4 M and 2 F) were reintroduced to Addo's Main Camp (approx. 13,400 ha) in November 2003 from the Kgalagadi Transfrontier Park and all were radiocollared (Hayward et al. 2007). By August 2005, there had been no increase in numbers despite 3 litters being born. This area was within the Thicket Biome and was vegetated by elements of spekboomveld (Vlok et al. 2003), with varying degrees of agriculture-derived disturbance resulting in areas

of open grassland and bushy areas interspersed within the densely vegetated thicket matrix.

Shamwari (33°30'S, 26°05'E) covered 19,746 ha and was located 40 km east of Addo in the Eastern Cape. Six lions (2 M and 4 F) were reintroduced in September and October 2000 from Madikwe and Pilanesberg National Parks (Hayward et al. 2007). Since then the population has risen to 20 with several removals by managers aimed at minimizing the impact of male coalitions on Shamwari's buffalo (*Syncerus caffer*) population. Shamwari consisted of areas of Thicket Biome interspersed with cleared grasslands and riparian vegetation (Vlok et al. 2003).

Madikwe (24°50'S, 26°15'E) was a 55,000-ha game reserve located in South Africa's North West Province. Madikwe comprised a variety of ecosystems from mountain plateau, rocky ravines, varied acacia, and broad-leaved bushveld to riverine forest and open savannah grassland (Hofmeyr et al. 2003). Lions were reintroduced from Pilanesberg and Etosha National Parks in 1994, and by 1998 over 30 lions had bred from the 11 initially reintroduced (Hofmeyr et al. 2003).

Makalali (29°09'S, 30°42'E) was located in South Africa's Limpopo Province and its undulating terrain supported mixed lowveld and mopane bushveld as the dominant vegetation types (Druce et al. 2004). An adult female and her 4 cubs were reintroduced from Kruger National Park in December 1994 and by 1999, when 2 unrelated males were introduced, 35 offspring had been produced of which 20 were removed (Druce et al. 2004).

METHODS

Wilson (1975) determined prey abundance via 24-hour waterhole counts during the 1974 dry season at Wankie. Prey abundance was estimated by aerial counts elsewhere. Aerial counts involved a helicopter with multiple (>2) observers travelling set transect routes across the study area and provided a total count of wildlife, which was then adjusted for cryptic and small species using calibrations derived from low level counts.

Researchers, game guides, and rangers located lion kills at each of the study sites. In Addo, we employed 96-hour continuous "follows" of radiocollared lions (Packer et al. 1990) to give the least biased account of predator diet (Mills 1992), while daily opportunistic locating of kills of radiocollared and uncollared lions occurred elsewhere. We used the number of kills observed at each site for each species as an independent test of the precision of our predictions.

We collected prey abundance and kill data for 1974 in Wankie (1 yr), November 2003 until October 2005 in Addo (2 yr), January 2001 until December 2004 in Shamwari (4 yr), January 1996 until December 1998 in Madikwe (3 yr), and between February 1998 and December 1998, and January 2000 until December 2001 in Makalali (3 yr). For each site, we analyzed these data as individual years, yielding 13 samples. Treating each year's data as a sample is justified as variations in the abundance of even one species of prey

can alter the number of individuals of that or other species killed.

We calculated the predicted number of kills of each species at each site during each time period by solving the Jacobs' index equation (Jacobs 1974):

$$D = \frac{r - p}{r + p - 2rp} \quad (1)$$

for r (proportion of total kills). This led to the equation:

$$R_i = \frac{D_i p_i + p_i}{1 - D_i + 2D_i p_i} \times \sum K \quad (2)$$

where R_i is the predicted number of kills of species i when we observed a total of $\sum K$ kills, D_i represents the Jacobs' index value of species i calculated by Hayward and Kerley (2005) using data from sites other than those used here, and p_i represents the proportional abundance of prey species i at a site. We used multiplication by $\sum K$ (a constant at each site based on the number of kills observed) to allow direct comparison between the predicted and observed number of kills. We excluded estimates for blesbok (*Damaliscus dorcas phillipsi*), bontebok (*D. dorcas dorcas*), lechwe (*Kobus leche*), and black wildebeest (*Connochaetes gnou*) because we had no previous Jacobs' index estimate for these species and therefore could not solve equation 2 for them.

We compared observed number of kills of each species with the predicted (expected, R_i) number of kills of that species at each site during each time period using the log-likelihood goodness of fit (G) test (Zar 1996) with the H_0 that there was no significant difference between the predicted and observed number of kills of each species. We opted for this test rather than the χ^2 test because the difference between the observed and expected values were frequently greater than the expected values (Zar 1996). These analyses are susceptible to Type II errors, so we view P values less than 0.10 conservatively and highlight this in our results.

We used linear regression to measure the precision of our predictions, where a significant gradient indicates a relationship between the predicted and observed number of kills at a site or of an individual species and the r^2 value illustrates the amount of variance explained by the relationship (effect size). A gradient (β) equalling 1.00 indicates the model's predictions concord exactly with the observed number of kills, however there is no way to statistically test the accuracy of the predictions with a hypothetical gradient of 1 because the residual sum of squares is always 0 and there is no variance. Consequently, we tested the accuracy of the predictions by comparing the 95% confidence intervals of the slope with the hypothetical gradient of 1.

RESULTS

The predictions of lion diet were precise in 9 of 13 tests. Our predictions explained $57.6 \pm 6.4\%$ (mean \pm 1 SE) of the variance between the number of predicted and observed kills in the combined data for all sites with a mean gradient (β) of 1.05 ± 0.06 . Excluding one outlying species at one site (warthog [*Phacochoerus africanus*] at Makalali 1998) and

the less rigorously collected data from Wankie increased the amount of variation explained to $64.5 \pm 5.2\%$.

The model precisely predicted the number of kills observed for each prey species in Wankie ($G = 29.49$, $df = 24$, $P = 0.23$; Table 1). There was a highly significant positive linear relationship between these 2 variables also, although only a small amount of variation in the data was explained ($r^2 = 0.28$, $\beta = 0.47$, $P < 0.01$; Table 1).

In Addo, the model precisely predicted the observed number of lion kills for all species in 2004 ($G = 15.73$, $df = 11$, $P = 0.15$) and 2005 ($G = 16.77$, $df = 10$, $P = 0.09$; Table 2). The positive linear relationships between predicted and observed kills for both years were highly significant (2004, $r^2 = 0.87$, $\beta = 0.93$, $P < 0.01$; 2005, $r^2 = 0.63$, $\beta = 1.24$, $P < 0.01$).

The model precisely predicted the observed number of kills at Shamwari in 2001 ($G = 30.68$; $df = 23$; $P = 0.14$) and 2003 ($G = 33.59$; $df = 23$; $P = 0.07$; Table 3). The low P value for 2003 was concerning given the susceptibility to Type II errors, however, the large sample size (24) resulted in a power of >0.92 (Zar 1996:109). The model failed to predict the observed number of kills at Shamwari in 2002 ($G = 39.61$; $df = 23$; $P = 0.016$). The exclusion of kudu (*Tragelaphus strepsiceros*), bushbuck (*T. scriptus*), and warthog was required for these differences to cease being significant ($G = 22.54$; $df = 20$; $P = 0.31$) with the number of kills being underpredicted on each occasion (Table 3). The model also failed to predict the number of lion kills in 2004 ($G = 38.01$; $df = 23$; $P = 0.026$) as kudu and warthog predation were again underpredicted (Table 3). When these species were excluded the differences ceased being significant ($G = 31.16$; $df = 21$; $P = 0.07$; power > 0.92). The additional exclusion of bushbuck reduces the likelihood of a Type II error ($G = 27.81$, $df = 20$, $P = 0.13$). Parametric positive linear relationships between the predicted and observed number of kills for each year were highly significant (2001, $r^2 = 0.77$, $\beta = 1.67$, $P < 0.01$; 2002, $r^2 = 0.73$, $\beta = 1.60$, $P < 0.01$; 2003, $r^2 = 0.68$, $\beta = 1.72$, $P < 0.01$; 2004, $r^2 = 0.78$, $\beta = 1.54$, $P < 0.01$).

The model precisely predicted the observed number of kills at Madikwe in 1996 ($G = 8.99$, $df = 20$, $P = 0.98$) and 1997 ($G = 16.45$, $df = 20$, $P = 0.69$; Table 4) but not in 1998 ($G = 78.59$, $df = 20$, $P < 0.01$). The exclusion of blue wildebeest, warthog, kudu, and gemsbok (*Oryx gazella*) reduced these differences in 1998 to insignificant levels ($G = 0.36$, $df = 16$, $P > 0.99$). The model overpredicted blue wildebeest and gemsbok kills and underpredicted kudu and warthog kills. Irrespectively, there were highly significant positive linear relationships between the predicted and observed number of kills in each year (1996, $r^2 = 0.43$, $\beta = 0.60$, $P < 0.01$; 1997, $r^2 = 0.65$, $\beta = 0.71$, $P < 0.01$; 1998, $r^2 = 0.50$, $\beta = 0.65$, $P < 0.01$).

The model failed to predict the observed number of kills at Makalali in 1998 ($G = 44.02$, $df = 13$, $P < 0.001$; Table 5). This significant difference was removed by excluding warthog ($G = 11.44$, $df = 12$, $P = 0.48$). The model was successful in 2000 ($G = 6.33$, $df = 15$, $P = 0.97$) and 2001 (G

Table 1. Potential prey species of lion in Wankie National Park, Zimbabwe (from Wilson 1975), their Jacobs' index values (from Hayward and Kerley 2005), their abundance (No.) based on 24-hour total counts at waterholes during the dry season, and the number of kills predicted by the model and observed by Wilson in 1974.

Species	Jacobs' index (D)	No.	Predicted No.	Observed No.
Baboon (<i>Papio cynocephalus</i>)	-0.89	1,004	0	0
Black rhinoceros (<i>Diceros bicornis</i>)	-1	30	0	0
Blue wildebeest (<i>Connochaetes taurinus</i>)	0.27	1,800	3	9
Buffalo (<i>Syncerus caffer</i>)	0.32	10,000	14	5
Common duiker (<i>Sylvicapra grimmia</i>)	-0.83	12	0	1
Common reedbuck (<i>Redunca aruninum</i>)	-0.57	250	0	0
Eland (<i>Tragelaphus oryx</i>)	0.18	1,600	2	4
Elephant (<i>Loxodonta africana</i>)	-0.87	10,500	1	0
Gemsbok (<i>Oryx gazella</i>)	0.7	120	1	0
Giraffe (<i>Giraffa camelopardis</i>)	0.24	552	1	3
Hippopotamus (<i>Hippopotamus amphibius</i>)	-0.45	5	0	0
Impala (<i>Aepyceros melampus</i>)	-0.73	8,000	1	0
Klipspringer (<i>Oreotragus oreotragus</i>)	-0.96	5	0	0
Kudu (<i>Tragelaphus strepsiceros</i>)	0.13	3,500	4	0
Porcupine (<i>Hystrix africaeustralis</i>)	0.58	2	0	0
Roan (<i>Hippotragus equines</i>)	0.15	600	1	0
Sable (<i>Hippotragus niger</i>)	-0.05	1,800	1	0
Sharpe's grysbok (<i>Raphicerus sharpie</i>)	-0.96	3	0	0
Steenbok (<i>Raphicerus campestris</i>)	-0.86	24	0	0
Tsessebe (<i>Damaliscus lunatus</i>)	0.01	100	0	2
Vervet monkey (<i>Cercopithecus aethiops</i>)	-1	246	0	0
Warthog (<i>Phacochoerus africanus</i>)	0.11	3,000	3	6
Waterbuck (<i>Kobus ellipsiprymnus</i>)	0.18	800	1	5
White rhinoceros (<i>Ceratotherium simum</i>)	-1	40	0	0
77 Zebra (<i>Equus burchelli</i>)	0.16	4,000	5	6

= 15.05, df = 14, $P = 0.36$). Again, there were significant relationships between the predicted and observed number of kills for 2000 and 2001 (2000, $r^2 = 0.76$, $\beta = 1.10$, $P < 0.01$; 2001, $r^2 = 0.30$, $\beta = 0.63$, $P = 0.03$). Such a relationship was not present in 1998 ($r^2 = 0.12$, $\beta = 0.89$, $P = 0.25$), although with the exclusion of warthog the relationship became highly positively significant ($r^2 = 0.59$, $\beta = 0.63$, $P < 0.01$).

There were no significant differences between our predictions and what was observed killed by lions in 9 out of 13 tests. The exclusion of one outlying prey species led to accurate predictions in another test. Other inaccurate tests required 2, 3, and 4 species to be excluded for the differences between the predicted and observed number of kills to cease

being significant. Warthog (erroneous in 4 out of 13 comparisons), kudu (3 out of 13), and bushbuck (1 out of 12) were each underpredicted in the number of kills, while the model significantly overpredicted the number of kills of blue wildebeest (1 out of 10) and gemsbok (1 out of 10). The model accurately predicted the rank of each prey species in each test (Tables 1–5; Fig. 1).

The model precisely predicted the number of kills of 6 of the 8 most common lion prey species (Fig. 1). Impala and zebra showed no relationship between the predicted and observed number of kills, although a significant positive relationship occurred for zebra with the exclusion of 2 outlying data points (Fig. 1). Based on the 95%

Table 2. Potential prey species of lion in Addo Elephant National Park, South Africa, in 2003–2004 and 2004–2005, their Jacobs' index values (from Hayward and Kerley 2005), their abundance in both years (No.) based on helicopter-derived total counts, and the number of kills predicted (Pred.) by the model and actually observed (Obs.).

Species	Jacobs' index (D)	2003–2004			2004–2005		
		No.	Pred.	Obs.	No.	Pred.	Obs.
Black rhinoceros (<i>Diceros bicornis</i>)	-1	7	0	0	15	0	0
Buffalo (<i>Syncerus caffer</i>)	0.32	355	27	16	310	14	18
Bushbuck (<i>Tragelaphus scriptus</i>)	-0.53	103	1	3	81	1	1
Cape grysbok (<i>Raphicerus melanotis</i>)	-0.96	1	0	0	0	0	0
Common duiker (<i>Sylvicapra grimmia</i>)	-0.83	55	0	3	9	0	1
Eland (<i>Tragelaphus oryx</i>)	0.19	106	7	5	88	3	5
Elephant (<i>Loxodonta africana</i>)	-0.87	344	1	0	310	1	0
Hartebeest (<i>Alcephalus busephalus</i>)	0.02	288	13	15	287	7	9
Kudu (<i>Tragelaphus strepsiceros</i>)	0.13	706	38	41	1,394	39	17
Ostrich (<i>Struthio camelus</i>)	-0.55	261	4	9	185	1	9
Warthog (<i>Phacochoerus africanus</i>)	0.11	298	16	23	674	19	20
Zebra (<i>Equus burchelli</i>)	0.16	36	2	0	14	0	2

Table 3. Potential prey species of lion in Shamwari Game Reserve, South Africa, in 2001, 2002, 2003, and 2004, their Jacobs' index values (from Hayward and Kerley 2005), their abundance (No.) based on helicopter-derived total counts, and the number of kills predicted by the model (Pred.) and actually observed (Obs.).

Species	Jacobs' index (D)	2001			2002			2003			2004		
		No.	Pred.	Obs.	No.	Pred.	Obs.	No.	Pred.	Obs.	No.	Pred.	Obs.
Baboon (<i>Papio cynocephalus</i>)	-0.87	0	0	0	0	0	0	0	0	0	122	0	1
Black rhinoceros (<i>Diceros bicornis</i>)	-1	13	0	0	14	0	0	16	0	0	18	0	0
Blue wildebeest (<i>Connochaetes taurinus</i>)	0.27	3	1	1	2	1	1	1	1	0	55	2	7
Buffalo (<i>Syncerus caffer</i>)	0.32	32	1	0	34	2	0	39	1	0	5	0	1
Bushbuck (<i>Tragelaphus scriptus</i>)	-0.53	750	5	8	1,000	8	19	1,000	5	7	930	9	19
Bushpig (<i>Potamochoerus larvatus</i>)	0.11	200	5	0	270	8	0	270	5	0	250	8	1
Cape grysbok (<i>Raphicerus melanotis</i>)	-0.96	75	0	0	80	0	0	75	0	0	50	0	0
Common duiker (<i>Sylvicapra grimmia</i>)	-0.83	900	2	6	925	2	6	925	1	1	850	2	3
Common reedbuck (<i>Redunca aruninum</i>)	-0.57	4	0	0	3	0	0	4	0	0	0	0	0
Eland (<i>Tragelaphus oryx</i>)	0.19	105	3	7	110	4	8	122	3	6	69	3	6
Elephant (<i>Loxodonta africana</i>)	-0.87	49	0	0	53	0	0	49	0	0	53	0	0
Gemsbok (<i>Oryx gazella</i>)	0.70	61	6	3	68	8	4	87	6	1	59	8	1
Giraffe (<i>Giraffa camelopardis</i>)	0.23	18	1	1	16	1	1	18	1	0	25	1	0
Hartebeest (<i>Alcephalus busephalus</i>)	0.02	132	3	5	130	3	7	157	2	1	112	3	3
Hippopotamus (<i>Hippopotamus amphibius</i>)	-0.55	16	0	0	18	0	0	21	0	0	15	0	0
Impala (<i>Aepyceros melampus</i>)	-0.73	694	2	4	891	4	2	977	2	7	656	3	4
Kudu (<i>Tragelaphus strepsiceros</i>)	0.13	800	19	36	900	26	46	942	16	31	900	29	46
Mountain reedbuck (<i>Redunca fulvorufula</i>)	-0.57	300	2	1	350	0	0	350	1	0	325	2	0
Nyala (<i>Tragelaphus angusi</i>)	-0.32	25	0	0	34	0	0	43	0	0	6	0	0
Ostrich (<i>Struthio camelus</i>)	-0.55	42	0	12	13	0	1	37	0	1	46	0	2
Springbok (<i>Antidorcas marsupialis</i>)	-0.59	264	1	1	270	2	3	335	1	1	132	1	1
Warthog (<i>Phacochoerus africanus</i>)	0.11	65	2	4	56	2	21	184	3	18	231	7	27
Waterbuck (<i>Kobus ellipsiprymnus</i>)	0.18	65	2	1	57	2	2	71	2	3	61	2	6
White rhinoceros (<i>Ceratotherium simum</i>)	-1	14	0	0	16	0	0	19	0	0	19	0	0
Zebra (<i>Equus burchelli</i>)	0.16	84	2	1	117	4	4	138	3	2	113	4	4

confidence intervals of the regression slopes (β), the model accurately predicted the number of buffalo, eland, blue wildebeest, and zebra kills and slightly underpredicted the number of hartebeest, impala, kudu, and warthog kills (Fig. 1).

DISCUSSION

We precisely predicted lion diet at Wankie in 1974, Addo in 2004 and 2005, Shamwari in 2001 and 2003, Madikwe in 1996 and 1997, and Makalali in 2000 and 2001. Thus, we

Table 4. Potential prey species of lion in Madikwe Game Reserve, South Africa, in 1996, 1997, and 1998, their Jacobs' index values (from Hayward and Kerley 2005), their abundance (No.) based on helicopter-derived total counts, and the number of kills predicted by the model (Pred.) and actually observed (Obs.).

Species	Jacobs' index (D)	1996			1997			1998		
		No.	Pred.	Obs.	No.	Pred.	Obs.	No.	Pred.	Obs.
Black rhinoceros	-1	16	0	0	19	0	0	21	0	0
Blue wildebeest	0.27	2,100	8	7	2,688	12	14	3,014	52	34
Buffalo	0.32	95	0	0	119	1	0	140	3	0
Bushbuck	-0.53	85	0	0	75	0	1	51	0	0
Eland	0.19	1,060	4	1	1,050	4	1	903	14	10
Elephant	-0.87	255	0	0	267	0	0	274	0	0
Gemsbok	0.7	650	8	1	739	10	3	681	36	2
Giraffe	0.23	155	1	1	130	1	0	100	2	0
Hartebeest	0.02	900	2	2	750	2	2	521	6	12
Hippopotamus	-0.55	1	0	0	6	0	0	9	0	0
Impala	-0.73	3,000	1	6	2,800	2	6	2,704	6	13
Kudu	0.13	2,000	6	3	2,300	9	5	2,321	32	37
Nyala	-0.32	35	0	0	25	0	0	26	0	0
Ostrich	-0.55	95	0	0	59	0	0	51	0	0
Sable	-0.05	35	0	1	26	0	1	20	0	0
Springbok	-0.59	300	0	1	100	0	1	78	0	0
Tsessebe	0.01	29	0	0	16	1	1	36	0	1
Warthog	0.11	1,501	5	4	1,501	5	5	2,001	27	50
Waterbuck	0.18	650	2	1	595	3	1	36	0	0
White rhinoceros	-1	82	0	0	80	0	0	78	0	0
Zebra	0.16	1,900	6	9	1,950	7	5	2,192	30	5

Table 5. Potential prey species of lion in Makalali in 1998, 2000, and 2001, their Jacobs' index values (from Hayward and Kerley 2005), their abundance (No.) based on helicopter-derived total counts, and the number of kills predicted by the model (Pred.) and actually observed (Obs.).^a

Species	Jacobs' index (<i>D</i>)	1998			2000			2001		
		No.	Pred.	Obs.	No.	Pred.	Obs.	No.	Pred.	Obs.
Blue wildebeest	0.21	293	11	4	346	7	11	294	13	15
Bushbuck	-0.53	54	1	3	21	0	0	47	0	0
Bushpig	0.11							1	0	0
Common duiker	-0.83	13	0	0	10	0	0	5	0	0
Eland	0.19	14	1	1	8	0	0	6	1	2
Giraffe	0.23	136	5	2	121	3	4	83	4	3
Hartebeest	0.02	10	1	0	3	1	1	1	0	0
Impala	-0.73	1,596	1	1	1,131	4	2	713	4	8
Kudu	0.13	233	7	10	284	5	2	273	9	3
Nyala	-0.32	35	0	0	22	0	0	18	0	0
Sable	-0.05	6	0	0	1	0	0	1	0	0
Warthog	0.11	167	5	36	222	4	4	121	4	15
Waterbuck	-0.86	195	6	5	152	3	5	120	5	3
Zebra	0.16	281	9	7	371	7	7	338	12	1

^a Data were collated from Druce et al. (2004).

were accurate in 9 out of 13 tests of our predictions and the 4 imprecise tests were largely caused by poor predictions of 2 (warthog and kudu) of the 32 species assessed. The 4 imprecise tests occurred at sites where lion diet was accurately predicted in other years.

We believe our results are adequate for the purposes of predicting lion diet given that opportunistic predation is likely to reduce the precision of our predictions. Moreover, our precision of prediction is highlighted by the minimal discrepancies between the proportion of total kills predicted to be made up of each prey item with that actually observed and the large amount of variance explained by the highly significant relationships between these variables (currently 64.5%). Furthermore, this technique is robust enough to precisely predict the diet of lions when prey abundance has been censused using disparate methods (aerial transects with variable counter numbers and waterhole counts), however in Addo, where data were most rigorously collected, the predictions were always precise. These predictions will improve with further refinement, through the addition of information from this and future studies to calculate more accurate Jacobs' index values. These results and techniques begin building realistic foraging models for large predators that 20 years ago were considered unlikely (Sunquist et al. 1987).

The lions at 4 of the test sites were reintroduced, along with some prey species. The naïveté of the prey and lions to their environment could affect the success of predation and therefore our predictions. This is unlikely to bias our results given the brief period (one generation) that it takes prey (moose, *Alces alces*) to lose their naïveté to recolonizing wolves (*Canis lupus*; Berger et al. 2001), the speed with which prey develop antipredatory strategies to reintroduced lions (<3 months; Hunter and Skinner 1998), and the comparable hunting success rate of reintroduced lions in Addo (10.7%; M. W. Hayward, unpublished data) to elsewhere (Schaller 1972, Bertram 1979, Funston et al. 2001).

Warthog are among the most common prey items of lions (Hayward and Kerley 2005) and the imprecision in 4 of our predictions may stem from inaccurate counts in some studies or some years. Given that studies used in this analysis most commonly used aerial counts to census warthog abundance and for studies used in the derivation of the Jacobs' index value for warthog (Hayward and Kerley 2005), the same hypothesized biases of undercounting such a small species would affect both datasets equally. Hence, erroneous counts are unlikely to be the cause of the discrepancy. Nonetheless, consistent, accurate and repeatable prey censuses are likely to increase the accuracy of our predictions.

Alternatively, the variation in the predictive power for warthog kills could have arisen through natural variation in lion predation rates arising through the opportunistic nature of predation or even associated with variation caused by rainfall patterns (Mills 1995). The greater number of warthog kills observed than predicted in the 4 tests may also be due to influxes of subadult lions into a small adult population, as occurred in Makalali in 1998 (Druce et al. 2004) and probably again when the next cohort of cubs dispersed in 2001. Warthogs are below the ideal prey weight range for lion, however, they are still taken in accordance with their abundance (Hayward and Kerley 2005). This may be due to their apparent lack of vigilance and relatively slow speed (Scheel 1993) which means they can be easily captured by subadult and nomadic lions, where cooperative hunting of larger species is less efficient and less likely to occur (Schaller 1972).

One final explanation for the discrepancy in warthog observation versus prediction is that the lion population had exceeded the ecological carrying capacity at sites where this discrepancy occurred (Shamwari 2002, 2004; Madikwe 1998; Makalali 1998), such that food was a limiting factor, forcing individuals to target suboptimal prey. New litters of cubs were born at Shamwari in 2002 and 2004 (Hayward et al. 2007), while 1998 was a year of below average rainfall (Anyamba et al. 2002). The only published study of the

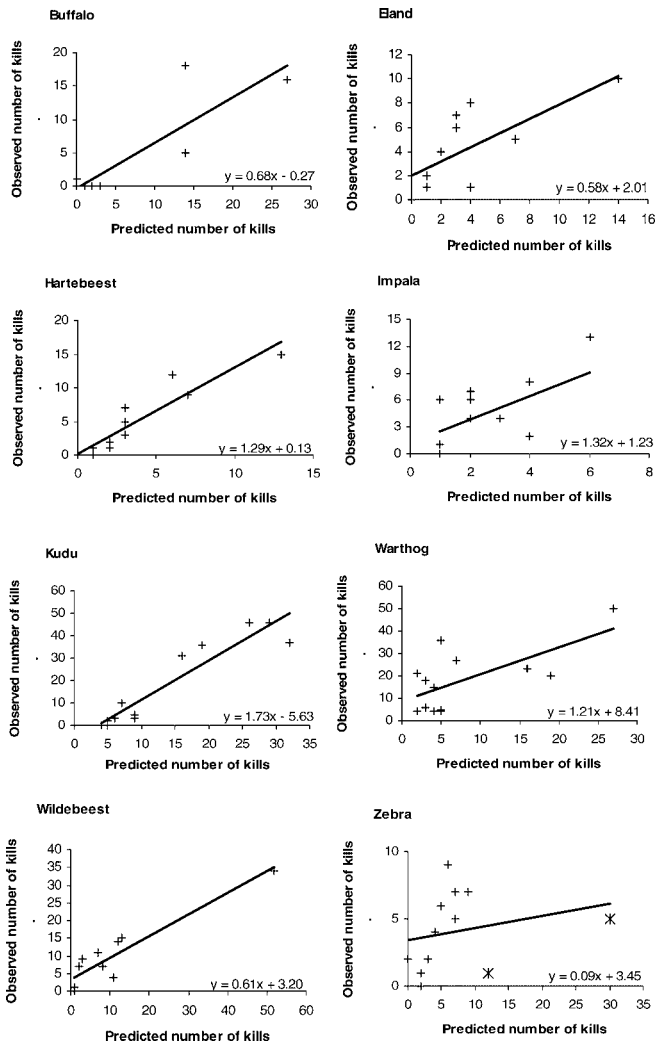


Figure 1. Linear regression lines and 95% confidence intervals (dashed) comparing the predicted and observed number of kills of buffalo ($r^2 = 0.763$, $n = 10$, $P = 0.001$), eland ($r^2 = 0.440$, $n = 12$, $P = 0.019$), hartebeest ($r^2 = 0.861$, $n = 12$, $P < 0.001$), impala ($r^2 = 0.325$, $n = 11$, $P = 0.672$), kudu ($r^2 = 0.875$, $n = 11$, $P < 0.001$), warthog ($r^2 = 0.450$, $n = 13$, $P = 0.012$), wildebeest ($r^2 = 0.861$, $n = 11$, $P < 0.001$), and zebra ($r^2 = 0.061$, $n = 13$, $P = 0.417$) at all sites. Excluding 2 outlying predictions of zebra kills (Makalali 2001 and Madikwe 1998) leads to a significant positive relationship ($y = 0.87x + 0.39$; $r^2 = 0.670$, $n = 11$, $P = 0.002$).

variation in lion predation during times of prey abundance and scarcity comes from Botswana's Chobe National Park where, during the wet season when migratory herds were present and food for lions was plentiful, warthogs comprised only 1% of the available prey and only made up 6% of kills (Viljoen 1993). When the migratory herds departed, warthog comprised 3% of available prey but made up 43% of lion kills (Viljoen 1993), providing support for the theory that lions take suboptimal prey in times of food shortage, as is predicted by optimal foraging theory (Krebs 1978). The opportunistic nature of lion predation, therefore, masks prey preferences (Hayward and Kerley 2005).

The number of kudu kills was underpredicted 3 times. Kudu are one of the most abundant prey species in South Africa's Eastern Cape Province, where few other medium-sized ungulates occur (Tables 2 and 3), and so they are killed

by lion more frequently than at the sites of the original Jacobs' index calculations (Hayward and Kerley 2005). Where elsewhere they occur at such low densities that it may be energetically uneconomical for lion to preferentially prey on them above other more abundant large ungulates (as occurs with roan; Hayward and Kerley 2005), in the Eastern Cape their relative abundance makes it an optimal strategy to preferentially hunt them.

Conversely, the overprediction of gemsbok kills arose from the calculation of Jacobs' index stemming from sites where it was the most common medium-sized ungulate among very few other potential prey species (e.g., Kalahari) such that it made up almost 15% of the available prey (Hayward and Kerley 2005). In situations where it is scarcer (e.g., Wankie and Shamwari; Tables 1 and 3), its rarity protects it from preferential predation.

We used the actual number of kills observed at a site (ΣK) as the constant for deriving a comparative predicted kill value for testing (eq. 2). In a management situation, where the total number of kills at a site is unknown, we suggest replacing ΣK with 100 to give the percentage of all kills made up of species i . Alternatively, where ΣK is unknown an estimate of the number of kills made by lions per year could be used. Estimates of the annual number kills per individual lion range from 15 to 50 kills per year (Schaller 1972, Bertram 1979), which is probably due to variations in pride size and sex ratio. The number of kills of one species may vary with predator numbers but the relative number, which is the basis for this present work, would remain constant.

There are various sources of bias that could affect our results. Aerial counts are thought to underestimate the abundance of small species, however lions rarely take such species (Schaller 1972, Radloff and du Toit 2004, Hayward and Kerley 2005) so this is unlikely to bias our predictions and tests. While numerous authors stress the frequency of undercounting kills of small species (Bertram 1979, Mills 1992), biases from this are likely to be counteracted by the hypothesized undercounting of small species during aerial counts because we use relative values of abundance and kill data (Hayward and Kerley 2005). Furthermore, it is energetically inefficient for lions to preferentially prey on small species compared to larger prey (Carbone et al. 1999).

Our initial predictions were made from throughout the distribution of the lion (Hayward and Kerley 2005), however, there were no published studies from South Africa's Thicket Biome or from reintroduction sites. We tested these predictions at sites with completely unique or modified habitats (especially the former agricultural lands of Addo and Shamwari) and they proved precise. This suggests that for lions, and probably other generalist predators, habitat definitions based on vegetation communities are less important than those based on available prey. Rather, habitat of large, generalist predators should refer to an adequate supply of prey with body masses within their preferred prey weight range, or habitat that can support this prey. As cervids are fundamental to the survival of the tiger (*Panthera tigris*) in the wild (Sunquist et al. 1987), so too are

adequately sized and abundant prey of the lion. We reinforce then that habitat refers to the biotic and abiotic factors that make up the area in which an animal lives (Sunquist and Sunquist 2001). Habitat features affect hunting success (Quinn and Cresswell 2004) and a suite of other autecological features that simplify living (e.g., shade, water, parasite loads), however, in the absence of sufficient numbers of suitably sized prey, predators are unlikely to be able to exist at a particular site.

MANAGEMENT IMPLICATIONS

We can now predict the diet of lions and determine if sufficient numbers of optimally sized prey species are available to sustain a reintroduced population. This in turn can be used in the development of management strategies to influence the impact of lions on particular prey species. For example, if prey species A is ranked higher in preference by lions than species B, which is of conservation concern, then it may be appropriate for managers to increase the relative abundance of species A to act as a buffer species in order to reduce the impact of lion predation on species B (Pech et al. 1995, Sinclair and Pech 1996).

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