J. Zool., Lond. (2005) **266**, 153–161 © 2005 The Zoological Society of London Printed in the United Kingdom doi:10.1017/S0952836905006710

Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism

C. Carbone[1]*, L. Frame[2], G. Frame[3], J. Malcolm[4], J. Fanshawe[5], C. FitzGibbon[6], G. Schaller[7], I. J. Gordon[8], J. M. Rowcliffe[1] and J. T. Du Toit[9]

[1] Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, U.K.
[2] P.O. Box 822, Cape May Court House, NJ 08210, U.S.A.
[3] Gateway National Recreational Area, 210 New York Avenue, Staten Island, NY 10305, U.S.A.
[4] Department of Biology, University of Redlands, P.O. Box 3080, Redlands, CA 92373-0999, U.S.A.
[5] Birdlife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, U.K.
[6] Rural Planning Services (RPS) Ltd, Willow Mere House, Compass Point Business Park, Stocks Bridge Way, St Ives, Cambridgeshire PE27 5JL, U.K.
[7] Wildlife Conservation Society, New York Zoological Society, Bronx Park, New York, NY 10460, U.S.A.
[8] Rangelands and Savannas Program, Sustainable Ecosystems, CSIRO – Davies Laboratory, PMB P.O., Aitkenvale, Queensland 4814, Australia
[9] Mammal Research Institute, Department of Zoology and Entomology,University of Pretoria, Pretoria 0002, South Africa

(Accepted 14 October 2004)

Abstract

Longer-term ecosystem level dynamics are often neglected in conservation studies involving single species. In this study, a retrospective analysis is presented on the feeding performance of African wild dogs *Lycaon pictus* in the Serengeti in relation to a competing species, the spotted hyena *Crocuta crocuta*, to test whether hyenas had an effect on feeding performance of wild dogs in this ecosystem. Our analysis is based on observations of over 700 wild dog kills recorded over a 20-year period (from 1964 to 1987) during which time there was a decline in wild dog numbers (ending with their local extinction in 1991) and a twofold increase in hyena density. Overall, the amount of time that dogs had access to the kill (access time) decreased with increasing numbers of hyenas attending kills, but access time increased with increasing hunting-group size of dogs and carcass mass. In addition, in the 1980s, dogs spent longer at kills than in the 1970s for a given set of conditions, including when hyenas were absent. Our analysis demonstrates a greater potential for group benefits than was found in a previous study (Carbone, Du Toit *et al*., 1997). Hunting-group sizes of between two and six dogs performed best when hyenas attended dog kills because the benefits of increased defence outweighed the costs of having to share the carcass with more dogs. Hunting-group sizes of wild dog and levels of hyena attendance at the kill broadly paralleled the population trends in these species, with hunting-group sizes of wild dog declining, followed by hyena attendance increasing. Despite the combined effects of increased hyena attendance and reduced hunting-group size, dogs in the 1980s typically spent longer feeding and consumed more of the carcass including the poorest sections. This suggests that dogs in the 1980s may have been under greater energetic stress.

Key words: hunting-group size, wild dog, *Lycaon pictus*, kleptoparasitism, hyena, interspecific competition

INTRODUCTION

There has been considerable interest in the influence of competition and predation among carnivores and the role this plays in the conservation of endangered carnivore species (Laurenson, 1994; Mills & Gorman, 1997; Palomares & Caro, 1999; Caro & Stoner, 2003). For subordinate species within carnivore guilds, these interactions may have a substantial impact on population demography. The local extinction of the African wild dog *Lycaon pictus* (Temminck) population in the Serengeti National Park, which occurred at the same time as a doubling of the density of a competing species, the spotted hyena *Crocuta crocuta* (Exleben) (Burrows, Hofer & East, 1995; Hofer & East, 1995), represents a potentially important example of this phenomenon. On the Serengeti plains, Tanzania, wild dogs declined from over 100 individuals in the 1960s to *c*. 40 in the 1970s (Burrows *et al*., 1994). A further decline occurred in the 1980s before their local extinction in the early 1990s (Burrows *et al*., 1994, 1995; Ginsberg, Mace & Albon, 1995).

Wild dogs are the smallest of the large vertebrate prey specialists among African carnivores (Carbone, Mace

*All correspondence to: C. Carbone.
E-mail: chris.carbone@ioz.ac.uk

et al., 1999; Carbone & Gittleman, 2002; Creel & Creel, 2002). Their size makes them particularly vulnerable to competition with larger members of the carnivore guild, especially spotted hyenas and lions *Panthera leo* (L.) and they have been found to avoid areas with high densities of large predators (Fanshawe & Fitzgibbon, 1993; Mills & Gorman, 1997). Wild dogs typically hunt in groups of between four and 10 (Schaller, 1972; Eaton, 1979; Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1995), although total pack sizes may be larger (Frame *et al*., 1979; Malcolm, 1979). Sociality in wild dogs may improve hunting success (van Orsdal, 1984; Scheel & Packer, 1991; Creel & Creel, 1995; Creel, 1997), ability to defend kills (Fanshawe & Fitzgibbon, 1993) and breeding success (Courchamp, Rasmussen & Macdonald, 2002; Malcolm & Marten, 1982), and this has led to the species being described as an obligate cooperator (Courchamp, Clutton-Brock & Grenfell, 1999; Courchamp, Grenfell & Clutton-Brock, 1999; Courchamp & Macdonald, 2001; Stephens, Sutherland & Freckleton, 1999).

Fanshawe & Fitzgibbon (1993) found that hyenas attended 85% of Serengeti wild dog kills in the 1980s. Under such circumstances, the potential impact of kleptoparasitism could be severe, however, this was never quantified. Carbone, Du Toit & Gordon (1997) developed a simple foraging model to assess the effects of kleptoparasitism on food intake by dogs and the benefits of group defence of kills. They predicted that while kleptoparasitism reduced feeding performance of wild dogs, the overall benefits of group defence did not outweigh the costs of sharing the carcass with more individuals. Thus, group defence of kills on its own was not believed to be a driving force for the evolution of sociality in this species. This work was recently criticized by Creel & Creel (2002) who argued that there may be net benefits to group defence, and that the approach of Carbone, Du Toit *et al*. (1997) may have been limited by a lack of data to properly parameterize the model. In this paper, interactions between wild dogs and spotted hyenas are re-examined using a long-term dataset spanning over 20 years in the Serengeti, based on over 700 wild dog kills (Kruuk, 1972; Schaller, 1972; Frame *et al*., 1979; Malcolm, 1979; Fanshawe & Fitzgibbon, 1993). These data were used to evaluate our previous model and to retrospectively assess changes in wild dog feeding performance associated with the population level decline in dog numbers and the co-occurring increase in the hyena numbers in the region.

METHODS

Database

Data were obtained from focal observations of wild dog kills from 5 studies in the Serengeti (Kruuk, 1972; Schaller, 1972; Frame *et al*., 1979; Malcolm, 1979; Fanshawe & Fitzgibbon, 1993) (summarized in Table 1). All records comprise the numbers of dogs present at the kill, the prey species and age class (used to estimate carcass weight: Schaller 1972; L. H. Frame, G. W. Frame & J. R. Malcolm, pers. obs.) and the number of hyenas attending the kill. In addition, data on access time (time from the first to last dog eating, Fanshawe & FitzGibbon, 1993; Carbone, Du Toit *et al*., 1997) were recorded for most of the data obtained from the 1970s and part of the data from the 1960s and 1980s. Data on the time individual wild dogs spent eating and the amount of carcass consumed were obtained predominantly from the 1970s (L. H. Frame, G. W. Frame & J. R. Malcolm, pers. obs.).

Table 1. Contents of the datasets. Authors and period of the studies were as follows: G. Schaller (1966–67) and H. Kruuk (1964–68); L. Frame, G. Frame & J. Malcolm (1975–78); J. Fanshawe & C. FitzGibbon (1986–89). +, Data available

Data types	Schaller & Kruuk	Frame, Frame & Malcolm	Fanshawe & FitzGibbon
Total no. of kills	156	399	158
Prey type	+	+	+
No. of dogs	+	+	+
No. of hyenas	+	+	+ (62 kills)
Time at kill	+ (38 kills)	+ (Total time and some records of individuals)	+ (62 kills)
Amount eaten	(Few records)	+	

Hyena attendance

Data on hyena attendance at dog kills were used to determine whether the frequency of hyena attendance increased in association with the recorded population increase in spotted hyenas over the period from the 1960s to the 1990s (Burrows *et al*., 1995). There were, however, differences in the local densities of hyenas during different studies in the 1960s; Kruuk (1972) found a higher frequency of hyena attendance at wild dog kills than Schaller (1972). This difference may have resulted from the fact that Kruuk's work focused on spotted hyenas, whereas Schaller's research concentrated on lions. In order to focus on long-term trends during the study, data were grouped according to the 3 periods (described as 1960s, 1970s and 1980s; Table 1) to focus on the long-term trends during the study.

Estimate of wild dog intake rate

Estimates of the amount of the carcass consumed by the dogs was obtained for 289 records (L. H. Frame, G. W. Frame & J. R. Malcolm, pers. obs.) (Table 1). The amount (kg) consumed was estimated by dividing the carcass into 9 sections assuming the following proportions of the total mass: hindlimbs (0.167), pelvis-lumbar region (0.073), forelimbs (0.081), viscera (0.106), ribcage (0.116), neck (0.04), head (0.014), skin (0.066) and bones (0.248) based on (Blumenschine & Caro, 1986). The proportion of each section consumed by the dogs was calculated for each kill record and multiplied by the proportion that that section contributed to the total carcass mass to estimate

Table 2. Definition of prey weight classes in Figs 3(a) & 4(a). Descriptions are given of the most common prey type, but the percentages include other species/age classes within the weight range. Weight estimates were obtained from Schaller (1972), Fanshawe & FitzGibbon (1993) and L. H. Frame, G. W. Frame & J. R. Malcolm (pers. obs.)

Weight class	Description	Percentage of total no. of prey captured	Mean estimated weight (kg)	Weight range (kg)
Small	Gazelle young	20.9	5.8	1–14
Medium	Adult gazelles and juvenile wildebeest	61.3	26.7	15–49
Large	Yearling wildebeest	9.5	63.8	50–99
Very large	Adult wildebeest and zebra	8.2	141.5	100–205

the total amount in kg consumed. The energetic value of the carcass was estimated by multiplying each section of the carcass by the corresponding estimated energy value (e.g. 6080 kJ/kg viscera and skin, 1130 kJ/kg for meat, and no value for bones; Creel & Creel, 2002). The energetic value obtained per dog per kill was calculated by dividing the total energy value of the consumed portion of the carcass (kJ) by the number of dogs eating. When estimating the energetic values of portions consumed, the total portion of edible mass on the carcass was taken into account (following Carbone, Du Toit *et al*., 1997; L. H. Frame, G. W. Frame & J. R. Malcolm, pers. obs.). The edible mass was calculated as the percentage of the total carcass mass of the prey as follows: for prey up to 10 kg, 91%; 10–14 kg, 89%; 14–20 kg, 82%; for 20+ kg, 65%. To establish estimates of broad patterns in feeding performance in relation to prey weight, individual prey weights were categorized into four weight classes (Table 2).

Foraging function

The data on the energy value of the carcass eaten (measured as kJ/dog/kill) and total time eating (access time, see below) was then used to parameterize a foraging intake function in order to make general predictions about the amount of meat that could be consumed for different hunting-group sizes, carcass masses and access times. In the foraging function, intake g (kJ of carcass/dog/kill) is defined using the following formula:

$$g = (k/N)\left(1 - e^{-\alpha(N/k)t}\right),$$

N is the number of dogs, k is the maximum kJ available on the carcass and t is access time (min) of the hunting group. The scaling factor α affects the rate at which intake g approaches the maximum share of the kill (k/N). In this function α also represents the maximum intake rate (kJ/min) (when $t = 0$). α was estimated using a function fitting program (using the Gauss–Newton algorithm) in which α was varied to produce the best fit between observed intake/dog/kill and the predicted intake. Here the exponent term (N/k) has been added to the original formula used by Carbone, Du Toit *et al*. (1997) to allow for the more realistic assumption that the rate of depletion increases with an increase in the number of dogs feeding.

The pattern in carcass depletion is also examined using a subset of the data (74 kills) with hunting groups of 3–5 dogs and carcasses offering 4–6 kg/dog.

Access time

A generalized linear model (GLM) with normal errors and identity link function was used to test the influence of the number of hyenas present, dog group size and the weight of meat available per dog, on access time. Data from approximately 350 records obtained in the 1970s and 1980s were used in this analysis (Table 1). All data (dependent and independent) had non-normal distributions and were $\log_{10}(x+1)$-transformed before analysis.

Bootstrapping analysis

A bootstrapping analysis was conducted to provide estimates of the feeding performance of wild dogs under a range of conditions broadly reflecting the conditions observed over the 20-year study period, and also to predict feeding performance in the 1980s for which feeding time, but not intake, was obtained. Food intake (kJ/dog/kill) was estimated from access time (using the GLM analysis described above) and the parameterized foraging function (see above). Values of hunting-group size, prey weight and levels of hyena attendance used to predict access times were obtained by randomly selecting with replacement from the frequency distributions observed in the dataset.

In this analysis, single dogs were restricted to prey of 25 kg or less, while pairs were restricted to prey with a maximum weight of 40 kg (based on previous results in Fanshawe & FitzGibbon 1993; Carbone, Du Toit *et al*., 1997). Intake per dog was set at a maximum of 11 kg/dog/kill or 110 800 kJ/dog/kill (accounting for viscera and meat eaten and amounts and energy values from Creel & Creel, 1995, 2002; L. H. Frame, G. W. Frame & J. R. Malcolm, pers. obs.).

The bootstrapping calculations were based on 1000 hunts for each hunting-group size (1–10 dogs) representing typical hunting-group sizes for dogs in the Serengeti (Kruuk, 1972; Schaller, 1972; Frame *et al*., 1979; Fanshawe & FitzGibbon, 1993).

The bootstrapping analysis used a prey frequency distribution based on 25 weight classes (ranging from 1 to 205 kg). Species and age classes of prey selected by the dogs varied little over the 20-year study period (see below), and so all prey data were combined to establish the prey distributions used for the bootstrapping analysis. Because Fanshawe & Fitzgibbon (1993) did not find a relationship between hyena attendance and prey weight, these variables were selected independently of each other in the bootstrapping analysis.

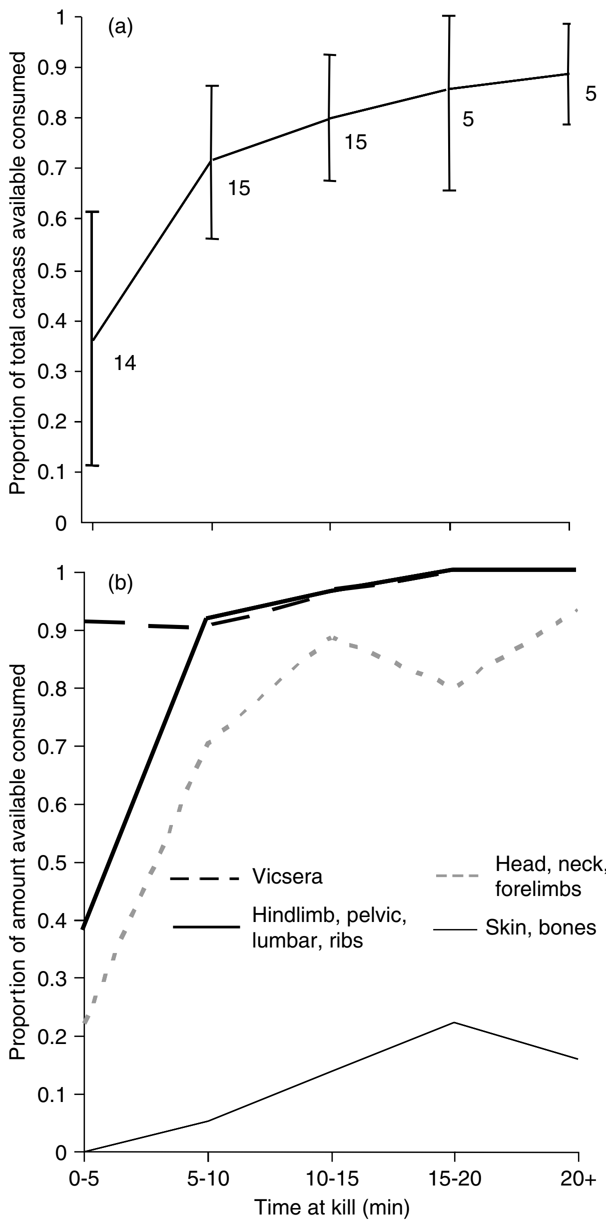

Fig. 1. The observed proportion of the carcass consumed against consumption time at kill (data grouped into 5-min intervals) for pack sizes of three to five wild dogs *Lycaon pictus*, with carcasses offering 4–6 kg/dog (corresponding to a prey mass range of 12–30 kg). (a) Total proportion of available carcass by weight. Numbers are sample sizes. Error bars, 1 ± SD. Typically, dogs in the 1970s spent between 5 and 15 min feeding on a kill. (b) Data separated into different sections of the carcass.

RESULTS

Wild dog energy intake

Our foraging function was fitted to 289 records of dog kills to calculate the one unknown parameter, the scaling constant α, which reflects the maximum intake rate (kJ/min). This analysis estimated $\alpha = 6808$ (SE = 289; $r^2 = 0.67$) which corresponds to a maximum intake rate for dogs of 6808 kJ/min. This function along with the estimate of α was used to predict energy intake (kJ/dog/kill) under varying wild dog group sizes and prey weights in relation to time feeding (access time) (see below).

Table 3. Parameter values and significance for a general linear model relating access time (min) to study where data were obtained from various sources (Fa&Fi, Fanshawe & FitzGibbon; Fr&Fr, Frame & Frame; Malc, Malcolm; see also Table 1). Hyena, number of hyenas *Crocuta crocuta* present at dog kills; dog, number of wild dogs *Lycaon pictus* present at the kill; meat, total amount of meat available per dog (kg/dog). All variables were $\log_{10}(x+1)$-transformed before analysis

Parameter		Estimate	χ^2	d.f.	P
Study	Fa&Fi	1.609	53.08	2	< 0.001
	Fr&Fr	1.006			
	Malc	0.967			
Hyena × study	Fa&Fi	– 1.284	6.57	2	< 0.05
	Fr&Fr	– 0.914			
	Malc	– 0.910			
Dogs		– 0.095	0.16	1	NS
Meat		– 0.349	2.38	1	NS
Dog × hyenas		0.865	7.37	1	< 0.01
Dogs × meat		0.936	10.17	1	< 0.005

The pattern in carcass depletion was examined by estimating the proportion of the carcass consumed across 5-min intervals (Fig. 1). There was a clear pattern in carcass depletion with typically 80% of the carcass being consumed within 10–15 min after the animal was killed (Fig. 1b). Edible portions of the viscera and meat were usually consumed first with skin and bone only being partially consumed after 15 min (Fig. 1b).

Access time

Time spent feeding at the carcass (access time) was negatively influenced by hyenas, although the strength of this response also varied between studies (significant study × hyenas term) (Table 3; Fig. 2). In general, dogs spent longer at kills in the 1980s (Fanshawe and FitzGibbon, 1993), but the difference between studies decreased when several hyenas were present. As a result of this effect, for future analyses, 1970s access times were defined as ‘short’ and 1980s access times as ‘long’. The effect of hyenas on access time was also dependent on the number of dogs in the group (significant number of dogs present × number of hyenas present term), reflecting a more severe effect on smaller groups. Finally, large groups of dogs tended to spend longer at kills when more meat was available per dog (significant number of dogs present × meat availability per dog term).

Prey weights

Wild dogs most commonly killed adult Thomsons gazelles *Gazella thomsoni* (34%), Thomsons gazelle young (21%) and wildebeest *Connochaetes taurinus* juveniles (27%) (summarized in Table 2). Overall, prey selection by wild

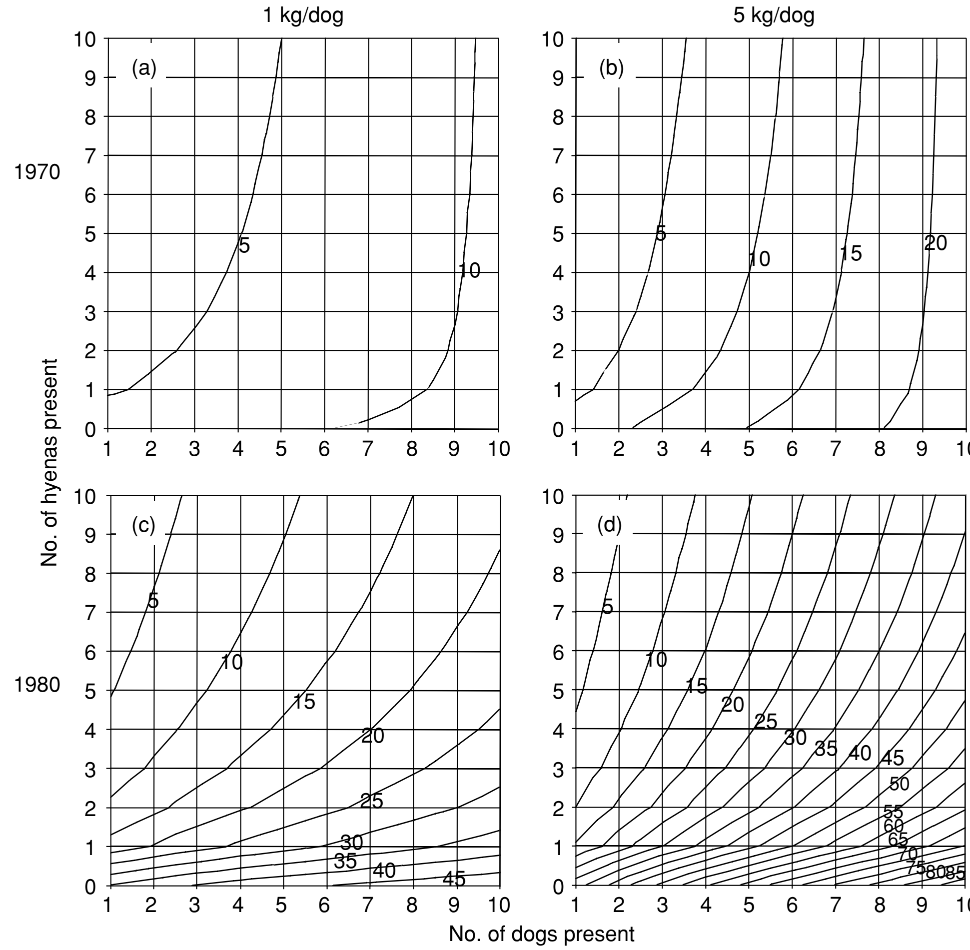

Fig. 2. Predicted response of access time at the kill (min, given on plot lines) in relation to study period (a, b, 1970s; c, d, 1980s), the amount of meat available per dog *Lycaon pictus* (a, c, 1 kg; b, d, 5 kg), the number of hyenas *Crocuta crocuta* present, and group size of dogs. Predicted values are derived from the statistical model given in Table 3.

dogs was consistent across the study period and there was no change in the proportion of these four prey weight classes selected across periods (Kruskal–Wallis $\chi^2 = 3.0348$, d.f. = 2, $P = 0.2193$; Fig. 3a).

Hyena attendance

During the 1960s and 1970s, hyenas were absent from most wild dog kills (55–60% of kills) (Fig. 3b). In the 1980s, 85% of kills had one or more hyenas attending the kills while 65% had two or more hyenas present. The levels of hyena attendance between the 1960s and 1970s were not different, but these periods did differ from the 1980s (Kruskal–Wallis $\chi^2 = 43.4$, d.f. = 2, $P < 0.0001$; Fig. 3b).

Hunting group size

In the 1960s, the most common hunting-group size was 12 or more dogs (representing > 35% of kills) (Fig. 3c). In the 1970s and 1980s this pattern changed dramatically and the most common group size was four, and in the 1980s singletons represented 15% of hunts (Fanshawe & FitzGibbon, 1993). Thus hunting-group sizes declined significantly after the 1960s, but did not vary significantly between the 1970s and 1980s (Kruskal–Wallis $\chi^2 = 223.3$, d.f. = 2, $P < 0.0001$). The main decline in the group size of wild dogs occurred before the increase in hyena attendance suggesting hyena attendance was not the original cause for the decline in dog group size.

Bootstrapping analysis and feeding performance

Our bootstrapping procedure used analyses of access time and energy intake rates to approximate feeding performance (energy intake, kJ/dog/kill) under a range of hunting-group sizes, prey weights and levels of hyena attendance. In Fig. 4(a) the following scenarios are examined according to the prey weight classes in Table 2: (a) all edible portions of the carcass consumed (e.g. as in the 1980s with no hyenas present); (b) with short access times (as in the 1970s) with lower hyena attendance as in the 1960s to 1970s; (c) with short access times and higher hyena attendance as in the 1980s. In Fig. 4(b), the average performance is approximated based on conditions found in

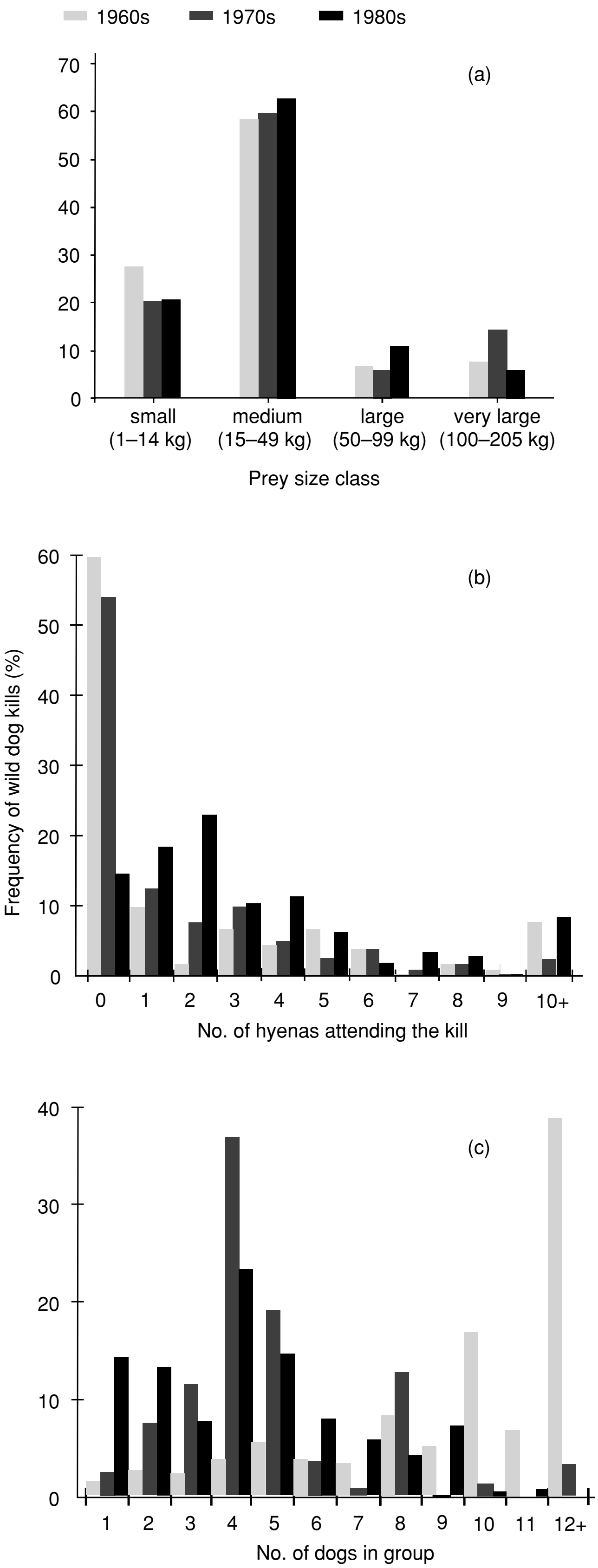

Fig. 3. The frequencies (%) of hunts by African wild dogs *Lycaon pictus* for different periods (see Table 1) according to: (a) prey weights taken; (b) number of hyenas attending dog kills; (c) number of dogs in the hunting group.

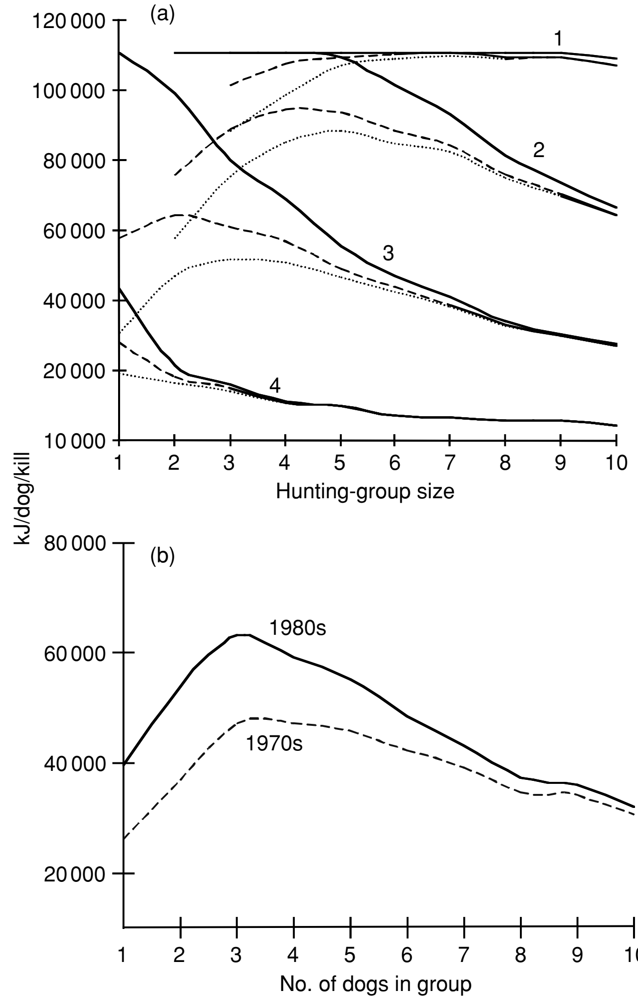

Fig. 4. Predicted mean intake (kJ/dog/kill) for different hunting-group sizes of wild dogs *Lycaon pictus* based on a bootstrapping analysis of observed frequencies conditions at the kill (see text for details). The results were analysed according to: (a) four prey weight classes (very large (1), large (2), medium (3) and small (4) (for definition of weight classes see Table 2)) with complete consumption (fine dashed lines), with short access times (as in the 1970s), and lower levels of hyena attendance (as in the 1970s) (course dashed lines), with short access times and higher hyena attendance (solid line); (b) two time periods: 1970s (short access times and lower hyena attendance, fine dashed line), 1980s (long access times and higher hyena attendance, solid line).

the 1970s and 1980s (e.g. long access times, but higher hyena attendance in the 1980s).

Individual dogs achieved the highest intake, on a per kill basis, when all edible portions were completely consumed. Group sizes of 2–6 dogs performed best with low and high levels of hyena attendance and when feeding on medium to very large prey. The best performing group size increased with increasing prey weight and to some extent with increased levels of hyena attendance. Overall, dogs in the 1980s, with groups sizes of between 1 and 6, consumed *c*. 23% more than dogs in the 1970s.

DISCUSSION

In this paper records of over 700 wild dog kills in the Serengeti were used to examine changes in the feeding performance of wild dogs in relation to differences in dog numbers, prey weight and different levels of hyena attendance at the kill.

Food intake and access time

Our analysis of wild dog food intake is based on using 289 records of wild dog kills to parameterise a foraging function (revised from Carbone, Du Toit *et al*., 1997). The model provided a good fit to the data, explaining 67% of the variance. This fit is impressive given the wide range of dog group sizes and carcass weights used in the analysis and highlights the potential value of using foraging theory to understand carnivore feeding ecology. Our foraging function analysis was used to derive a maximum consumption rate of 6808 kJ/dog/min (corresponding to *c*. 0.5 kg/dog/min) from data for which the number of dogs attending the kill and the amount of the carcass consumed at the point of leaving was known. This result, however, is not very different from recent direct estimates of a maximum consumption rate of 0.8 kg/dog/min for dogs in Zimbabwe (Pole, 2000). Therefore, we assume our estimates of wild dog intake are similar for other periods in the Serengeti and for other areas in Africa.

Three hundred and fifty kill records were also analysed to estimate access time in relation to the number of dogs and hyenas present, carcass mass, and study period (e.g. 1970s *vs* 1980s). Fanshawe & FitzGibbon (1993) found that access time for wild dogs varied with the ratio of dogs to hyenas, decreasing with an increase in the relative number of hyenas. In addition to hyena attendance, access time was found to increase with both dog numbers and carcass mass. Also, importantly, dogs in the 1980s spent far longer feeding at the kill than dogs in the 1970s for a given set of conditions. This latter finding was surprising, but may in part reflect the fact that most kills (85%) had at least one hyena in attendance. Leaving a carcass early would not have been a good strategy to avoid hyenas because of the high likelihood that they would be present at the next kill. In addition, in the 1980s, dogs typically spent longer at the carcass even in the absence of hyenas and it is estimated that they consumed virtually all edible portions of the carcass during most kills.

Prey weight, hyena attendance and dog group size

Despite the differences in hunting-group size during the study, patterns in the prey weights killed varied little. The most common prey weight range was between 15 and 49 kg, representing 61% of the total prey killed. This was largely made up of adult gazelle and juvenile wildebeest.

Hyena attendance was similar in the 1960s and 1970s but increased substantially in the 1980s. During this latter period, over 80% of kills had one or more hyenas present. Trends in the hunting-group size of dogs showed the reverse pattern. In the 1960s, dog groups typically contained 12 or more individuals (Schaller, 1972; Kruuk, 1972). Group sizes declined to 4–8 in the 1970s and 1–5 in the 1980s (Fig. 3). The patterns in the numbers of dogs in hunting groups and the numbers of hyenas attending kills of wild dogs, therefore, broadly parallels patterns in the population sizes of both species during the study. This provides a rare example of population level processes influencing behavioural interactions between two competing carnivore species. The increase in hyena attendance, however, occurred after the hunting-group size of dogs declined, suggesting that other mechanisms were involved in the population decline of wild dogs.

Feeding performance of wild dogs

While there are no records of energy intake (kJ/dog/kill) from dogs during the 1960s and 1980s, it was possible to use our analyses of foraging and access time to approximate performance across the entire range of feeding conditions including those during the 1980s. Examining feeding performance in relation to group size and hyena attendance, singletons have the highest intake when all of the available portions of the carcass were consumed (Fig. 4). When hyenas are competing for the kill, for all but the smallest prey, group sizes of 2–6 dogs performed best. Intermediate group sizes performed best because, under these conditions, the benefits of carcass defence outweighed the costs of having to share the carcass with more dogs. These findings provide compelling evidence that group defence of food represents an important force for sociality, even in the absence of other potential advantages such as improved hunting success and cooperative rearing of pups. Carbone, Du Toit *et al*. (1997) predicted that intermediate-sized groups may benefit by being efficient at hunting a wider range of prey, however, they did not predict any net benefit to group defence of kills. In this study, it was possible to use the extensive dataset to parameterize and refine the models and make more accurate predictions of the effects of increasing group size on wild dog intake.

Our analysis was used to predict average performance during the 1970s and during 1980s when levels of hyena attendance were higher. Despite the higher levels of hyena attendance, dogs in the 1980s remained longer at the kill and had a higher level of food intake per kill. This would have resulted, however, in the dogs consuming a higher proportion of bone and sinew, and given that this occurred even in the absence of hyenas, suggests that dogs in the 1980s were energetically stressed.

Carcass depletion and kleptoparasitism

There was a clear indication of a slowing down in intake rate as the total carcass mass becomes consumed with time spent feeding (Fig. 1). Marginal value theorum (Charnov, 1976) predicts that animals trade-off declining energetic intake from a resource patch against the time spent finding a new patch. Given that wild dog kills represent resources patches, dogs in the 1980s might be expected to feed longer on kills if they have a lower expectation of success during the next hunt (e.g. if the likelihood of hyena attendance is high or if the time between kills was greater).

Typically around two-thirds of the best sections of the carcass were consumed in the first 10–15 min after capture. This suggests that kleptoparasitism will only affect the feeding performance of wild dogs when hyenas quickly find and take-over dog kills. This is unlikely to happen unless hunting-group sizes are small and hyena densities are high. Such conditions were found in the Serengeti in the late 1980s (Fanshawe & FitzGibbon, 1993). Under such circumstances, kleptoparasitism may have a severe impact on the survival of wild dogs. Gorman *et al*. (1998) argued that given the extremely high levels of energy expenditure of wild dogs, a loss of 25% of food intake owing to kleptoparasitism would be unsustainable in the long term.

Our retrospective analysis of the Serengeti data endorses the view that conserving rare African carnivores (e.g. wild dogs and cheetahs *Acinonyx jubatus*) requires an understanding of population changes among more dominant members of the carnivore guild (i.e. hyenas and lions). It was found that associated with a decline in the numbers of dogs and the increase in the numbers of hyenas, there was a decline in the hunting-group size of wild dogs and an increase in the levels of hyena attendance at dog kills. Strong evidence was found that hyena attendance at kills reduced the time that dogs had access to their kills, particularly when the hunting-group sizes of dogs were small. In the 1980s, however, when dogs were faced with lower kill rates, they showed greater resistance to hyena takeovers, probably owing to increased energetic stress. Our results support the notion that for large groups of wild dogs, kleptoparasitism from spotted hyena would not have a substantial affect on feeding performance. However, kleptoparasitism could have a substantial impact on declining populations with small group sizes of wild dogs, as was the case in the early 1990s in the Serengeti.

Acknowledgements

We thank Charlotte Watts for her advice on formulating the foraging function and Josh Ginsberg for helpful discussions. We especially thank Hans Kruuk for providing us with original data, Valerie Olson for her helpful comments on a previous version of the manuscript. IJG was supported by the Scottish Executive Environment, and Rural Affairs Department.

REFERENCES

Blumenschine, R. J. & Caro, T. M. (1986). Unit flesh weights of some East African bovids. *Afr. J. Ecol*. **24**: 273–284.

Burrows, R., Hofer, H. & East, M. L. (1994). Demography, extinction and intervention in a small population: the case of the Serengeti wild dogs. *Proc. R. Soc. Lond. B Biol. Sci*. **256**: 281–292.

Burrows, R., Hofer, H. & East, M. L. (1995). Population-dynamics, intervention and survival in African wild dogs (*Lycaon pictus*). *Proc. R. Soc. Lond. B Biol. Sci*. **262**: 235–245.

Carbone, C., Du Toit, J. T. & Gordon, I. J. (1997). Feeding success in African wild dogs: Does kleptoparasitism by spotted hyenas influence hunting-group size? *J. Anim. Ecol*. **66**: 318–326.

Carbone, C. & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science* **295**: 2273–2276.

Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. (1999). Energetic constraints on the diet of terrestrial carnivores. *Nature (Lond.)* **402**: 286–288.

Caro, T. M. & Stoner, C. (2003). The potential for interspecific competition among African carnivores. *Biolo. Conserv*. **110**: 67–75.

Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theor. Popul. Biol*. **9**: 129–136.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**: 405–410.

Courchamp, F., Grenfell, B. & Clutton-Brock, T. (1999). Population dynamics of obligate cooperators. *Proc. R. Soc. Lond. B Biol. Sci*. **266**: 557–563.

Courchamp, F. & Macdonald, D. W. (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Anim. Conserv*. **4**: 169–174.

Courchamp, F., Rasmussen, G. S. A. & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol*. **13**: 20–27.

Creel, S. (1997). Cooperative hunting and group size: assumptions and currencies. *Anim. Behav*. **54**: 1319–1324.

Creel, S. & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav*. **50**: 1325–1339.

Creel, S. & Creel, N. M. (2002). *The African wild dog: behavior, ecology, and conservation*. Princeton, NJ: Princeton University Press.

Eaton, R. L. (1979). Interference competition among carnivores: a model for the evolution of social behavior. *Carnivore* **2**: 9–16.

Fanshawe, J. H. & Fitzgibbon, C. D. (1993). Factors influencing the hunting success of an African wild dog pack. *Anim. Behav*. **45**: 479–490.

Frame, L. H., Malcolm, J. R., Frame, G. W. & van Lawick, H. (1979). Social organisation of African wild dogs *Lycaon pictus* on the Serengeti plains, Tanzania 1967–78. *Z. Tierpsychol*. **50**: 225–249.

Ginsberg, J. R., Mace, G. M. & Albon, S. D. (1995). Local extinction in a small and declining population: wild dogs in the Serengeti. *Proc. R. Soc. Lond. B Biol. Sci*. **262**: 221–228.

Gorman, M. L., Mills, M. G., Raath, J. P. & Speakman, J. R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature (Lond.)* **391**: 479–481.

Hofer, H. & East, M. L. (1995). Population dynamics, population size, and the commuting system in Serengeti spotted hyaenas. In *Serengeti* **II**: *dynamics, management and conservation of an ecosystem*: 332–363. Arcese, A. R. E. S. P. (Ed.). Chicago: University of Chicago Press.

Kruuk, H. (1972). The spotted hyena. Chicago: University of Chicago Press.

Laurenson, M. K. (1994). High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal-care. *J. Zool. (Lond.)* **234**: 387–408.

Malcolm, J. R. (1979). *Social organisation and communal rearing in African wild dogs*. PhD thesis, Harvard University.

Malcolm, J. R. & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dog (*Lycaon pictus*). *Behav. Ecol. Sociobiol*. **10**: 1–13.

Mills, M. G. L. & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol*. **11**: 1397–1406.

Palomares, E. & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *Am. Nat*. **153**: 492–508.
Pole, A. (2000). *The behaviour and ecology of African wild dogs* (***Lycaon pictus***) *in an environment with reduced competitor density*. Ph D, University of Aberdeen, U. K.
Schaller, G. B. (1972). *The Serengeti lion: a study of predator–prey relations*. Chicago: University of Chicago Press.
Scheel, D. & Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. *Anim. Behav*. **41**: 697–709.
Stephens, P. A., Sutherland, W. J. & Freckleton, R. P. (1999). What is the Allee effect? *Oikos* **87**: 185–190.
van Orsdal, K. G. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *Afr. J. Ecol*. **22**: 79–99.