

# Prey preferences of the lion (*Panthera leo*)

Matt W. Hayward\* and Graham I. H. Kerley

Terrestrial Ecology Research Unit, Department of Zoology, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth, 6031, Eastern Cape, South Africa

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## Abstract

Lions *Panthera leo* are generally thought to prey on medium to large ungulates. Knowledge of which species are actually preferred and which are avoided is lacking, however, as is an understanding of why such preference or avoidance may arise. An analysis of 32 studies over 48 different spatial locations or temporal periods throughout the distribution of the lion shows that it preferentially preys upon species within a weight range of 190–550 kg. The most preferred weight of lion prey is 350 kg. The mean mass of significantly preferred prey species is 290 kg and of all preferred species is 201 kg. Gemsbok, buffalo, wildebeest, giraffe and zebra are significantly preferred. Species outside the preferred weight range are generally avoided. Species within the preferred weight range that are not significantly preferred (such as roan, sable and eland) generally have features that reduce predation either morphologically (e.g. sable horns), ecologically (e.g. roan and sable occurring at low density), or behaviourally (e.g. the large herd size and increased vigilance of eland). Warthog are below the preferred weight range yet are taken in accordance with their availability and this is probably due to their sympatry with lion, their relatively slow evasion speed and their lower level of vigilance. Plots of prey preference against prey body mass follows a bell curve with a right skew that, we argue, is caused by collective hunting by lions of larger-bodied prey. Our methods can be used on all large predators and are likely to be useful in assessing competition in sympatric communities of predators, cooperative hunting and predicting predator diets. This will allow us to move beyond descriptive dietary studies to improve our predictive understanding of the mechanisms underlying predator–prey interactions.

**Key words:** buffalo, gemsbok, giraffe, Jacobs' index, optimal foraging, predation preference, preferred prey weight range, zebra, wildebeest, warthog, lion, *Panthera leo*

## INTRODUCTION

The strategies of a predator are forged by natural selection to maximize nutrient intake while being tempered by a wide range of ecological constraints, such as prey density and habitat, that differ throughout its geographical distribution (Sunquist & Sunquist, 1997). As long as a predator can increase its survival chances or reproductive success by hunting more efficiently, natural selection will favour efficient, optimally foraging predators (J. R. Krebs, 1978).

For lions *Panthera leo* L. this means preying upon a broad range of medium- and large-sized mammals (Hanby & Bygott, 1991). Yet a review of the literature reveals they commonly take species as small as warthog (e.g. Savuti, Botswana; Viljoen, 1993) and as large as buffalo (e.g. Kafue National Park, Zambia; Mitchell, Shenton & Uys, 1965). Lions also take unusual prey items such as

seals (Bridgford, 1985), rhinoceroses (W. M. Elliot, 1987; Brain, Forge & Erb, 1999; Matipano, 2004) and elephant (Ruggiero, 1991a).

A summary such as this reveals very little about the ecology of the lion, other than its catholic tastes. These dominant prey species may be the only ones present or may be the most abundant. Alternatively, these data may reflect innate preferences by lions. If two species are equally abundant, why is one preferred? To determine how and why a predator selects its prey, cognisance of prey availability is imperative. If a predator kills a species more frequently than expected based on its availability then we can consider it a preferred prey species, while if the predator takes proportionally fewer prey than expected based on availability then it is an avoided prey species.

This definition of preference is potentially misleading, as a kill signifies not just prey availability but also its vulnerability (Schaller, 1972). The capture of prey by a predator involves behaviours relating to searching, stalking, attacking and subduing, and the susceptibility of a prey species to a particular predator relates to the matching of these events (J. P. Elliott, McTaggart Cowan &

\* All correspondence to: M. W. Hayward.  
E-mail: hayers111@aol.com

Holling, 1977). Whether a predator initiates this series of behaviours depends on the difference between the energy expenditure required during the hunt and that gained in its ingestion (J. P. Elliott *et al.*, 1977). This energy differential must also be weighted against the potential risks associated with capturing it.

### Factors affecting prey preferences

Factors affecting the vulnerability of prey to a certain predator are its abundance, size, temporal and spatial distribution, defences and anti-predatory tactics (Sunquist & Sunquist, 1997). Environmental factors that influence hunting success in lions include grass/shrub cover, time of day, moon presence and terrain (van Orsdol, 1984; Stander & Albon, 1993; Funston, Mills & Biggs, 2001). Features of the predator that affect hunting success include hunting-group size and composition, and hunting method used (Sunquist & Sunquist, 1997). Climatic conditions are also influential (Mills, Biggs & Whyte, 1995). Unfortunately the majority of these are difficult to measure (Sunquist & Sunquist, 1997), such that Radloff & du Toit (2004) suggest that the complexity of the interactions between these factors, compounded by opportunistic predatory behaviour, will confound attempts to explain predator-prey relationships in terms other than body mass.

### Encounter rate

At each site, there is a given amount of energy available as food for carnivores and higher herbivore density means more food for predators (Sunquist & Sunquist, 1997). High encounter rate reflects similar habitat use, activity patterns and temporal and spatial distribution patterns (Sunquist & Sunquist, 1997). Lions have a very diverse habitat tolerance ranging from semi-desert to dense woodland (Stuart & Stuart, 2000). They hunt mostly at night or in cooler daytime periods although they are highly opportunistic (Schaller, 1972). Lions are also able to travel long distances in search of prey (Eloff, 1984) and regularly hunt in groups (Schaller, 1972). This suggests that lions have a relatively high encounter rate with their prey. We can therefore expect that lions will encounter the full range of potential prey species occurring in their habitat, and a re-analysis of Scheel's (1993, table 1) data suggest that there is significant linear relationship between herd availability and encounter rate ( $r^2 = 0.978$ ,  $n = 10$ ,  $P < 0.001$ ).

### Body mass of prey

Although large felids can subsist on small, abundant prey, they are morphologically specialized to take prey their own size or larger, and readily do so (Sunquist & Sunquist, 1997). Larger vertebrate predators tend to forage optimally on larger-bodied prey (see review by Pyke, Pulliam & Charnov, 1977) as energy maximizers (Griffiths, 1975), and so are expected to take the largest prey that could

safely be killed (Sunquist & Sunquist, 1997). Prey digestibility and nutrient quality are unlikely to be important as large predators possess constant and efficient digestive systems (Ewer, 1973), so profitability for carnivores is correlated with prey size (Lendrem, 1986). Studies from the Serengeti confirm this for lions as their preference for wildebeest and zebra during the migration, and warthog and buffalo during prey scarcity suggests they are risk-sensitive foragers that maximize food intake (Scheel & Packer, 1995) such that their modal prey size is 150 kg (Packer, 1986). Differences in food habits of a species between sites reflects prey availability and vulnerability (Sunquist & Sunquist, 1997).

Conversely, larger-bodied prey species are also thought to avoid predation through their larger size (Schaller 1972; J. P. Elliott *et al.*, 1977; Ruggiero 1991a; Sinclair, 1995b), which would reduce the size of preferred prey. Smaller prey depend less on their ability to evade predators at the subduing stage, and instead aim to evade predators during search, stalk and attack phases (J. P. Elliott *et al.*, 1977).

### Herd size

Larger groups convey safety from predation by increased detection of the predator through increased group vigilance (Hamilton, 1971) or by the confusion effect (Estes, 1976), suggesting predators should prefer solitary individuals over large herds, as occurs in Kruger National Park (Funston, Mills & Biggs, 2001). Conversely, predators can more easily locate large groups, either visually or through their smell (Krause & Godin, 1995), and approach closer to them (Walther, 1969), suggesting herding species will be preferentially preyed upon. Small groups of kob detected lions hunting at night significantly more than larger groups of topi (van Orsdol, 1984), despite topi being the most vigilant prey species (Schaller, 1972).

### Habitat use of prey

Habitat features are also important drivers of prey selection. All felids use physical environmental features extensively to get as close as possible to prey while hunting (Sunquist & Sunquist, 1997). Grass to 0.4 m height was required for a successful daytime hunt (J. P. Elliott *et al.*, 1977) and hunting success increased with grass up to 0.8 m (van Orsdol, 1984). Yet it is difficult to classify and compare habitat constraints amongst sites (Sunquist & Sunquist, 1997).

Localized features, driven by climate-induced habitat change, affect the susceptibility of prey to a predator. Drought is known to increase the susceptibility of buffalo to lion predation (Prins & Iason, 1989), while wet periods decrease this susceptibility for buffalo, as well as for waterbuck and kudu (Smuts, 1978). Increased water availability led to increased lion predation on roan antelope (Harrington *et al.*, 1999) probably through altered habitat conditions (Mills & Funston, 2003). Similarly, rainfall variation affects zebra and wildebeest predation rates in the Serengeti (Scheel & Packer, 1995) and both

species declined in high rainfall years in the Kruger due to increased lion and hyena predation (Smuts, 1978; Mills & Shenk, 1992).

### Anti-predator behaviour

A species' anti-predatory strategy can involve crypsis (e.g. kudu), speed of evasion (e.g. tsessebe, topi, hartebeest), mobbing predators (e.g. springbok, Thomson's gazelle) or active defence (e.g. warthog, zebra stallions, gemsbok and buffalo herd bulls) (Estes, 1991). Analysing the degree of crypsis a species uses in avoiding predation requires knowledge of the visual acuity of the predator relative to the pelage colour and pattern of the prey. Similarly, colours and patterns providing crypsis in an open grassland are unlikely to do so in denser vegetation, so habitat features also need to be accounted for.

The minor amount of published work on prey evasion speed suggests that lion have an initial acceleration advantage but this is lost within the first few seconds, after which Thomson's gazelle rapidly outpace them, followed by zebra with wildebeest only fractionally faster than lion (J. P. Elliott *et al.*, 1977). Buffalo also have a slight speed advantage over lion (Prins & Iason, 1989), while warthog are relatively slow compared to the ungulates (Estes, 1999).

Migratory or nomadic prey species are largely unaffected by top-down, predatory influences (Schaller, 1972; Kruuk, 1972; Mills, 1990), however resident herbivores at low density can be regulated by predation (Fryxell, Greever & Sinclair, 1988). Yet variation in movement patterns within sites, such as the sedentary and nomadic wildebeest populations in the Kalahari (Mills & Retief, 1984), precludes this from being investigated more broadly.

The result of anti-predatory strategies from the predator's perspective varies from an unsuccessful hunt to bodily harm and even death. Elephant and rhinoceros actively defend themselves and their young (Makacha & Schaller, 1969; Ruggiero, 1991a; Berger & Cunningham, 1994). Buffalo are known to mob predators and lions have been killed by them (Mangani, 1962; Beyers, 1964; Mitchell *et al.*, 1965; Makacha & Schaller, 1969). Giraffe, sable (Wilson, 1981) and gemsbuck (Eloff, 1964) have also been observed killing lions and a thorough literature search is likely to reveal more such incidents. Any injury that incapacitates a predator has serious consequences on its survival chances (Sunquist & Sunquist, 1997). These species, and hippopotamus, therefore constitute the greatest category of threat to predators based on their size, strength and aggressive nature.

### Aims and summary

In 1978, Smuts stated that 'predation needs to be analysed for each particular situation and its influence may vary not only spatially, but also temporally within a certain area'. Since then, numerous studies have done just that and enough data has accumulated to investigate the issue of

lion prey preferences from a species, rather than population perspective. In this study therefore, the aim was to use kill and prey availability data collected from various studies conducted throughout the distribution of the lion to determine which, if any, prey species the lion prefers and those it avoids. Further, why particular species are preferred or avoided is discussed. Our results will allow us to predict the diet of the lion at other sites of natural or reintroduced populations, and thereby facilitate the expansion of predator dietary ecology beyond the descriptive to the predictive. These same techniques can be used on all predators, to predict their diet at unstudied sites and to investigate other features such as predator coexistence.

By necessity, our analyses are generalized and descriptive because of the nature of the data we are restricted in using. Consequently, it was not possible to use varying ecological conditions or migratory/sedentary behaviour of prey because this information is rarely stated in the studies used, there are migratory or sedentary populations within individual species (e.g. wildebeest; Estes, 1976; Mills & Retief, 1984), or not a large enough sample size was available. Numerous studies have explored factors that make certain species susceptible to predation (e.g. J. P. Elliott *et al.*, 1977; Stander & Albon, 1993; Mills & Shenk, 1992; Funston, Mills & Biggs, 2001). Hence, rather than reanalyse this work, our study attempts to explain the preference and avoidance of prey by lions and relate this to general characteristics of those species.

### METHODS

A literature survey revealed 32 different studies describing the diet of the lion which included some measure of prey availability (either actual or relative) (Table 1). Several of these studies were conducted over a long-term and these allowed temporally separated prey preferences to be calculated as prey abundance changed over time (Table 1). Others provided detailed information on prey and availability of lions in different study regions (Table 1). Such partitioning has been used previously in the study of carnivore ecology (see Creel & Creel, 2002). Consequently, 48 assessments of prey preference were calculated from sites throughout the distributional range of the lion. We do not believe that autocorrelation exists by using data from the same area at different prey abundance, as one of the fundamental rules of whether a species is captured and killed is the probability of coming in contact with the predator and this varies with prey density.

Numerous studies provided excellent descriptive information on lion diet but insufficient or no information on prey availability (Mitchell *et al.*, 1965; Eloff, 1973; 1984; Smuts, 1979; McBride, 1984; Stander, 1992; Scheel, 1993; Scheel & Packer, 1995; Funston, Mills, Biggs *et al.*, 1998; Cronje, Reilly & MacFadyen, 2002). Unless other sources could be found that provided prey

**Table 1.** Sites and sources of prey preference data used in this study

| Country                  | Site  | Years/Period  | Source  |
|--------------------------|---|---|---|
| Botswana                 | Savuti, Chobe National Park                     | Wet season<br>Dry season  | Viljoen, 1993<br>Viljoen, 1993  |
| Central African Republic | Manovo-Gounda-St. Floris National Park          | 1982–84   | Ruggiero, 1991 <i>b</i>   |
| Congo                    | Albert National Park                            | 1950s   | Bourliere & Verschuren, 1960  |
| India                    | Gir Forest, Gujarat                             | 1970s   | Joslin, 1984  |
| Kenya                    | Nairobi National Park                           | 1986–89<br>1966<br>1967<br>1968–72  | Chellam & Johnsingh, 1993<br>Foster & McLaughlin, 1968<br>Foster & McLaughlin, 1968<br>Rudnai, 1974   |
| Namibia                  | Masai-Mara Game Reserve<br>Etosha National Park | 1973–74<br>1975–78<br>Unstated  | Saba, 1979<br>Berry, 1981<br>Stander & Albon, 1993  |
| South Africa             | Hluhluwe-Umfolozi                               | 1965–68<br>Umfolozi<br>Hluhluwe<br>1990s  | Steele, 1970<br>Whateley & Brooks, 1985<br>Whateley & Brooks, 1985<br>Maddock <i>et al.</i> , 1996  |
|                          | Kalahari Gemsbok National Park                  | 1971–82<br>1974–82  | Eloff, 1984<br>Mills, 1984  |
|                          | Kruger National Park                            | 1956–65 North<br>1956–65 South<br>1956–65 Central<br>1969<br>1970<br>1971<br>Early 1990s<br>1990s | Pienaar, 1969<br>Pienaar, 1969<br>Pienaar, 1969<br>Bryden, 1976<br>Bryden, 1976<br>Bryden, 1976<br>Mills & Biggs, 1993<br>Harrington <i>et al.</i> , 1999 |
|                          | Madjuma Game Reserve                            | 1998<br>1999  | Power, 2002<br>Power, 2002  |
|                          | Phinda Resource Reserve                         | 1992–96   | Hunter, 1998  |
|                          | Timbavati Game Reserve                          | 1964<br>1965<br>1966<br>1967  | Hirst, 1969<br>Hirst, 1969<br>Hirst, 1969<br>Hirst, 1969  |
| Tanzania                 | Lake Manyara<br>Ngorongoro<br>Selous            | 1967–68<br>1970–72<br>1974  | Makacha & Schaller, 1969<br>J. P. Elliott & McTaggart Cowan, 1978<br>Rodgers, 1974  |
|                          | Serengeti                                       | 1993–2002<br>1950s<br>1965–66<br>1966–69 Masai Pride<br>1966–69 All                               | Creel & Creel, 2002<br>Wright, 1960<br>Kruuk & Turner, 1967<br>Schaller, 1972<br>Schaller, 1972   |
| Uganda                   | Queen Elizabeth (Ruwenzori) National Park       | Ishashi Pride<br>Mweya Pride  | Van Orsdol, 1982, 1984<br>Van Orsdol, 1982, 1984  |
| Zambia                   | Kafue National Park                             | 1962–64   | Mitchell <i>et al.</i> , 1965   |
| Zimbabwe                 | Mana Pools National Park                        | 1968–69<br>1981–84<br>1985–89   | Dunham, 1992<br>Dunham, 1992<br>Dunham, 1992  |

availability at the appropriate time, these studies could not be used in this analysis (see Table 2).

The data collected in these studies was derived from both incidental observations and continuous follows. Continuous follows are widely regarded as the superior method of ascertaining the diet of a predator (Bertram, 1979; Mills, 1992; although see also Radloff & du Toit, 2004). Incidental observations are biased toward larger prey; however, this bias against smaller items is generally alleviated by the undercounting of small prey species in aerial counts. Furthermore, even continuous studies find only a small proportion of kills are small species (Schaller, 1972; Packer, Scheel & Pusey, 1990; Hanby, Bygott &

Packer, 1995; Scheel & Packer, 1995). Consequently both types of data were used.

Many indices have been used to describe selectivity; however, none is generally superior to the rest and none is without bias and increasing error at small proportions (Chesson, 1978; Strauss, 1979). As a result, many researchers have overstated the accuracy of their preference results (Norbury & Sanson, 1992). This is particularly the case with the most commonly used techniques, such as the forage ratio and Ivlev's electivity index (Ivlev, 1961). These indices and their variations suffer from several problems including non-linearity, bias to rare food items, increasing confidence intervals with increasing

**Table 2.** Assumptions made in determining prey availability for studies where it is not implicitly stated. Page and table numbers relate to the source of the information

| Study and section   | Assumptions made or source of availability data  |
|---|--|
| Bourliere & Verschuren (1960)<br>Chellam & Johnsingh (1993)   | Data taken from Bourliere (1963)<br>Wild prey availability data taken from Khan <i>et al.</i> (1996) and livestock taken from original paper.<br>Body mass of chital and sambar taken from Nowak & Paradiso (1983)   |
| Dunham (1992)   | Availability data comes from Durham (1994). Elephant and hippopotamus were excluded because they were scavenged  |
| Mills (1984)<br>Eloff (1984)<br>Mills & Biggs (1993)          | Availability data comes from Mills & Retief (1984)<br>Availability data comes from Mills (1990) – dunes<br>Giraffe and hippopotamus were assumed to be in equal abundance from Mills & Biggs (1993 Fig. 2) and buffalo abundance came from Donkin (2000). Similarly kudu and waterbuck were assumed to be of equal abundance. This is irrelevant as no individuals of these species were preyed upon by lions      |
| Mitchell <i>et al.</i> (1965)<br>Rudnai (1974)<br>Saba (1979) | Availability data taken from Dowsett (1966)<br>Availability data taken from 1967 game census (Foster & McLaughlin, 1968)<br>Availability data taken from 1976 in Ottichilo <i>et al.</i> (2000) and wildebeest and zebra numbers from Sinclair (1995a) based on presence in the Mara for 3–4 months  |
| Schaller (1972)   | Resident prey of the 115 km <sup>2</sup> range of the Masai pride is given in table 34 (p. 430), however there is no mention of migratory species that were preyed upon. The total migratory population of wildebeest (400,000), zebra (132,500) and Thomson's gazelle (165,000) were multiplied by the proportion of time they spent around Seronera (p. 211) to give their availability in the Masai pride range |
| Steele (1970)<br>Van Ordsol (1984)                            | Availability data taken from Brooks & Macdonald (1983)<br>Prey availability for large species taken from Van Ordsol (1982) and density per km for duiker, hippopotamus, elephant and reedbuck were calculated from Petrides & Swank (1965)   |
| Wright (1960)   | Availability data comes from Grzimek & Grzimek (1960)  |

heterogeneity, being unbound or undefined, and lacking symmetry between selected and rejected values (Jacobs, 1974). Confidence intervals also become excessive for proportions below *c.* 10% (Strauss, 1979). There are methods that minimize these biases (Krebs, 1989) and we have chosen Jacobs' index:

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the proportion of the total kills at a site made up by a species and *p* is the proportional availability of the prey species (Jacobs, 1974). The resulting value ranges from +1 to –1, where +1 indicates maximum preference and –1 maximum avoidance (Jacobs, 1974). The mean Jacobs' index for each prey species across studies was calculated ( $\pm 1$  SE wherever mean is shown) and these values were tested for significant preference or avoidance using *t*-tests against a mean of 0 if they conformed to the assumptions of normality (Kolmogorov–Smirnov test) (e.g. Palomares *et al.*, 2000; Hayward, de Tores & Banks, 2005). Where transformation could not satisfy these assumptions, the sign test (Zar, 1996) was used, although the biological relevance of non-significant results where several –1 (maximum avoidance) values were coupled with a fractionally positive one must be questioned. The value of this kind of analysis is that it is not biased by the results from one particular area; it is not overly influenced by the available community of prey species because for a species to be significantly preferred or avoided it must be so in diverse communities throughout its range; and that it takes into account of varying hunting group sizes and sex ratios by being collected in populations that hunt as fission–fusion groups.

Several assumptions were made when calculating the availability of prey from various studies and these are listed in Table 2. Sources of error arise in preference indices via inaccurate availability or choice data. Such errors may occur in various studies here where availability data is not taken for the exact time period during which the prey data were collected. However, such errors are minimal given the frequency with which studies presented actual availability or coincided with other studies that did.

The resulting mean Jacobs' index values were analysed using multiple regression of 3 variables that were initially considered to influence lion predation after several other variables were found to be partially correlated (see Results). Significant relationships were plotted using distance weighted least-squares and linear-regression fits of transformed data. Lions are generally thought to eat prey of medium body size and consequently  $\frac{3}{4} \times$  mean adult female body mass of prey species was used (Table 3) to take account of calves and sub-adults eaten. This value was used by Schaller (1972) to ascertain food intake in lions and was confirmed by Scheel (1993) who found 25% of kills in the Serengeti were calves or juveniles. Weights were taken from Stuart & Stuart (2000).

Social organization of prey species was taken to be an indicator of the ability of the prey to detect predators. This was a categorical variable with 1 relating to solitary individuals, 2 relating to species that exist in pairs, 3 relating to small family grouping species, 4 to small herds (10–50) and 5 relating to large herds (> 50; Table 3). This is a simplification as solitary males exist alongside larger breeding herds and smaller bachelor herds of several species. Yet mean herd size of each sex is not provided

**Table 3.** Jacobs' index values, number of studies recording the species as a potential prey item ( $n$ ), mean percentage availability of each species (out of a total of 4,581,156 species records), mean percentage that each species comprised of the total kills recorded (22,684), body mass ( $3/4$  of mean female body mass) and categories of herd size, habitat density and injury threat to predators used in modelling. Specifics of each category are described in the text and their details were derived from Stuart & Stuart (2000) and Estes (1991). Symbols  $^+$  refers to significantly preferred and  $^-$ , significantly avoided

| Species                                     | Jacobs' index<br>( $\pm 1$ SE) | $n$ | Availability (%)<br>( $\pm 1$ SE) | Prey (%)<br>( $\pm 1$ SE) | Body<br>mass (kg) | Herd<br>size | Habitat | Threat |
|---|--------------------------------|-----|-----------------------------------|---------------------------|-------------------|--------------|---------|--------|
| Aardvark <i>Orycteropus afer</i>            | 0.03 (0)                       | 1   | 0.24 $\pm$ 0                      | 0.25 $\pm$ 0              | 40                | 1            | 2       | 0      |
| Baboon <i>Papio cynocephalus</i>            | -0.89 (0.11)                   | 5   | 4.22 $\pm$ 1.89                   | 1.25 $\pm$ 0.56           | 12                | 5            | 2       | 1      |
| Black rhinoceros <i>Diceros bicornis</i>    | -1 (0)                         | 2   | 1.19 $\pm$ 0.84                   | 0 $\pm$ 0                 | 800               | 1            | 3       | 2      |
| Blue duiker <i>Cephalophus monticola</i>    | -1 (0)                         | 1   | 0.01 $\pm$ 0                      | 0 $\pm$ 0                 | 3                 | 1            | 3       | 0      |
| Buffalo <i>Syncerus caffer</i>              | 0.32 (0.10) $^+$               | 30  | 13.29 $\pm$ 2.43                  | 20.65 $\pm$ 3.77          | 432               | 5            | 2       | 2      |
| Bushbuck <i>Tragelaphus scriptus</i>        | -0.53 (-0.20) $^-$             | 9   | 1.14 $\pm$ 0.31                   | 1.94 $\pm$ 0.52           | 23                | 1            | 3       | 0      |
| Bushpig <i>Potamochoerus larvatus</i>       | 0.11 (0.26)                    | 2   | 1.75 $\pm$ 1.24                   | 1.91 $\pm$ 1.35           | 46                | 3            | 3       | 1      |
| Chital deer <i>Axis axis</i>                | -0.81 (0.19)                   | 2   | 42.14 $\pm$ 29.80                 | 21.48 $\pm$ 15.19         | 30                | 5            | 1.5     | 0      |
| Common duiker <i>Sylvicapra grimmia</i>     | -0.83 (0.07) $^-$              | 7   | 1.84 $\pm$ 0.65                   | 0.22 $\pm$ 0.08           | 16                | 1            | 2.5     | 0      |
| Eland <i>Tragelaphus oryx</i>               | 0.18 (0.14)                    | 24  | 1.23 $\pm$ 0.25                   | 2.33 $\pm$ 0.48           | 345               | 5            | 2       | 1      |
| Elephant <i>Loxodonta africana</i>          | -0.87 (0.12)                   | 4   | 3.23 $\pm$ 1.14                   | 1.01 $\pm$ 0.36           | 1600              | 3            | 2       | 2      |
| Gemsbok <i>Oryx gazella</i>                 | 0.70 (0.06) $^+$               | 4   | 14.80 $\pm$ 7.40                  | 23.29 $\pm$ 11.65         | 158               | 4            | 1       | 2      |
| Giraffe <i>Giraffa camelopardalis</i>       | 0.24 (0.10) $^+$               | 24  | 3.71 $\pm$ 0.76                   | 6.32 $\pm$ 1.29           | 550               | 3            | 2       | 2      |
| Grant's gazelle <i>Gazella granti</i>       | -0.56 (0.22) $^-$              | 8   | 7.08 $\pm$ 2.68                   | 1.31 $\pm$ 0.49           | 38                | 4            | 1       | 0      |
| Hartebeest <i>Alcephalus buselaphus</i>     | 0.02 (0.13)                    | 17  | 9.55 $\pm$ 2.19                   | 9.66 $\pm$ 2.22           | 95                | 4            | 1.5     | 0.5    |
| Hippopotamus <i>Hippopotamus amphibius</i>  | -0.45 (0.33)                   | 4   | 6.12 $\pm$ 3.06                   | 5.75 $\pm$ 2.88           | 750               | 3            | 1.5     | 2      |
| Impala <i>Aepyceros melampus</i>            | -0.73 (0.05) $^-$              | 34  | 39.52 $\pm$ 6.78                  | 9.94 $\pm$ 1.70           | 30                | 4            | 2       | 0      |
| Klipspringer <i>Oreotragus oreotragus</i>   | -0.96 (0.01) $^-$              | 4   | 0.89 $\pm$ 0.44                   | 0.02 $\pm$ 0.01           | 10                | 2.5          | 3       | 0      |
| Kob <i>Kobus kob</i>                        | -0.31 (0.26)                   | 4   | 43.07 $\pm$ 21.53                 | 27.89 $\pm$ 13.95         | 47                | 4            | 2       | 0      |
| Kudu <i>Tragelaphus strepsiceros</i>        | 0.13 (0.12)                    | 25  | 3.20 $\pm$ 0.64                   | 7.47 $\pm$ 1.49           | 135               | 3            | 2       | 0      |
| Nilgai <i>Boselaphus tragocamelus</i>       | -1 (0)                         | 1   | 0.31 $\pm$ 0                      | 0                         | 120               | 3            | 2       | 0      |
| Nyala <i>Tragelaphus angasi</i>             | -0.32 (0.14)                   | 7   | 19.91 $\pm$ 7.52                  | 15.95 $\pm$ 6.03          | 47                | 3            | 2       | 0      |
| Oribi <i>Ourebia ourebi</i>                 | -0.72 (0.28)                   | 2   | 5.53 $\pm$ 3.91                   | 0.90 $\pm$ 0.64           | 14                | 2            | 1       | 0      |
| Ostrich <i>Struthio camelus</i>             | -0.55 (0.17) $^-$              | 11  | 1.23 $\pm$ 0.37                   | 1.25 $\pm$ 0.38           | 70                | 3            | 1.5     | 0      |
| Porcupine <i>Hystrix africaeaustralis</i>   | 0.58 (0)                       | 1   | 0.47 $\pm$ 0                      | 2.0 $\pm$ 0               | 10                | 1            | 2       | 1.5    |
| Puku <i>Kobus vardonii</i>                  | -0.58 (0)                      | 1   | 0.26 $\pm$ 0                      | 1.0                       | 47                | 4            | 1       | 0      |
| Red duiker <i>Cephalophus natalensis</i>    | -1 (0)                         | 1   | 1.78 $\pm$ 0                      | 0                         | 10                | 1            | 3       | 0      |
| Reedbuck <i>Redunca sp.</i>                 | -0.57 (0.15) $^-$              | 17  | 1.60 $\pm$ 0.39                   | 0.61 $\pm$ 0.15           | 30                | 3            | 3       | 0      |
| Roan <i>Hippotragus equinus</i>             | 0.15 (0.17)                    | 16  | 0.65 $\pm$ 0.19                   | 1.53 $\pm$ 0.46           | 220               | 3.5          | 2       | 0.5    |
| Sable <i>Hippotragus niger</i>              | -0.05 (0.20)                   | 12  | 0.94 $\pm$ 0.27                   | 2.18 $\pm$ 0.63           | 180               | 4            | 2       | 0.5    |
| Sambar deer <i>Cervus unicorn</i>           | -0.16 (0.84)                   | 2   | 1.72 $\pm$ 1.22                   | 7.39 $\pm$ 5.23           | 200               | 4            | 2       | 0      |
| Sharpe's grysbok <i>Raphicerus sharpei</i>  | -0.96 (0.03) $^-$              | 4   | 1.16 $\pm$ 0.67                   | 0.04 $\pm$ 0.02           | 7                 | 1            | 2.5     | 0      |
| Springbok <i>Antidorcas marsupialis</i>     | -0.59 (0.32)                   | 4   | 50.09 $\pm$ 25.05                 | 29.38 $\pm$ 14.69         | 26                | 5            | 1       | 0      |
| Steenbok <i>Raphicerus campestris</i>       | -0.86 (0.08) $^-$              | 4   | 4.34 $\pm$ 1.94                   | 0.07 $\pm$ 0.03           | 8                 | 1.5          | 1.5     | 0      |
| Thomson's gazelle <i>Gazella thomsoni</i>   | -0.62 (0.17) $^-$              | 9   | 19.21 $\pm$ 6.79                  | 10.33 $\pm$ 3.65          | 15                | 5            | 1       | 0      |
| Topi/tsessebe <i>Damaliscus lunatus</i>     | 0.01 (0.13)                    | 13  | 5.43 $\pm$ 1.51                   | 5.56 $\pm$ 1.54           | 90                | 3            | 2       | 0      |
| Vervet monkey <i>Cercopithecus aethiops</i> | -1 (0)                         | 4   | 0.96 $\pm$ 0.48                   | 0 $\pm$ 0                 | 3.5               | 4            | 2       | 0      |
| Warthog <i>Phacochoerus africanus</i>       | 0.11 (0.09)                    | 39  | 4.06 $\pm$ 0.65                   | 8.07 $\pm$ 1.29           | 45                | 3            | 2       | 0      |
| Waterbuck <i>Kobus ellipsiprymnus</i>       | 0.18 (0.12)                    | 30  | 2.85 $\pm$ 0.52                   | 7.98 $\pm$ 1.46           | 188               | 3.5          | 2       | 0.5    |
| White rhinoceros <i>Ceratotherium simum</i> | -1 (0)                         | 2   | 1.94 $\pm$ 1.37                   | 0 $\pm$ 0                 | 1400              | 2            | 1.5     | 2      |
| Wildebeest <i>Connochaetes taurinus</i>     | 0.27 (0.08) $^+$               | 38  | 17.14 $\pm$ 2.78                  | 25.99 $\pm$ 4.22          | 135               | 5            | 1       | 0      |
| Zebra <i>Equus burchellii</i>               | 0.16 (0.07) $^+$               | 40  | 11.24 $\pm$ 1.78                  | 15.19 $\pm$ 2.40          | 175               | 3            | 2       | 1      |

in the majority of studies analysed here and nor are rates of predation for each sex or age class. Hence we were limited to the information provided. None the less, it is still meaningful and similar categorization has been used previously (e.g. Funston, Mills & Biggs, 2001).

A predator must encounter a prey species in order to kill it and habitat type may affect predation rates. Also the density of vegetation may affect the detectability of prey. Although inherently difficult to classify (Sunquist & Sunquist, 1997), a categorical variable of habitat density was used, with 1 referring to open grasslands, 2 referring to savanna, and 3 to densely vegetated areas. Obviously a species may overlap these habitat types and in this case

an average of habitat use was applied (Table 3). Again by necessity, this is a simplification; however, it serves to highlight general trends.

Finally, the anti-predatory strategy a species uses will affect its chances of becoming prey. Unfortunately, the lack of studies comparing crypsis or evasion speed of prey species (J. P. Elliott *et al.*, 1977; Prins & Iason, 1989 excepted) meant the threat of injury to a hunter was all that could be analysed. The categories of threat used were 0 (no threat), 1 (minor threat or active defence of young), 2 (severe threat; known deaths attributed to predators caused by this species) (Table 3). Information for each of these categories comes from Estes (1991) and Stuart & Stuart

(2000), and Nowak & Paradiso (1983) for Indian prey species. Categorization as used here is fairly rudimentary; however, it serves to illustrate general trends adequately.

The analysis of this data was not separated by the sexes or the group size of the hunting lions as no study looked solely at the prey of solitary hunters or groups or either sex. We aimed to investigate lion diet from a population perspective whereby a population at each site contains both males and females hunting as individuals or groups, thereby taking account of hunting preferences of both individuals and groups of males and females. We expect our results to reflect the mean hunting group size at a site (e.g. 2 in the Serengeti; Schaller, 1972) and the variation in hunting group size (1–11; Packer *et al.*, 1990) of both males and females. The data available never indicated the group size or sex of each kill and we leave such detailed analyses to individual study sites where data has been collected with this in mind (e.g. Radloff & du Toit, 2004). Similarly, as several of the studies used looked at seasonal variation (e.g. Viljoen, 1993) and others included varying climatic conditions (e.g. Hirst, 1969; Bryden, 1976; Dunham, 1992), we expect the mean Jacobs' index value for a species to reflect the variable susceptibility of prey in drought or above average rainfall.

Generalized linear and additive models were not used because of the requirement that there be 10 samples for each predictor variable (Burnham & Anderson, 2002). As Jacobs' index for individual prey species was the dependent variable, our analysis is limited to prey species that also have their availability recorded.

## RESULTS

Jacobs' index scores for 22 684 kills of 42 species recorded as prey in the literature are shown in Fig. 1 and Table 3. Zebra are recorded as lion prey in 40 studies, with warthog (39), blue wildebeest (38), impala (34), buffalo (30) and waterbuck (30) also frequently taken (Table 3). Springbok account for 50.1% of available prey at the four sites where it was recorded, and kob account for 43.1% in the four floodplain sites it was recorded (Table 3). Impala (39.5% of prey available at 34 sites), Thomson's gazelle (19.2% at 9 sites), blue wildebeest (17.1% at 38 sites), gemsbok (14.8% at 4 sites), buffalo (13.3% at 30 sites) and zebra (11.2% at 40 sites) were the other most abundant prey species (Table 3).

Springbok were the most commonly killed prey (29.4% at the 4 sites it occurred), closely followed by kob (27.9% at 4 sites). Both of these species are taken proportionally less than they are available (Table 3). Blue wildebeest (26.0% at 38 sites), gemsbok (23.3% at 4 sites) and buffalo (20.7% at 30 sites) were taken proportionally more than often than they were available (Table 3). A plot of the percentage that each species made up of the diet of lion and its body mass shows lions predominately eat prey ranging from 40 to 251 kg with a peak at 115 kg (Fig. 2). The mean body mass of the eight most frequently killed lion prey is  $160 \pm 73$  kg.

**Table 4.** Regression statistics for the multiple regression model Jacobs' index =  $-1.04 + 0.09$  (herd size) +  $0.23$  ( $\log_{10}$ (body mass)) -  $0.03$  ( $\log_{10}$ (availability)). Standard error of estimate = 0.481;  $r^2 = 0.174$ . Analysis of variance  $F_{3,38} = 2.67$ ,  $P = 0.061$ . All variables satisfied multiple normal distribution and had constant variances (normality test  $P = 0.292$ ; constant variance test  $P = 0.532$ ; Power = 0.994). Body mass (*italicized*) predicted the Jacobs' index value at  $\alpha = 0.05$

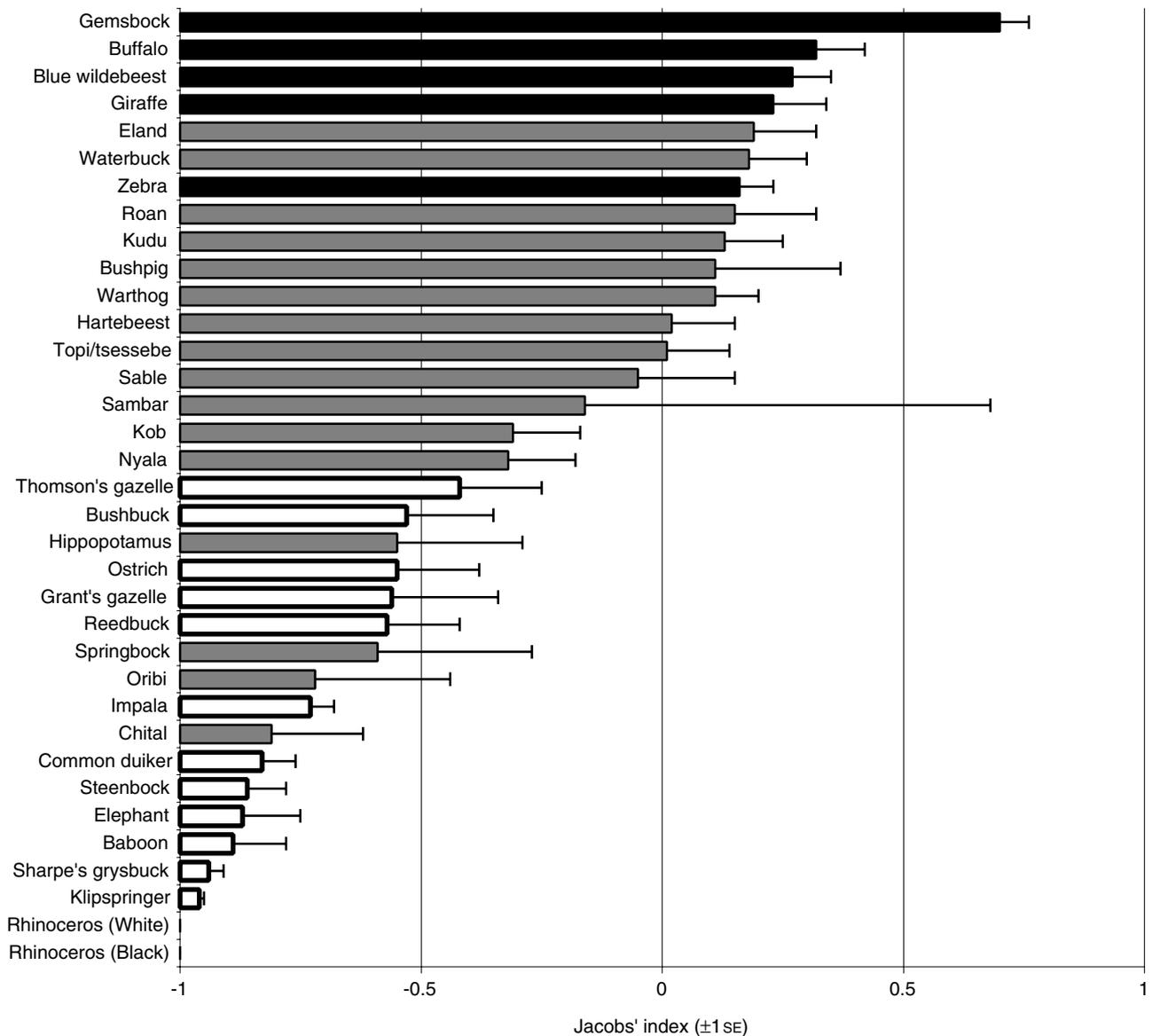
| Variable                            | Coefficient  | SE           | <i>t</i>     | Probability  |
|-------------------------------------|--------------|--------------|--------------|--------------|
| Constant                            | -1.039       | 0.255        | -4.688       | < 0.001      |
| $\log_{10}$ (availability)          | -0.031       | 0.124        | -0.252       | 0.803        |
| <i>Log<sub>10</sub> (body mass)</i> | <i>0.228</i> | <i>0.112</i> | <i>2.033</i> | <i>0.049</i> |
| Herd size                           | 0.092        | 0.068        | 1.351        | 0.185        |

Gemsbok ( $t = 11.05$ , d.f. = 3,  $P = 0.008$ ), buffalo ( $t = 3.25$ , d.f. = 28,  $P = 0.003$ ) blue wildebeest ( $t = 3.61$ , d.f. = 37,  $P < 0.001$ ), giraffe ( $t = 2.31$ , d.f. = 23,  $P = 0.030$ ) and zebra ( $t = 2.45$ , d.f. = 39,  $P = 0.019$ ) are significantly preferred (Fig. 1). Eland, kudu, warthog, waterbuck, roan, topi, tsessebe, hartebeest and sable are all preyed upon in accordance with their abundance (Fig. 1). A greater sample size through time from India's remnant Gir Forest lion population is required to ascertain whether sambar, chital or nilgai are preferred or avoided.

Conversely, klipspringer ( $t = -65.54$ , d.f. = 3,  $P < 0.001$ ), Sharpe's grysbok ( $t = -37.22$ , d.f. = 3,  $P < 0.001$ ), elephant (Sign test  $Z = 2.47$ ;  $n = 8$ ;  $P = 0.013$ ), steenbok ( $t = -10.51$ , d.f. = 3,  $P = 0.002$ ), common duiker ( $t = -12.00$ , d.f. = 7,  $P < 0.001$ ), impala ( $t = -13.77$ , d.f. = 33,  $P < 0.001$ ), reedbuck ( $t = -3.89$ , d.f. = 16,  $P = 0.001$ ), Grant's gazelle ( $t = -2.57$ , d.f. = 7,  $P = 0.037$ ), ostrich ( $t = -3.23$ , d.f. = 10,  $P = 0.009$ ), bushbuck ( $t = -2.93$ , d.f. = 10,  $P = 0.012$ ) and Thomson's gazelle ( $t = -3.70$ , d.f. = 9,  $P = 0.006$ ) are all significantly avoided by lion. Rhinoceros (black and white), baboon and vervet monkey are also avoided (Fig. 1); however, these differences were not significant according to the sign test ( $P > 0.05$ ). It is likely that greater sample sizes would result in kob, nyala, hippopotamus, springbok and oribi also being significantly avoided (Fig. 1).

A strong positive correlation was found between body mass and predator injury threat category ( $r = 0.65$ ;  $P < 0.05$ ), no doubt as a result of larger prey species being able to inflict more damage on lions than smaller species. Irrespectively, there was no relationship between predator injury threat and Jacobs' index values ( $r^2 = 0.057$ ;  $P = 0.211$ ). Similarly, there was a negative correlation between herd size class and habitat density category ( $r = -0.50$ ;  $P < 0.05$ ) indicating that species that live in big herds prefer open habitat. Nonetheless, there was no relationship between Jacobs' index values and habitat density category ( $r^2 = 0.071$ ;  $P = 0.163$ ).

Subsequently, a multiple regression model of relative availability, body mass and herd size category revealed body mass significantly contributed to the prediction of the Jacobs' index dependent variable (Table 4). A distance weighted least squares regression plot of mean Jacobs' index values against body mass ( $3/4$  mass of adult female)



**Fig. 1.** Lion *Panthera leo* dietary preferences based on Jacobs' index (mean  $\pm$  1 SE) of 48 lion populations at differing prey densities. Black bars, species taken significantly more frequently than expected based on their availability (preferred); grey bars, species taken in accordance with their relative abundance; unfilled bars, species taken significantly less frequently than expected based on their availability (avoided). Only species recorded in lion diet more than once are included.

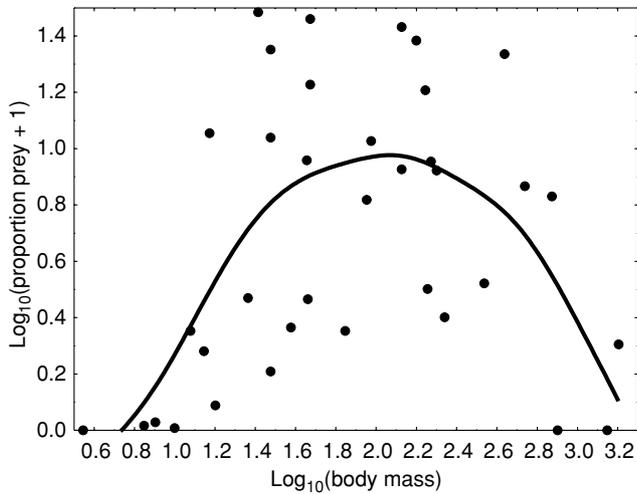
shows the preferred weight range of lion prey is between 190 kg and 550 kg (Fig. 3). Instead of a clear peak in preference the distribution is skewed to the right (Fig. 3). Exclusion of the megaherbivores (> 600 kg) led to a significant linear relationship between Jacobs' index and body mass (Fig. 4). This relationship still existed for prey species with body masses ranging from 30 kg to 600 kg (i.e. excluding many significantly avoided species) ( $r^2 = 0.583$ ;  $n = 19$ ;  $P < 0.001$ ). While herd size was not considered by the multiple regression to be useful in predicting the Jacobs' index of a species, there is still a significant linear relationship between the two variables (Fig. 5).

The most preferred weight of lion prey species appears to be approximately 350 kg (Fig. 3). The mean body mass

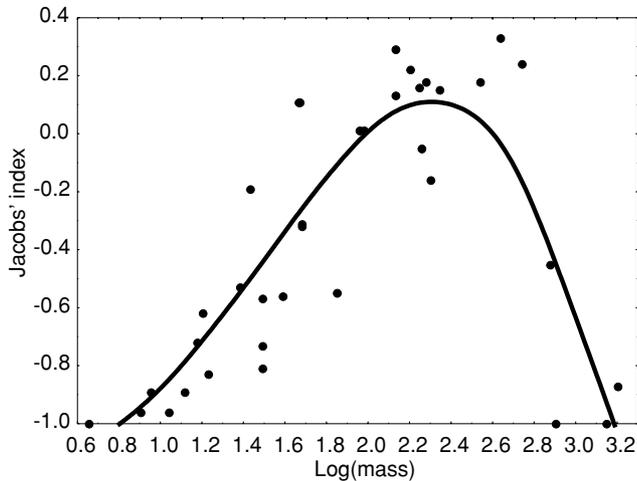
of the significantly preferred prey species was  $290 \pm 84$  kg and for all preferred species was  $201 \pm 44$  kg. There is no relationship between prey availability and lion prey preference (Table 4).

## DISCUSSION

Lions prefer large prey species within a weight range of 190 to 550 kg (Fig. 3) irrespective of their availability (Table 4), yet they predominately take prey substantially smaller than this (Fig. 2) reflecting their opportunistic hunting behaviour. In the Serengeti, they preferred prey ranging from 170 to 250 kg (Sinclair, Mduma & Brashares, 2003), which is lower but comparable to that



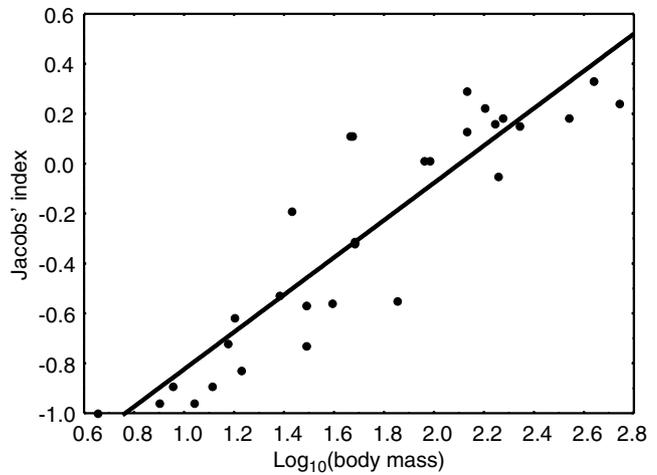
**Fig. 2.** Distance weighted least-squares relationship between mean percentage of lion *Panthera leo* diet ( $\log_{10} + 1$ ) and prey body mass ( $0.75 \times$  adult female body mass) ( $r = 0.19$ ,  $P = 0.28$ ).



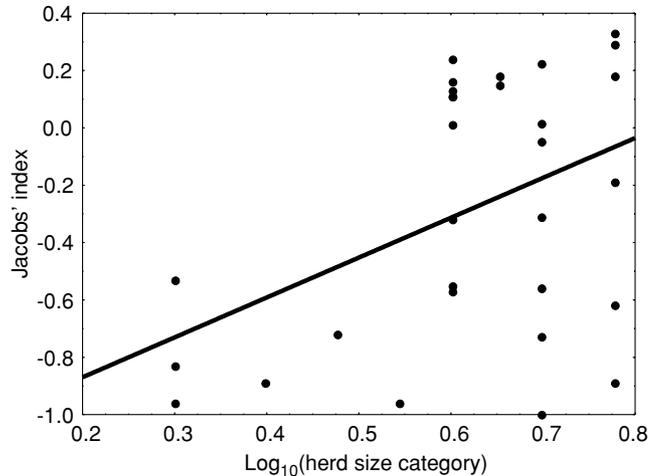
**Fig. 3.** Distance weighted least squares relationship between lion *Panthera leo* prey preference (mean Jacobs' index) and the  $\log_{10}$  of prey body mass ( $r = 0.401$ ,  $P = 0.015$ ).

found here for lions throughout their range. While the modal prey size of felids is usually less than their body weight (Packer, 1986), lions are expected to take prey  $> 45\%$  of their body mass as they are larger than Carbone *et al.*'s (1999) 21.5 kg threshold, but the preferred weight range of lions is greater than 100% of their body mass.

This weight range encompasses adults of larger antelope, buffalo and the young of massive (or mega-) herbivores, such as hippopotamus, elephant and white and black rhinoceros. Within this range they prefer species that weigh 350 kg (Fig. 4) which is much larger than the largest recorded weight of lion (260 kg according to Berry, 1983 in Estes, 1991: 369). This is far heavier than the 100–200 kg previously hypothesized (Bertram, 1979). The preferred weight range calculated here is likely to be an underestimate given that males of most species are preferentially taken (Schaller, 1972; Rudnai, 1974; Mills, 1984; Prins & Iason, 1989), and we have conservatively



**Fig. 4.** Linear relationship between lion *Panthera leo* prey preference (mean Jacobs' index) and the  $\log_{10}$  of prey body mass excluding elephant, rhinoceros and hippopotamus ( $r^2 = 0.823$ ,  $P < 0.001$ ,  $y = 1.57 + 0.75x$ ).



**Fig. 5.** Linear relationship between lion *Panthera leo* prey preference (mean Jacobs' index) and prey herd size ( $r^2 = 0.186$ ,  $P < 0.017$ ,  $y = -1.15 + 1.39x$ ).

used Schaller's (1972) figure of three-quarters of the female body mass in our analyses.

We had hypothesized that lion prey preferences would follow a normal distribution when plotted against prey body mass based on optimal foraging theory (Pulliam, 1974). We expected some species to be too small for lions to obtain enough energy from hunting to be sustainable (Rosenzweig, 1966; J. P. Elliott *et al.*, 1977; Earle, 1987) and others to be too large to easily and safely be taken (J. P. Elliott *et al.*, 1977). Generalized capture success curves reflect this distribution with peak efficiency between inefficient small and excessively large prey sizes (D. S. Wilson, 1975). This is also supported by long-term data from the Serengeti where carnivores are inefficient at catching prey outside their preferred size range (Sinclair *et al.*, 2003). In essence, our data support two predictions of optimal foraging theory (J. R. Krebs, 1978: 29); namely that lions prefer more profitable prey (Fig. 4) and largely

ignore unprofitable prey which are outside the optimal set (Fig. 3) regardless of how common they are. That they do take such prey reflects their opportunistic hunting behaviour (Schaller, 1972).

The body mass distribution of lion prey species shows a skew to the right which we suggest stems from the group hunting strategy of lions which enables exceptionally large prey items to be taken (see review by Gittleman, 1989). Other predators that hunt as groups, such as African wild dog *Lycaon pictus*, spotted hyena *Crocuta crocuta*, Indian dhole *Cyon alpinus*, bush dogs *Speothos venaticus*, and grey wolf *Canis lupus*, are also likely to exhibit a skewed preference toward larger bodied prey in plots similar to Fig. 4, as group hunting predators are able to kill larger prey relative to their own size (Kruuk, 1975). This prediction was partially met by Radloff & du Toit (2004) who found a significant linear relationship between predator and prey body mass in the Mala Mala Game Reserve. There, group hunting species, such as lions and wild dogs, killed the broadest range of prey, from the largest to the smallest, with a predator:prey body mass ratio ranging from 1:1.0 for lionesses to 1:2.1 for lions and 1:1.2 for wild dogs (Radloff & du Toit, 2004). We have essentially shown this occurs for lion throughout their range (Fig. 2), but it is clearly not their preferred option, which is to kill increasingly large prey (Fig. 4).

We also hypothesize that individually hunting predators, such as caracal *Caracal caracal*, leopard *Panthera pardus*, tiger *P. tigris*, jaguar *P. onca*, mountain lion *Felis concolor*, Ethiopian wolf *Canis simensis* and red fox *Vulpes vulpes* would have optimal preference for prey species with body masses closer to the mean of their own species and with less of a skew toward large bodied prey. For solitary hunting cheetah and leopard at Mala Mala, the predator:prey ratio was less than 1:1 (Radloff & du Toit, 2004).

While body mass in predators is governed by the frequency distribution of the size of available prey (McNab, 1971), diverse communities of prey require predators to have evolved competition avoidance or minimization mechanisms. These may be morphological, through the segregation of prey by body mass; ecological, through habitat segregation; or behavioural, via the use of refuges (e.g. Durant, 1998). The linear relationship between Jacobs' index and prey body mass with exclusion of the megaherbivores (Fig. 4) suggests that lions increasingly prefer larger prey species, irrespective of other ecological or behavioural features of the prey. For example, there seems to be no preference for water dependent prey species given that buffalo, giraffe and wildebeest are water dependent and preferred and gemsbok is water independent and also preferred (Table 5). Avoided species can also be water dependent (impala and kob) or independent (springbok) (Table 5). The nominally water independent larger species (roan, sable and eland) are all taken in accordance with their availability (Table 5). This could not be analysed separately because the exact nature of water dependency is not known for most species and variation exists within species (e.g. there are water dependent and independent populations of wildebeest in the Kalahari; Mills & Retief, 1984).

**Table 5.** Comparison between species preferred, avoided and killed in accordance with their abundance separated by their water dependency (if recorded in Estes 1991)

|                                       | Water dependent   | Water independent  |
|---------------------------------------|---|--|
| Preferred prey                        | Buffalo<br>Giraffe<br>Warthog<br>Wildebeest<br>Zebra  | Gemsbok  |
| Taken in accordance with availability | Bushpig<br>Hippopotamus<br>Kob<br>Nyala<br>Topi/tsessebe<br>Waterbuck   | Eland<br>Hartebeest<br>Kudu<br>Oribi<br>Roan<br>Sable<br>Springbok |
| Avoided prey                          | Black rhinoceros<br>Bushbuck<br>Grant's gazelle<br>Impala<br>Klipspringer<br>Reedbuck sp.<br>White rhinoceros | Ostrich<br>Steenbok<br>Thomson's gazelle                           |

The preference of lions for specific prey species is also interesting. Blue wildebeest, with males weighing 250 kg (Stuart & Stuart, 2000), are within the lion's preferred body mass range, occur in large herds, occur in habitat used by lion, and are unlikely to cause injury to hunting lions. Their maximum speed is very similar to that of lions and much slower than other potential prey species, and their ability to detect predators is much lower than zebra and gazelles (J. P. Elliott *et al.*, 1977). Consequently, they are one of the most preferred prey species. The degree of preference is limited by the synchronous breeding exhibited by wildebeest that minimizes predation on calves (Estes, 1976), although they are below the preferred weight range, and by the migratory nature of various populations (see Estes, 1976; Mills & Retief, 1984). Mills & Shenk (1992) concluded that the sedentary behaviour of wildebeest in Kruger meant lion predation impacted on their population more severely than on the semi-migratory zebra.

Buffalo are a much riskier species to hunt (e.g. Mangani, 1962; Mitchell *et al.*, 1965; Packer, 1986) and have a slightly faster maximum speed than lions (Prins & Iason, 1989); however, the returns in energy investment make the risks rewarding, such that some lions hunt buffalo almost exclusively (Makacha & Schaller, 1969; Funston, Mills, Biggs *et al.*, 1998). Large buffalo herds are easy to detect through their noise and smell, and this may increase the preference of lion for buffalo. Lion in the Serengeti rely on buffalo while the migratory species are absent (Scheel & Packer, 1995) and buffalo seem to be much more susceptible to predation during droughts (Mills *et al.*, 1995). Studies where availability data were not included suggest that buffalo are also preferentially preyed upon (e.g. McBride, 1984; Scheel & Packer, 1995).

The inclusion of this data is likely to positively increase the Jacobs' index value of this species.

Gemsbok occur in arid, prey-impooverished environments, such as the Kalahari and Etosha, where they are independent of water. With so little other medium-sized to large prey available, gemsbok are highly preferred as prey by lion. Despite their formidable horns, gemsbok are within the preferred weight range, occur in herds and in a habitat where lions are relatively abundant.

There have been suggestions that the stripes of zebra evolved to reduce the risk of predation (see review by Ruxton, 2002). Kingdon (1984) discounted this hypothesis because he contended that zebra were killed in proportion to their availability. Our data support this and zebra should be preferentially preyed upon by lion based on their size, grouping strategy and habitat choice, while tempered slightly by their active predator defence, leading to a 28.6% hunt failure, and their relatively high detection distance (J. P. Elliott *et al.*, 1977). Lions have 6 s when attacking zebra before they start being outrun as the zebra reaches top speed (J. P. Elliott *et al.*, 1977). In Etosha and the Kruger, lions preferentially prey upon zebra foals (Stander, 1992; Mills & Shenk, 1992). Once wildebeest and zebra were encountered there was no difference in the likelihood of either becoming prey. However, lions encountered wildebeest more frequently than zebra during continuous follows (0.71 wildebeest encounters per zebra encounter compared to 0.51 wildebeest per zebra in the population; Mills & Shenk, 1992; Tables 1 & 4). This greater than expected encounter rate, coupled with a better ability to determine the outcome of hunts (measured by proportion of encounters that did not lead to hunts; Mills & Shenk, 1992), may further assist in explaining why wildebeest are more preferred than zebra despite differences in body mass predicting otherwise.

Giraffe are at the upper end of the preferred weight range and are preyed upon more frequently than expected based on their availability. Between 50% and 75% of calves are preyed upon in their first few months (Estes, 1999). The height of giraffe, and the associated increased predator detection capability, and the threat of injury to predators from its hooves, which are actively used in defending adults and offspring, would be expected to minimize the preference. This is not the case.

Klipspringer, grysbok, steenbok, common duiker, impala, reedbuck, Grant's gazelle, ostrich, bushbuck and Thomson's gazelle are all less than half of the preferred body mass of lion prey and are significantly avoided. This is not to say that these species are unimportant items in the diet of lion as many of them are commonly taken (Table 3, Fig. 2). Rather they are killed less frequently than expected based on their availability. Whether this is the result of active avoidance (not attacked when encountered) by lion or by a reduced encounter rate is unknown, although re-analysis of data presented in Funston, Mills & Biggs (2001) suggests the former. Encounters of small prey (steenbok, duiker, hare and porcupine) led to hunts on 68.7% of occasions (46 hunts of 67 encounters from Table 2; Funston, Mills & Biggs, 2001). For impala, only 61.3% of 312 encounters led to hunts (Funston, Mills & Biggs,

2001). Medium-sized prey (wildebeest, zebra, kudu and waterbuck) were encountered on 420 occasions and hunted on 76.2% of them, while buffalo, were encountered 104 times and hunted on 84.6% of occasions (Funston, Mills & Biggs, 2001). Separate analysis of wildebeest and zebra found that 61.2% of 98 encounters led to hunts of wildebeest while 77.9% of 140 zebra encounters led to hunts (Mills & Shenk, 1992). This reanalysis illustrates that larger prey species are preferentially hunted over smaller species. Furthermore, lions invest more energy in capturing larger prey (31.6 min per stalk of wildebeest and zebra) compared to small prey (6.9 min per stalk of gazelles) (J. P. Elliott *et al.*, 1977).

Yet within the preferred weight range, there exists species that are not preferred. Optimal foraging theory suggests that a predator should be able to distinguish between items of differing profitability and prefer the most profitable types (J. R. Krebs, 1978). For roan and sable this lack of preference may be because of their low abundance throughout their range (Stuart & Stuart, 2000), reducing their encounters with lions to the point that searching becomes too energetically costly (Sunquist & Sunquist, 1997), although during altered environmental conditions they can be substantially taken (Harrington *et al.*, 1999). The large body mass of eland coupled with their active defence against predators, their vigilance (through large herd size) and their weaponry (Estes, 1991), probably reduce their likelihood of predation, such that they are killed in accordance with their abundance. Waterbuck weigh between 250 and 270 kg (195 kg adjusted) which puts them within the preferred prey weight range and their requirement for grassland habitat near water (Stuart & Stuart, 2000) means they are likely to be encountered by lion frequently. Yet they are only preyed upon by lion in accordance with their abundance, possibly arising from taste aversion stemming from its lack of scent glands that results in a greasy, musky smelling coat (Estes, 1999).

Warthog are well below the preferred weight range of lion prey and so would be expected to be avoided, yet they are taken in accordance with their abundance. It is unlikely that this is an artefact of censusing or counting kills as the underestimation of the population size of small species is likely to be counteracted by the undercounting of the carcasses of these small species which are almost totally consumed. More likely is that warthogs are common in habitats where lions are, and are slower and have less endurance than most savanna ungulates (Estes, 1999). Confounding this is the use of burrows by warthogs, although this is by no means a secure refuge (Estes, 1999).

Analyses such as this can only be achieved by using the results of numerous detailed studies from different parts of the lions distribution and in different time periods. This highlights the importance of replicated dietary studies for other predators which take into account prey availability. While South Africa and Tanzania lead the way in such studies on lions (Table 1), it is crucial to increase the number of studies from other parts of Africa.

The methods used here can be used on all other large predators to determine their preferred weight range

of prey, as well as determining if other characteristics influence predation patterns. Eventually, the degree of competition in a community of predators, as occurs in Africa, Australia, North America, Asia or South America, can be investigated. Comparison between such predators may also shed light on the evolution of cooperative hunting. Additionally, wildlife managers can use this data to predict what lions will eat when reintroduced by solving Jacobs' index with the value calculated here and the game count data of the site in question, thereby allowing them to plan rather than simply respond. Consequently, the information presented here will allow us to move beyond descriptive dietary studies to improving our predictive understanding of the mechanisms underlying predator/prey interactions.

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