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# PREY PREFERENCES OF THE AFRICAN WILD DOG *LYCAON PICTUS* (CANIDAE: CARNIVORA): ECOLOGICAL REQUIREMENTS FOR CONSERVATION

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Valuable conservation research on the African wild dog (*Lycaon pictus*) has identified that its current endangerment is primarily due to human persecution, although habitat alteration, interference competition with other large predators, and disease also are factors. Numerous studies have thus determined what should be avoided to sustain an African wild dog population, yet in this study we identify what is needed to conserve a wild dog population by using Jacobs' index to determine its preferred prey species. Twenty-four assessments of wild dog prey preference were calculated from 18 studies involving 4,874 kills of 45 species from throughout its distributional range. Wild dogs prefer prey within a bimodal body mass range of 16–32 kg and 120–140 kg, which is abundant and less likely to cause injury when hunted. This bimodal range follows that of optimal wild dog pack sizes based on energetic costs and benefits. Greater kudu (*Tragelaphus strepsiceros*) and Thomson's gazelle (*Gazella thomsonii*) are killed by wild dogs wherever they coexist and are significantly preferred. Impala (*Aepyceros melampus*) and bushbuck (*Tragelaphus scriptus*) also are significantly preferred. Our results allow wildlife managers to more accurately assess the survival chances of reintroduced or small wild dog populations by determining if sufficient preferred prey are available. These techniques are applicable to all adequately studied large predators.

Key words: endangered species, Jacobs' index, optimal foraging, predation, preferred prey weight range, prey selection

The African wild dog (*Lycaon pictus*) is a gregarious, cooperatively hunting, obligate carnivore (Malcolm 1999) that is naturally rare (Creel et al. 2004). It originally occurred throughout sub-Saharan Africa outside forests and extreme deserts, but populations have been greatly reduced (to 5,750 individuals in 600–1,000 packs—Woodroffe et al. 2004) and highly fragmented over the past 40 years (Fanshawe et al. 1997), predominantly through persecution by humans but more recently via competition with larger carnivores and, possibly, disease (Creel and Creel 1996; East and Hofer 1996; Fanshawe et al. 1997; Mills and Gorman 1997). Today the African wild dog is listed as endangered (McNutt et al. 2004) and is largely restricted to conservation areas (Lindsey et al. 2004).

Wild dog body mass (17–36 kg—Stuart and Stuart 2000) spans the 21.5-kg threshold considered necessary for obligate carnivory on large vertebrates (Carbone et al. 1999). The wild dog's pack hunting strategy may allow its metabolic requirements to be met by hunting larger vertebrates than could be captured by a solitary dog. Although hunting success is positively related to hunting group size (Creel 1997; Creel and Creel 1995), 1 individual can capture prey as large as an adult female greater kudu (*Tragelaphus strepsiceros*—Courchamp et al. 2002).

For its size, the wild dog consumes more meat per day than any other carnivore (3.04 kg—Mills and Harvey 2001). Wild dogs have been recorded preying on species as small as hares (*Lepus*—Creel and Creel 2002) and bat-eared foxes (*Otocyon megalotis*—Rasmussen 1996) up to the size of juvenile African buffalo (*Syncerus caffer*) and eland (*Taurotragus oryx*—Creel and Creel 2002). Within this range of species, however, wild dogs are thought to concentrate on prey weighing between 10 and 120 kg (Creel and Creel 2002).

Wild dogs hunt daily (Creel and Creel 2002) at dawn and dusk (Malcolm 1999). Sight is thought to be their most important predatory sense (Estes and Goddard 1967; Kühme 1965); however, research in denser habitats revealed similar

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**TABLE 1.**—Sites and sources of African wild dog prey preference data used in this study.

| Country | Site | Period | No. kills | Source |
|---|---|---|---|---|
| Kenya | Aitong | 1989 | 29 | Fuller et al. (1995) |
| South Africa | Hluhluwe–Umfolozi Park | Early 1980s | 85 | Whateley and Brooks (1985) |
| | | 1992–1994 | 346 | Krüger (1996) |
| | Kruger National Park | 1956–1965 South | 1,399 | Pienaar (1969) |
| | | 1956–1965 Central | 422 | Pienaar (1969) |
| | | 1956–1965 North | 929 | Pienaar (1969) |
| | | Early 1990s | 52 | Mills and Biggs (1993) |
| | Madikwe Game Reserve | 1996 | 69 | M. Hofmeyr (in litt.) |
| | | 1997 | 76 | M. Hofmeyr (in litt.) |
| | | 1998 | 78 | M. Hofmeyr (in litt.) |
| | Pilanesberg National Park | 1999–2001 | 137 | van Dyk and Slotow (2003) |
| | Shambala Private Game Reserve | 2002 | 56 | Rhodes and Rhodes (2004) |
| | Shamwari Game Reserve | 2004 | 58 | J. O'Brien (pers. comm.) |
| | | 2005 | 47 | J. O'Brien (pers. comm.) |
| | Timbavati Game Reserve | 1964–1968 | 19 | Hirst (1969) |
| Tanzania | Ngorongoro Crater | 1965–1966 | 50 | Estes and Goddard (1967) |
| | Selous Game Reserve | 1993–1999 | 180 | Creel and Creel (2002) |
| | Serengeti National Park | Late 1950s | 100%[a] | Wright (1960) |
| | | 1965–1966 | 42 | Kruuk and Turner (1967) |
| | | 1966–1969 migration[b] | 131 | Schaller (1972) |
| | | 1966–1969 resident[b] | 66 | Schaller (1972) |
| Zambia | Kafue National Park | 1960–1963 | 96 | Mitchell et al. (1965) |
| Zimbabwe | Wankie (Hwange) National Park | 1972–1973 | 75 | Wilson (1975) |
| | Savé Conservancy | 1990s | 430 | Pole et al. (2004) |

[a] Only percentages provided.
[b] Migration refers to annual period when migratory herds were present at Schaller's (1972) Serengeti study site and resident refers to periods when the migrants were away and only resident fauna was present.

hunting success rates, suggesting that auditory and olfactory cues also assist (Creel and Creel 1995; Krüger 1996). Estimates of hunting success rates vary from 13% to 100% ($\bar{X} = 44\%$—Creel 1997; Creel and Creel 1995; Estes 1967; Estes and Goddard 1967; Fanshawe and Fitzgibbon 1993; Fuller and Kat 1993; Kruuk and Turner 1967; Kühme 1965; Malcolm and van Lawick 1975; van Lawick 1971). This high success rate relative to other members of Africa's large predator guild reflects a high predictability of the outcome of the hunt and the very high energy expenditure (Gorman et al. 1998), which severely penalizes unsuccessful hunts (Bertram 1979).

One, generally dominant, member leads the pack in its chase and often seizes the prey before the other pack members arrive to kill by disembowelment (Estes 1967). Members of the hunting pack also may capture vulnerable prey opportunistically during the chase (Estes and Goddard 1967). Multiple kills in large packs are not uncommon ($\bar{X} = 1.8$ kills per hunt, $n = 266$—Creel and Creel 2002).

As cursorial hunters, wild dogs tend to take slow individuals, such as the young, pregnant, old, sick, or injured (Kruuk 1972; Pole et al. 2004; Schaller 1972) or males in poor condition (Fitzgibbon and Fanshawe 1989), more frequently than do stalking predators. Their cooperative behavior during these chases allows individuals to cut corners during their quarry's directional changes and thereby increase hunting success (Bertram 1979; Kruuk and Turner 1967). In denser habitats, there is no evidence of wild dogs selecting substandard prey (Krüger 1996).

Wild dogs lose up to 50% of their kills in open habitats to kleptoparasitism, especially by spotted hyenas (*Crocuta crocuta*—Kruuk 1972). Such high losses are energetically costly because losing 25% of kills necessitates an increase in hunting time from 3.5 to 12 h per day (Gorman et al. 1998). The infrequency of scavenging (3% of the diet—Schaller 1972) by wild dogs and their crepuscular activity pattern probably evolved to minimize interactions with dominant competitors, because lion (*Panthera leo*) predation is the most common cause of wild dog death in some populations (Ginsberg et al. 1995; Mills and Gorman 1997).

Here we used dietary and prey abundance data collected from throughout the wild dog's distribution to test which prey species African wild dogs prefer and which they avoid. If a species is killed more frequently than it exists in the prey population then it can be considered preferred, whereas if it is taken less frequently then it is avoided. Obviously, this is a simplification because this reflects not just the predator's preference but also the ease with which prey is captured. Further, we tested why particular prey species were preferred or avoided using various ecological characteristics (Jaksic et al. 1992) and assessed whether prey preferences could be another factor threatening wild dogs with extinction.

## MATERIALS AND METHODS

A literature survey revealed 16 published and 2 unpublished studies from 5 of the 14 countries with extant populations describing diets of African wild dogs with some measure of prey abundance (actual or relative; Table 1). Several studies were long term, allowing temporally separated prey preferences to be calculated with changes in prey abundance (Table 1). Others provided information from different regions of a study area (Table 1). Consequently, 24 assessments of prey preference were calculated from throughout the distribution of the wild dog. We do not believe autocorrelation exists by using data from the same area at different prey densities, because 1 of the fundamental factors determining whether a species is captured and killed is the probability of coming in contact with the predator, and this varies with prey density.

The unpublished data came from 2 South African sites. Shamwari Game Reserve covers 19,746 ha in the Eastern Cape Province of South Africa and wild dogs were reintroduced there in 2000. The 55,000-ha Madikwe Game Reserve in the North West Province had wild dogs reintroduced in 1995 (Hofmeyr et al. 2003; Woodroffe and Ginsberg 1997).

Numerous studies provided information on wild dog diet but insufficient information on prey abundance (Childes 1988; Cronje et al. 2002; Fuller and Kat 1990; Rasmussen 1996, 1999; Wilson 1966). Unless other sources could be found that provided prey abundance at the appropriate time (Table 2), these studies could not be used.

There are many electivity indices; however, none is considered superior to the rest or without bias and increasing error at small proportions (Chesson 1978; Strauss 1979). Consequently, researchers have often overstated the accuracy of their preference results (Norbury Sanson 1992), particularly when employing the most commonly used techniques: the forage ratio and Ivlev's electivity index (Ivlev 1961). These indices and their variants suffer from nonlinearity, bias to rare food items, increasing confidence intervals with increasing heterogeneity, being unbound or undefined, and lacking symmetry between selected and rejected values (Jacobs 1974). Confidence intervals also become excessive for proportions below about 10% (Strauss 1979). There are methods that minimize these biases (Krebs 1989) and we have chosen Jacobs' index:

$$D = \frac{r_i - p_i}{r_i + p - 2r_i p_i},$$

where $r_i$ is the proportion of the total kills at a site made up by species i and $p_i$ is the proportional abundance of that species of the total prey population (Jacobs 1974). Jacobs' index produces values between +1 (maximum preference) and −1 (maximum avoidance). A Jacobs' index value was calculated for each prey species recorded in each study. The mean of these Jacobs' index values for each prey species was then calculated (±1 *SE*) 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 (Palomares et al. 2001), or the sign test (Zar 1996) where they did not.

This analysis is not biased by results from 1 particular area and 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. Furthermore, this method also accounts for varying hunting group sizes and sex ratios by being collected from populations that hunt in different-sized groups with different sex ratios. This technique investigates predation by African wild dogs as a species, rather than individual populations.

Multiple regression was conducted on transformed variables that were noncorrelating (tested using Spearman's correlation—Zar 1996), to determine which factors influenced prey preferences of African wild dogs. Significant relationships were plotted using distance-weighted least squares and linear regression fits of transformed data. Variables used were prey relative abundance at a site (as a measure of prey availability), prey body mass, herd size, preferred habitat type, and threat of injury to predator.

Three-fourths of mean adult female body mass of prey species was used as a species' body mass to account for predation on calves and subadults following Schaller (1972). Mammalian weights were taken from Stuart and Stuart (2000) and Schaller (1972) was used for ostrich (*Struthio camelus*) body mass.

**TABLE 2.**—Assumptions made in determining prey abundance for studies where it is not implicitly stated.

| Source | Assumptions made or source of abundance data |
|---|---|
| Fuller et al. (1995) | Abundance data from Ottichilo et al. (2000) with blue wildebeest and Burchell's zebra estimates from Caro (1994) |
| Kruuk and Turner (1967) | Abundance data from Schaller (1972) |
| Mills and Biggs (1993) | Giraffe and hippopotamus assumed to be in equal abundance from Mills and Biggs (1993:256, figure 3); African buffalo abundance from Donkin (2000). Similarly kudu and waterbuck were assumed to be of equal abundance |
| Mitchell et al. (1965) | Abundance data from Dowsett (1966) |
| Pole et al. (2004) | Abundance data from Ph.D. dissertation by A. Pole as personal communication from I. Gordon |
| Schaller (1972) | Abundance data from Schaller (1972:382, table 32), separated into seasons when migrating herds were present (January–June) and when only resident wildlife was present (July–December). |

Social organization is an indicator of a species' ability to detect predators (Hayward and Kerley 2005). 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).

Habitat type may affect predation rates through the density of vegetation affecting the detectability of prey and evasion speed. Habitat was treated as a categorical variable with 1 referring to open grasslands, 2 referring to savannah, and 3 to densely vegetated areas. Obviously a species may overlap these habitat types and then an average of habitat use was applied (Table 3).

Finally, the antipredatory strategy a species employs will affect its chances of becoming prey. There has been no comparison of crypsis between predator and prey species or between the evasion speed of predators and prey (but see Elliott et al. 1977; Prins and Iason 1989). This meant that the threat of injury to a hunter was all that could be analyzed, where larger species are more likely to stand and fight predators than smaller ones (Geist 1974). The categories of threat used were 0 (no threat), 1 (minor threat or active defense of young), 2 (severe threat; death of the predator a likely result—Estes 1999; Stuart and Stuart 2000; Table 3).

## RESULTS

Jacobs' index scores were calculated from 4,874 wild dog kills of 45 species (Table 3). Greater kudu, Thomson's gazelle (*Gazella thomsonii*), and steenbok (*Raphicerus campestris*) were killed by wild dogs in every study where they were present, whereas impala (*Aepyceros melampus*), common duiker (*Sylvicapra grimmia*), and bushbuck (*Tragelaphus scriptus*) were preyed upon in more than 80% of the sites where they occurred (Fig. 1). Conversely, giraffe (*Giraffa camelopardalis*) and ostrich were never killed by African wild dogs despite occurring in at least 10 sites investigated here (Fig. 1). Although less frequently recorded as potential prey

**Table 3.**—Jacobs' index values for prey species of African wild dogs recorded in >1 study, number of studies recording the species as a potential prey item ($n_p$) and actual prey item ($n_a$), mean relative (%) abundance of each species, mean percentage that each species comprised of the total kills recorded, body mass (three-fourths of mean adult female body mass), and categories of herd size, habitat density, and injury threat to wild dogs used in modeling. Specifics of each category are described in the text and their details were derived from Stuart and Stuart (2000) and Estes (1999).

| Species | Prey preference[a] | Jacobs' index ($\bar{X} \pm SE$) | $n_p$ | $n_a$ | Abundance (%) ($\bar{X} \pm SE$) | Kills (%) ($\bar{X} \pm SE$) | Mass (kg) | Herd size | Habitat | Threat |
|---|---|---|---|---|---|---|---|---|---|---|
| Antelope, roan (*Hippotragus equinus*) | | −1.00 ± 0.00 | 5 | 0 | 0.63 ± 0.29 | 0 ± 0 | 220 | 3.5 | 2 | 1.5 |
| Antelope, sable (*H. niger*) | | −0.63 ± 0.17 | 9 | 4 | 1.01 ± 0.41 | 1.01 ± 0.61 | 180 | 4 | 2 | 1.5 |
| Baboon, yellow (*Papio cynocephalus*) | − | −1.00 ± 0.00 | 8 | 0 | 1.39 ± 0.24 | 0 ± 0 | 12 | 5 | 2 | 1 |
| Blesbok (*Damaliscus dorcas phillipsi*) | | −0.55 ± 0.21 | 7 | 3 | 2.45 ± 0.78 | 1.73 ± 0.82 | 53 | 4 | 1 | 0.5 |
| Bontebok (*D. d. dorcas*) | | −1.00 ± 0.00 | 3 | 0 | 2.63 ± 2.24 | 0 ± 0 | 45 | 4 | 1 | 0.5 |
| Buffalo, African (*Syncerus caffer*) | − | −0.98 ± 0.02 | 20 | 2 | 5.36 ± 1.44 | 0 ± 0 | 432 | 5 | 2 | 2 |
| Bushbuck (*Tragelaphus scriptus*) | | 0.27 ± 0.17 | 15 | 13 | 1.37 ± 0.40 | 6.27 ± 2.37 | 23 | 1 | 3 | 0 |
| Bushbuck (excluding Shambala)[b] | + | 0.36 ± 0.15 | 14 | 13 | 1.46 ± 0.40 | 6.72 ± 2.49 | | | | |
| Bushpig (*Potamochoerus larvatus*) | − | −1.00 ± 0.00 | 8 | 0 | 4.05 ± 2.17 | 0 ± 0 | 46 | 3 | 3 | 1 |
| Cheetah (*Acinonyx jubatus*) | | −1.00 ± 0.00 | 4 | 0 | 0.75 ± 0.63 | 0 ± 0 | 30 | 1 | 1.5 | 1 |
| Duiker, blue (*Cephalophus monticola*) | | −1.00 ± 0.00 | 3 | 0 | 1.06 ± 0.11 | 0 ± 0 | 3 | 2 | 3 | 0 |
| Duiker, common (*Sylvicapra grimmia*) | | 0.15 ± 0.22 | 8 | 7 | 5.09 ± 2.53 | 11.38 ± 4.56 | 16 | 1 | 3 | 0 |
| Eland (*Taurotragus oryx*) | − | −0.71 ± 0.14 | 16 | 4 | 2.89 ± 0.68 | 1.42 ± 1.10 | 345 | 5 | 2 | 2 |
| Elephant, African savannah (*Loxodonta africana*) | − | −1.00 ± 0.00 | 9 | 0 | 4.06 ± 2.88 | 0 ± 0 | 1,600 | 3 | 2 | 2 |
| Gazelle, Grant's (*Gazella granti*) | | −0.06 ± 0.40 | 5 | 3 | 2.55 ± 1.08 | 4.88 ± 2.04 | 38 | 4 | 1 | 0 |
| Gazelle, Thomson's (*Gazella thomsonii*) | + | 0.68 ± 0.13 | 6 | 6 | 17.83 ± 6.36 | 62.38 ± 8.67 | 15 | 5 | 1 | 0 |
| Gemsbok (*Oryx gazella*) | − | −1.00 ± 0.00 | 9 | 0 | 2.52 ± 0.73 | 0 ± 0 | 158 | 4 | 1 | 2 |
| Giraffe (*Giraffa camelopardalis*) | − | −1.00 ± 0.00 | 15 | 0 | 2.06 ± 0.73 | 0 ± 0 | 550 | 3 | 2 | 2 |
| Grysbok, Cape (*Raphicerus melanotis*) | | −1.00 ± 0.00 | 3 | 0 | 6.98 ± 6.07 | 0 ± 0 | 7 | 1 | 2.5 | 0 |
| Grysbok, Sharpe's (*R. sharpei*) | | −0.73 ± 0.17 | 5 | 2 | 1.71 ± 0.92 | 0.25 ± 0.16 | 7 | 1 | 2.5 | 0 |
| Hartebeest (*Alcelaphus buselaphus*) | − | −0.56 ± 0.15 | 14 | 7 | 3.31 ± 0.91 | 2.00 ± 1.18 | 95 | 4 | 1.5 | 1 |
| Hippopotamus (*Hippopotamus amphibius*) | − | −1.00 ± 0.00 | 9 | 0 | 2.58 ± 1.88 | 0 ± 0 | 750 | 3 | 1.5 | 2 |
| Hyena, brown (*Hyaena brunnea*) | | −1.00 ± 0.00 | 4 | 0 | 0.24 ± 0.13 | 0 ± 0 | 38 | 1 | 1.5 | 1 |
| Impala (*Aepyceros melampus*) | | 0.06 ± 0.11 | 24 | 23 | 28.11 ± 4.73 | 34.00 ± 6.11 | 30 | 4 | 2 | 0 |
| Impala (excluding Serengeti sites)[b] | + | 0.25 ± 0.09 | 19 | 19 | 31.31 ± 5.69 | 42.20 ± 6.49 | | | | |
| Klipspringer (*Oreotragus oreotragus*) | − | −0.97 ± 0.03 | 6 | 1 | 0.78 ± 0.22 | 0.01 ± 0.01 | 10 | 2.5 | 3 | 0 |
| Kudu, greater (*Tragelaphus strepsiceros*) | + | 0.35 ± 0.10 | 18 | 18 | 7.91 ± 1.31 | 23.63 ± 4.36 | 135 | 3 | 2 | 0.5 |
| Lechwe (*Kobus leche*) | | −1.00 ± 0.00 | 3 | 0 | 0.56 ± 0.11 | 0 ± 0 | 60 | 4 | 1 | 1 |
| Leopard (*Panthera pardus*) | | −1.00 ± 0.00 | 4 | 0 | 0.50 ± 0.23 | 0 ± 0 | 17 | 1 | 2.5 | 3 |
| Lion (*Panthera leo*) | | −1.00 ± 0.00 | 4 | 0 | 1.43 ± 0.76 | 0 ± 0 | 110 | 3 | 2 | 3 |
| Nyala (*Tragelaphus angasii*) | | −0.48 ± 0.22 | 10 | 4 | 6.47 ± 4.41 | 12.18 ± 8.01 | 47 | 3 | 2 | 0.5 |
| Oribi (*Ourebia ourebi*) | | −0.88 ± 0.12 | 4 | 1 | 2.47 ± 1.38 | 0.52 ± 0.52 | 14 | 2 | 1 | 0 |
| Ostrich (*Struthio camelus*) | − | −1.00 ± 0.00 | 13 | 0 | 1.21 ± 0.43 | 0 ± 0 | 70 | 3 | 1.5 | 1 |
| Reedbuck, mountain (*Redunca fulvorufula*) | − | −0.77 ± 0.15 | 7 | 2 | 2.69 ± 1.03 | 0.42 ± 0.42 | 23 | 3 | 2.5 | 0 |
| Reedbuck, southern (*R. arundinum*) | | −0.41 ± 0.21 | 10 | 5 | 2.24 ± 1.47 | 3.20 ± 2.51 | 32 | 3 | 1.5 | 0 |
| Rhinoceros, black (*Diceros bicornis*) | − | −1.00 ± 0.00 | 7 | 0 | 0.82 ± 0.67 | 0 ± 0 | 800 | 1 | 2 | 2 |
| Rhinoceros, white (*Ceratotherium simum*) | − | −1.00 ± 0.00 | 7 | 0 | 0.56 ± 0.18 | 0 ± 0 | 1,400 | 2 | 1.5 | 2 |
| Springbok (*Antidorcas marsupialis*) | − | −0.68 ± 0.15 | 8 | 3 | 2.03 ± 0.71 | 1.09 ± 0.46 | 26 | 5 | 1 | 0 |
| Steenbok (*Raphicerus campestris*) | | −0.34 ± 0.36 | 5 | 3 | 0.74 ± 0.28 | 0.80 ± 0.50 | 8 | 1.5 | 1.5 | 0 |
| Topi−tsessebe (*Damaliscus lunatus*) | − | −0.69 ± 0.18 | 12 | 4 | 1.76 ± 0.88 | 1.10 ± 0.59 | 90 | 3 | 2 | 1 |
| Vervet monkey (*Chlorocebus aethiops*) | | −1.00 ± 0.00 | 2 | 0 | 1.56 ± 1.06 | 0 ± 0 | 3.5 | 4 | 2 | 0 |
| Warthog (*Phacochoerus africanus*) | | −0.52 ± 0.11 | 20 | 12 | 5.01 ± 0.66 | 3.30 ± 0.91 | 45 | 3 | 2 | 1.5 |
| Waterbuck (*Kobus ellipsiprymnus*) | | −0.35 ± 0.15 | 21 | 12 | 2.45 ± 0.53 | 4.21 ± 1.61 | 188 | 3.5 | 2 | 1.5 |
| Wildebeest, black (*Connochaetes gnou*) | | −1.00 ± 0.00 | 3 | 0 | 0.98 ± 0.98 | 0 ± 0 | 100 | 4 | 1 | 1 |
| Wildebeest, blue (*C. taurinus*) | − | −0.70 ± 0.08 | 24 | 15 | 19.87 ± 4.32 | 7.56 ± 2.89 | 135 | 5 | 1 | 1.5 |
| Zebra, Burchell's (*Equus burchellii*) | − | −0.88 ± 0.07 | 24 | 5 | 10.00 ± 1.02 | 0.58 ± 0.41 | 175 | 3 | 2 | 1.5 |
| Zebra, mountain (*E. zebra*) | | −1.00 ± 0.00 | 3 | 0 | 50.16 ± 49.84 | 0 ± 0 | 178.5 | 3 | 1.5 | 1.5 |

[a] +, significantly preferred; −, significantly avoided.
[b] Sites were excluded from analysis (see "Results" for reasons for their exclusion).

items, African savannah elephant (*Loxodonta africana*), black and white rhinoceros (*Diceros bicornis* and *Ceratotherium simum*, respectively), hippopotamus (*Hippopotamus amphibius*), yellow baboon (*Papio cynocephalus*), bushpig (*Potamochoerus larvatus*), and gemsbok (*Oryx gazella*) were never recorded as prey (Fig. 1).

Thomson's gazelle made up 62% of kills at sites where they occurred, with impala (42%), greater kudu (24%), and nyala (*Tragelaphus angasii*; 12%) also frequently killed (Table 3). Similarly, where they occurred impala (28% of available prey), blue wildebeest (*Connochaetes taurinus*; 19%), Thomson's gazelle (18%), and Burchell's zebra (*Equus burchellii*; 10%)

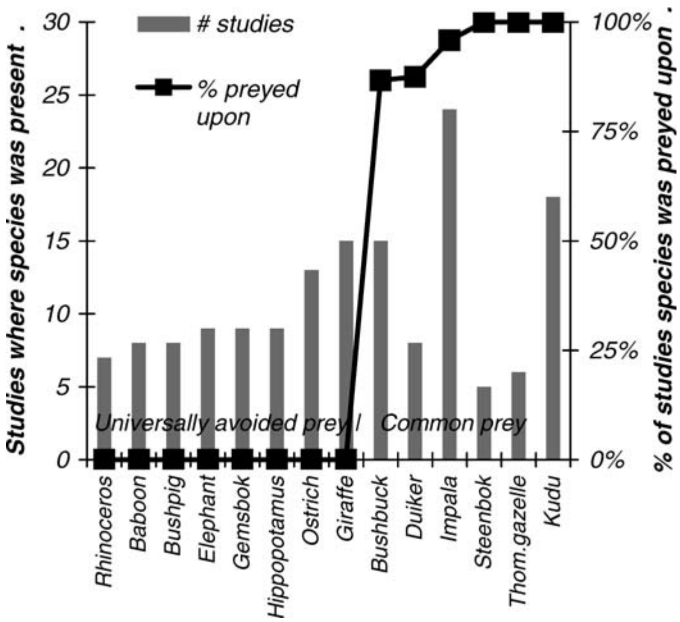


**FIG. 1.**—Commonly killed and avoided prey of African wild dogs showing the number of studies from which data were compiled (gray bars) and percentage of studies reporting that species was preyed upon (black symbols). Rhinoceros refers to both black and white species, and duiker refers to the bush duiker.

were the most common prey available to wild dogs (Table 3). Several of these species were preyed upon more frequently than expected based on their abundance, although overall there was a significant positive relationship between the proportional abundance of wild dog prey at a site and the relative frequency with which it was killed (Spearman's $R = 0.556$, $n = 16$, $P = 0.025$).

Thomson's gazelle ($t = 5.228$, $d.f. = 5$, $P = 0.003$) and greater kudu ($t = 3.586$, $d.f. = 17$, $P = 0.002$) were significantly preferred by African wild dogs when all data were included (Fig. 2). The exclusion of data from Shambala, where bushbuck made up less than 0.2% of available prey, led to bushbuck being significantly preferred ($t = 2.381$, $d.f. = 13$, $P = 0.033$). Impala are important prey everywhere except the Serengeti, where the larger Grant's gazelle (*Gazella granti*) is killed in preference to it (Kruuk and Turner 1967; Schaller 1972). When the Serengeti sites were excluded, impala were significantly preferred ($t = 2.653$, $d.f. = 18$, $P = 0.016$).

African wild dogs significantly avoided predation on yellow baboon (sign test, $Z = 2.474$, $n = 8$, $P = 0.013$), African buffalo ($Z = 4.249$, $n = 20$, $P < 0.001$), bushpig ($Z = 2.474$, $n = 8$, $P = 0.013$), topi–tsessebe (*Damaliscus lunatus*; $Z = 2.021$, $n = 12$, $P = 0.043$), eland (*Tragelaphus oryx*; $Z = 2.750$, $n = 16$, $P = 0.006$), African savannah elephant ($Z = 2.474$, $n = 8$, $P = 0.013$), gemsbok ($Z = 2.474$, $n = 8$, $P = 0.013$), giraffe ($Z = 3.328$, $n = 15$, $P < 0.001$), hartebeest (*Alcelaphus buselaphus*; $Z = 2.405$, $n = 14$, $P = 0.016$), hippopotamus ($Z = 2.667$, $n = 9$, $P = 0.008$), klipspringer (*Oreotragus oreotragus*; $Z = 2.041$, $n = 6$, $P = 0.041$), ostrich ($Z = 3.328$, $n = 13$, $P < 0.001$), black and white rhinoceros ($Z = 2.268$, $n = 7$, $P = 0.013$ for both), springbok

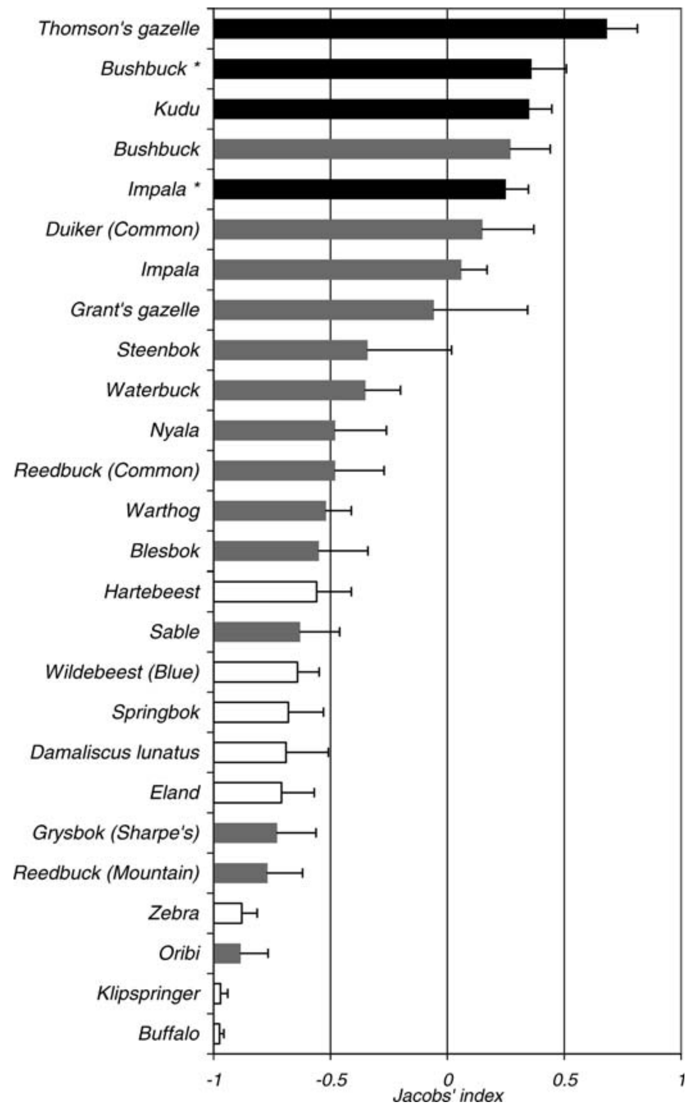


**FIG. 2.**—Dietary preferences of the African wild dog based on Jacobs' index (mean ± 1 *SE*) from 22 wild dog populations at differing prey densities. Black bars represent species preyed upon significantly more frequently than expected based on their abundance (i.e., preferred), gray bars indicate species preyed upon in accordance with their abundance or not significantly preferred or avoided, and unfilled bars show species killed significantly less frequently than expected based on their abundance (i.e., avoided). Jacobs' index values for bushbuck and impala that excluded anomalous sites are shown with an asterisk (*). African elephant, yellow baboon, black wildebeest, blue duiker, bontebok, brown hyena (*Hyaena brunnea*), bushpig, Cape grysbok, cheetah, gemsbok, giraffe, hippopotamus, lechwe, leopard, lion, mountain zebra, ostrich, black and white rhinoceros, roan antelope, and vervet monkey (*Chlorocebus aethiops*) all have Jacobs' index values of $-1 \pm 0$ and are not plotted.

(*Antidorcas marsupialis*; $Z = 2.268$, $n = 7$, $P = 0.023$), blue wildebeest ($Z = 3.878$, $n = 24$, $P < 0.001$), and Burchell's zebra ($Z = 3.878$, $n = 24$, $P < 0.001$).

Bontebok (*Damaliscus dorcas dorcas*), blesbok (*D. d. phillipsi*), blue duiker (*Cephalophus monticola*), common duiker, Grant's gazelle, Cape and Sharpe's grysbok (*Raphicerus melanotis* and *R. sharpie*, respectively), lechwe

**Table 4.**—Regression statistics for the multiple regression model of African wild dog prey preferences (Jacobs' index) against relative prey abundance, prey body mass and the habitat of prey species for species with more than 2 estimates of Jacobs index. The final regression equation was: Jacob's index = 0.76 + 0.40(log abundance) − 0.29(log body mass) − 0.03(habitat). Standard error of estimate = 0.330; $R^2 = 0.402$; analysis of variance $F = 6.711$, $d.f. = 3, 30$, $P = 0.001$. Prey abundance and body mass (italicized) predicted the Jacobs' index value at $\alpha = 0.05$.

| Variable | Coefficient | *SE* | $t_{(d.f.=41)}$ | *P* |
|---|---|---|---|---|
| Constant | 0.756 | 0.330 | −2.278 | 0.029 |
| Log (abundance) | *0.401* | *0.147* | *2.827* | *0.008* |
| Log (body mass) | *−0.298* | *0.043* | *−3.204* | *0.003* |
| Habitat | −0.030 | 0.101 | −0.298 | 0.767 |

(*Kobus leche*), nyala, oribi (*Ourebia ourebi*), southern and mountain reedbuck (*Redunca arundinum* and *R. fulvorufula*, respectively), roan and sable antelope (*Hippotragus equinus* and *H. niger*, respectively), steenbok, warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), black wildebeest (*Connochaetes gnou*), mountain zebra (*Equus zebra*), and several large carnivores are currently classed as being preyed upon in accordance with their abundance (Fig. 2). However, a larger sample size is likely to lead to bontebok, blue duiker, Cape grysbok, lechwe, oribi, roan antelope, black wildebeest, mountain zebra, and the large carnivores becoming significantly avoided if the existing trends continue (Fig. 2).

A multiple linear regression performed on prey abundance, prey body mass, and habitat with Jacobs' index as the dependent variable was conducted after herd size correlated significantly and negatively with habitat (Spearman's $R = -0.48$) and prey abundance ($R = 0.39$), and body mass correlated positively with threat ($R = 0.88$, $P < 0.05$ for each). This led to the predictive equation:

$$\text{Jacob's index} = 0.76 + 0.40(\log \text{abundance}) - 0.29(\log \text{body mass}) - 0.03(\text{habitat})$$

($R^2 = 0.402$, $F = 6.711$, $d.f = 3, 30$, $P = 0.001$). Prey abundance and body mass significantly predicted the Jacobs' index value (Table 4), with more abundant prey being increasingly preferred (Fig. 3).

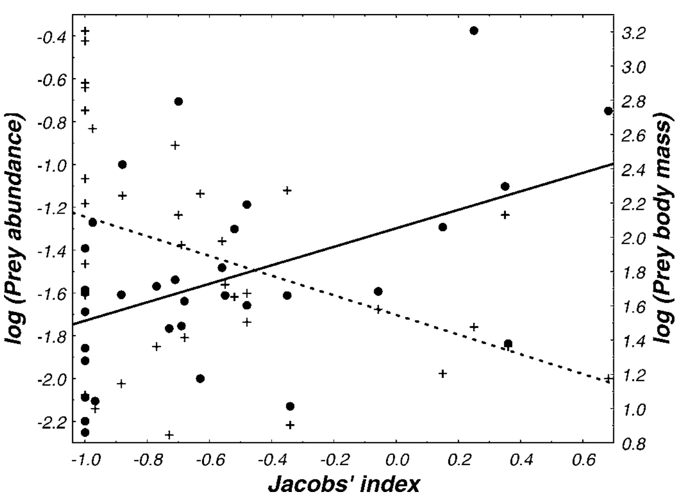


**Fig. 3.**—Linear plot of African wild dog prey preferences (mean Jacobs' index value of each prey species) against arcsin-transformed prey abundance data (black dots and line; $r^2 = 0.23$, $n = 30$, $P = 0.005$; $y = -1.30 + 0.43x$) and log-transformed prey body mass (crosses and dashed line; $r^2 = 0.17$, $n = 30$, $P = 0.011$; $y = 1.56 + 0.55x$). Only prey species with more than 3 estimates of Jacobs' index were included and large predators also were excluded. Jacobs' index values for bushbuck and impala that excluded anomalous sites are used.

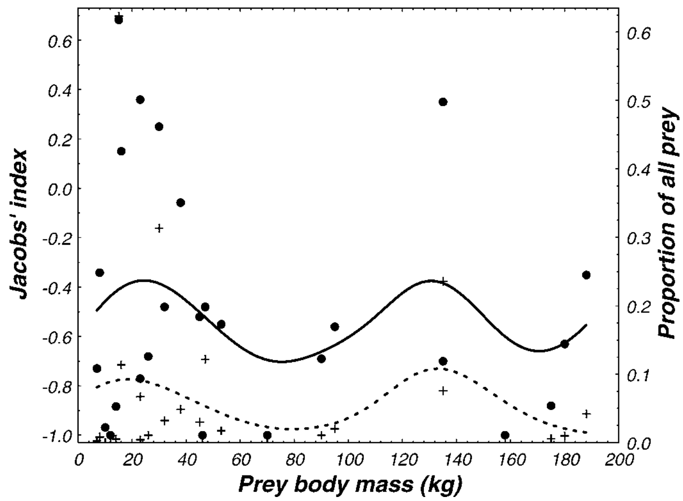


**Fig. 4.**—Distance-weighted least squares regression fit of body mass of African wild dog prey species weighing less than 200 kg plotted against Jacobs' index values (circles and solid line) and the proportion that a species comprises of wild dog prey at sites where it occurs (crosses and dotted line). Large predators were excluded, along with species with <3 estimates of Jacobs' index. Jacobs' index values for bushbuck and impala that excluded anomalous sites were used. The regression statistics for log (body mass) were $r = 0.116$, $P = 0.571$; and log (prey proportion) were $r = 0.266$, $P = 0.232$. These are presented to allow comparison with other members of Africa's large predator guild (e.g., Hayward and Kerley 2005).

A more detailed look at the body mass of wild dog preferred prey (between 0 and 200 kg) revealed bimodal peaks with preferred ranges of 16–32 kg and 120–140 kg, and modes at 24 and 132 kg (Fig. 4). There are 10 potential prey species within this body mass range occurring in sympatry with wild dogs in Africa (Fig. 4) and 4 of these are significantly preferred (Fig. 2). Although the plot of prey body mass against Jacobs' index values is not significant (Fig. 4), we have included it for its scientific interest and to allow comparison with other large African predators. This distribution is reflected by the body mass of prey that wild dogs actually kill (Spearman's $R = 0.839$, $n = 26$, $P < 0.05$; Fig. 4).

The mean body mass ($\pm 1$ *SE*) of significantly preferred wild dog prey is 50.8 ± 28.3 kg. Preferred wild dog prey exists in moderately sized herds (category 3 ± 0.9), in savannah habitat (category 2 ± 0.4), and offers little threat (category 0 ± 0.3). Of these variables, only the threat of injury from preferred and avoided prey differed significantly (Mann–Whitney $U = -2.91$, $d.f. = 4, 16$, $P = 0.004$). Taking 17 kg as the mean adult female body mass of African wild dogs (lower range of adult body mass from Stuart and Stuart [2000]), then the ratio of predator body mass to preferred prey varied between 1.41 and 7.76 based on the maximal preferred body mass of prey (Fig. 4), or 2.99 based on the mean body mass of preferred prey.

## Discussion

African wild dogs are opportunistic, rate-maximizing predators (Creel and Creel 2002; Krüger 1996) that prefer to prey on Thomson's gazelle, greater kudu, impala, and bushbuck. Three of these preferred species inhabit the denser vegetation of savannah woodlands and thickets, and would therefore require more effort in detection but less in capture (Reich 1981) than plains inhabitants. This preference for prey species that occur in dense vegetation supports the idea that smell and hearing are as important predatory senses as sight (Creel and Creel 1995). It is unlikely that wild dogs would preferentially prey upon these species to minimize the risk of kleptoparasitism given the speed that wild dogs consume their prey (Creel and Creel 2002).

Geographic variation in wild dog diet has been linked to the most abundant small to medium-sized prey species in an area (Ginsberg and Macdonald 1990). Our data support this, with prey abundance significantly predicting the Jacobs' index preference value, although prey with large body masses are avoided (Fig. 3). The relationship between prey abundance and preference is reinforced with evidence that wildebeest calves are the dominant prey when they are most abundant during the January calving season in Ngorongoro Crater, but are rarely taken outside this time (Estes and Goddard 1967). Similarly, in Savé Conservancy peaks of greater kudu and impala predation occurred during calving seasons (Pole et al. 2004). Prey selection in Hluhluwe was also based on prey body mass and abundance (Krüger 1996).

The bimodal peak in the wild dog's preferred weight range reflect peaks in gross benefits of foraging success in varying pack sizes found for packs of 3 (a minor peak), 10, and 20 dogs (Creel 1997). The dearth of small (3) packs may be due to factors other than food provisioning, such as pup guarding (Courchamp et al. 2002). This also illustrates the benefits of group hunting because the right-skewed distribution of body mass of lion prey reflected its cooperative hunting strategy (Hayward and Kerley 2005) and such a skew for wild dogs suggests similar benefits of cooperation (Fig. 4). Conversely, the bimodal peaks may be driven by a lack of prey weighing between 60 and 130 kg (Fig. 4), despite multiple regression finding wild dogs prefer the most abundant medium-sized prey available (Table 4). The 3 species within this weight range (ostrich, topi–tsessebe, and hartebeest) are universally avoided by all large African predators (Hayward 2006; Hayward and Kerley 2005; Hayward et al. 2006a, 2006b. If this bimodal distribution is an artifact of missing prey, then the ideal weight of wild dog prey is likely to be nearer 80 kg. These bimodal peaks in prey body masses also have been observed at individual sites (e.g., Radloff and du Toit 2004).

The preferred body mass of prey in Mala Mala Game Reserve near Kruger (29.8 kg—Radloff and du Toit 2004) was similar to the lower maxima found here. The predator to prey body mass ratio there was 1:1.2 (Radloff and du Toit 2004), which is lower than that we determined for wild dog predation overall (1.41–7.76). In Selous, the range of prey body masses taken by wild dogs was 0.5–208 kg with a mean of 48.5 kg (Creel and Creel 1995), which corresponds closely to the mean of preferred prey species calculated in this study (50.8 kg). Despite the richness of prey species recorded (see "Introduction") and encompassed by this range, the African wild dog only preferentially preys upon 4 species.

Impala are 1 of the few prey species within the wild dog's preferred weight range in Selous and hunting behavior illustrates their preferential status. Although opportunistic predation on other species occurs, impala are most frequently hunted (40% of all hunts), are most frequently killed (54% of all kills), and are hunted with most success (64%—Creel and Creel 1995). The decline in wild dog numbers in Kruger in the 1960s has been suggested as leading to a population explosion of impala (Estes and Goddard 1967) that still has not been redressed. Impala and greater kudu were commonly taken by wild dogs in Letaba Ranch, near Kruger (Cronje et al. 2002). Impala also comprised 88% of wild dog kills in Klaserie Private Nature Reserve, also adjoining Kruger (Kruger 1988).

Evidence supports the preference wild dogs have for other prey also. In Hluhluwe, bushbuck occur closer to roads than other prey species and, because wild dogs forage along these roads, they capture them more frequently than expected based on their profitability (Krüger 1996).

Although the spectrum of prey taken by wild dogs is considered similar to that of the other potentially competing, sympatric predators (Creel and Creel 1996), wild dogs are the only predator that significantly prefer greater kudu (Hayward 2006; Hayward and Kerley 2005; Hayward et al. 2006a, 2006b). However, wild dogs do compete in preference with leopard (*Panthera pardus*) for bushbuck (Hayward et al. 2006), with cheetah (*Acinonyx jubatus*) for Thomson's gazelle (Hayward et al., in press), and with both for impala. Wild dogs are not thought to be limited by food availability (Ginsberg et al. 1995; Mills and Biggs 1993), but whether this partitioning of preferred prey species among Africa's large predators is sufficient to avert competition affecting wild dogs seems unlikely given their inherent rareness (Creel et al. 2004), susceptibility to kleptoparasitism (Gorman et al. 1998), and direct predation by larger competitors (Ginsberg et al. 1995).

Species outside the preferred prey weight range of African wild dogs were hunted but not killed in Selous (Creel and Creel 1995). Common duikers are at the lower end of this range (Fig. 4). In Kruger, flight of common duiker and steenbok frequently failed to elicit chases from wild dogs (Reich 1981). Similarly, the effort expended in chasing suboptimal prey in Kruger is minimal compared to larger prey (longest chase of common duiker = 120 m cf. 1,500 m for zebra—Reich 1981). Notwithstanding this, larger species are taken and some packs appear to preferentially prey on these (e.g., zebra by the Ghengis pack in the Serengeti—Malcolm and van Lawick 1975).

Cheetah, southern and mountain reedbuck, and springbok are all within the preferred weight ranges of wild dog prey but are not significantly preferred. For cheetah, this is probably because of its predatory nature and rarity. Springbok probably occur in habitats too arid for wild dogs to consistently prey upon them and they, in addition to the 2 reedbucks, probably occur at a density too low to be preferentially preyed upon in favor of more abundant prey (Table 3).

Models of prey selection based solely on hunting energetics failed to fully describe the observed patterns of prey selection of wild dogs in Selous because they took no account of injury risk (Creel and Creel 2002). We found that wild dogs significantly preferred prey offering minimal injury risk, which validates this concern and highlights conclusions that the costs of hunting also must be considered when assessing the benefits of cooperative hunting (Creel 1997, 2001a) and optimal foraging. The potential risk of injury may further explain the cooperative hunting behavior of wild dogs (Creel and Creel 2002) despite their being capable of capturing all but the largest prey species (Courchamp et al. 2002).

A great deal of important conservation-related research on African wild dogs has focused on what places populations at risk; namely persecution, competition, and disease (Carbone et al. 1997; Courchamp et al. 2002; Creel 2001b; Creel and Creel 1996; Gorman et al. 1998; Mills and Gorman 1997; Woodroffe and Ginsberg 1999). Adequate densities of prey within the preferred weight range (especially Thomson's gazelle, greater kudu, impala, and bushbuck) also are important to conserve wild dog populations.

The distributions of the 2 tragelaphids and impala reflect that of the African wild dog. These prey species are also savanna–woodland browsers (Anderson 1997; Owen-Smith 1997). Given this tight association, it seems likely that these species coevolved together and savanna–woodlands are the preferred habitat of African wild dogs.

Manipulation of the abundance of the wild dog's preferred prey species at the expense of the preferred prey of dominant competitors may be a method of managing predators to maximize the likelihood of wild dog conservation. A natural experiment occurred with the decline of the Serengeti Thomson's gazelle population during the 1970s and 1980s through competition with the expanding blue wildebeest population (Borner et al. 1987; Ottichilo et al. 2000). The Serengeti cheetah population declined simultaneously (Kelly et al. 1998) and this was linked to the decline in prey base (Hayward et al. 2006b). The Serengeti wild dog population also went extinct then but causes other than dietary competition were attributed (disease, handling stress, etc.—Woodroffe and Ginsberg 1999). These latter threatening processes are among the small-population factors of Caughley's (1994) dichotomy that may ultimately drive a population extinct, but only after factors of his declining-population paradigm, such as a reduced prey base, have initiated a population decline. Given that Thomson's gazelle were the only preferred prey species of the wild dog in the Serengeti, a decline in prey base is likely to have initiated a decline in wild dogs before small-population factors ultimately drove the population extinct.

Prey abundance is known to influence carnivore demography (Fuller and Sievert 2001); however, with the more detailed understanding of preferred prey presented here, our power to predict carrying capacity, minimum viable population sizes, and area requirements is likely to increase. The methods used here are applicable to all well-studied, large predators.

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