Communal hunting and pack size in African wild dogs, *Lycaon pictus*

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Abstract. African wild dogs are 20–25 kg social carnivores whose major prey are ungulates ranging from 15 to 200 kg. In the Selous Game Reserve, Tanzania, wild dog pack size ranged from three to 20 adults (3–44 including yearlings and pups). Data from 905 hunts and 404 kills showed that hunting success, prey mass and the probability of multiple kills increased with number of adults. Chase distance decreased with number of adults. None the less, the distribution of per capita food intake across adult pack size was U-shaped, with a minimum close to the modal pack size. A similar result has been used to conclude that cooperative hunting does not favour sociality in lions (Packer et al. 1990, *Am. Nat.*, **136**, 1–19), and to argue that cooperative hunting is not responsible for group living in any carnivore (Caro 1994, *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*). Daily per capita food intake only accounts for variation in the benefits to cooperative hunting, ignoring variation in costs. For Selous wild dogs, per capita food intake per km chased peaked close to the modal adult pack size (where per capita food intake per day was near its minimum). Thus, the energetics of cooperative hunting favour sociality in Selous wild dogs. Analyses that incorporate variation in both costs and benefits of hunting may show that cooperative hunting favours sociality in other species where its influence has previously been rejected.

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In this paper, we present data on prey selection, hunting success, hunting effort and food intake for African wild dogs in the Selous Game Reserve. We determine optimal hunting group size using the traditional evolutionary currency, daily per capita food intake. We then show that inclusion of hunting costs substantially affects predictions for optimal hunting group size. Wild dogs are well suited for a test of the effects of communal hunting on pack size (Packer & Ruttan 1988), because common prey are risky to attack (e.g. warthogs, *Phacochoerus aethiopicus*; Fig. 1) or large relative to the dogs (e.g. yearling wildebeest, *Connochaetes taurinus*, outweigh a wild dog by a ratio of 6:1; Fig. 1).
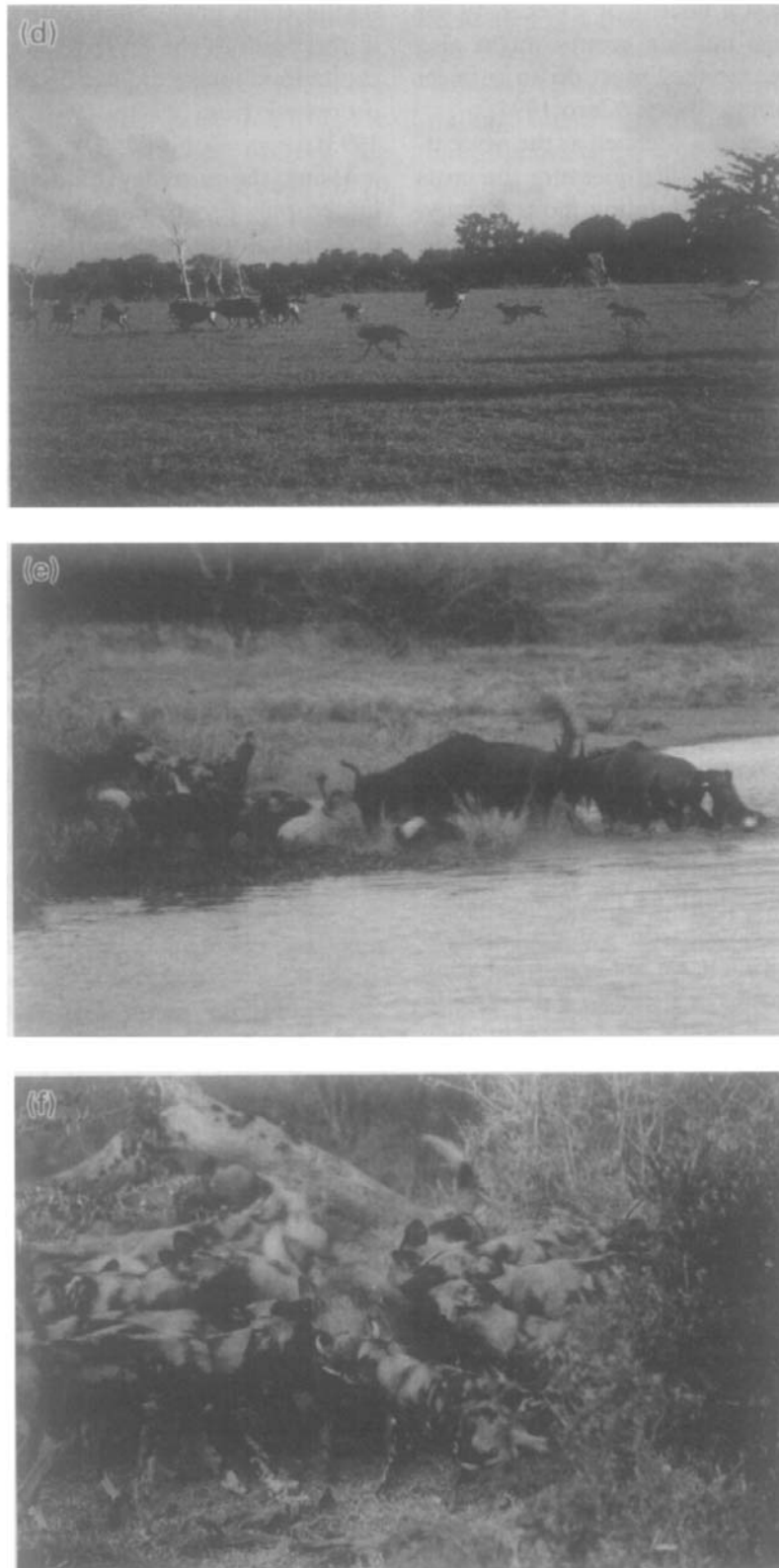
Communal hunting is one of the most conspicuous aspects of the behaviour of large social

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carnivores. Influential early studies of carnivore ecology suggested that communal hunting might favour sociality, either by increasing the size of prey that could be killed or by improving hunting success (Schaller 1972; Kruuk 1975). For example, Ngorongoro spotted hyaenas, *Crocuta crocuta*, typically hunted alone when pursuing Thomson's gazelles, *Gazella thomsoni*, but formed groups averaging 10·8 hyaenas when hunting zebras, *Equus burchelli* (Kruuk 1972). Wolves, *Canis lupus*, typically hunt Dall sheep, *Ovis dalli*, alone, but tackle moose, *Alces alces*, in groups (Murie 1944; Mech 1970). Associations between hunting group size and prey size are common among carnivores (Gittleman 1989), but are not universal. For example, lion, *Panthera leo*, hunting group size had no effect on species hunted or captured in Etosha National Park (Stander 1992a).

An association between hunting group size and prey size could result from a beneficial increase in the vulnerability of large prey to large hunting groups. An association between group size and prey size, however, does not clarify whether

Figure 1. (a-c)

Figure 1. (d-f)

Figure 1. Sequence of hunting behaviour in communal hunts by African wild dogs. (a) Group travels slowly in search of prey (compare gait with c). (b) Wildebeest herd in 'pinwheel' formation, attacked from several angles. (c) Gait in full speed chase at 60 km/h (compare with a). (d) Dogs follow several lines of pursuit: should the herd swing left, the wild dog in the foreground is positioned to intercept the wildebeest calf. (e) Several wild dogs distract an adult female wildebeest while another attacks her calf. (f) Large or well-armed prey such as warthogs can only be killed if the head is restrained.

hunting large prey is a benefit or a necessity for larger groups. Large hunting groups might also take large prey because they must do so to meet their needs, regardless of costs (Caro 1994).

Data on hunting success (defined as the percentage of hunts that end in kills) measure the costs and benefits of communal hunting more directly. Studies relating hunting success to group size have had variable results. Ngorongoro spotted hyaenas succeeded in 15% of solitary hunts of wildebeest calves, but in 74% of group hunts (Kruuk 1972). Serengeti lions hunting Thomson's gazelle succeeded in 15% of solitary hunts, but in 32% of communal hunts (Schaller 1972). In Etosha National Park, female lions' hunting success significantly increased across group sizes of one to seven, for each of the five most common prey (Stander & Albon 1993). Male Serengeti cheetahs showed no clear effects of group size on hunting success for large or small prey (Caro 1994). Kalahari spotted hyaenas showed no increase in hunting success across group sizes of one to seven when challenging gemsbok or wildebeest, which comprise 68% of their prey (Mills 1985, 1990).

Associations between group size and prey size or hunting success have been widely used to argue that communal hunting favours sociality, although these associations do not demonstrate that communal hunting has a net benefit. Sharing of prey in larger groups can lead to a decrease in daily per capita food intake even when hunting success or prey mass increases (Schaller 1972; Kruuk 1975; Packer et al. 1990; Caro 1994). The relationship between daily per capita food intake and group size has been measured for only three social carnivores. In Serengeti lions, foraging group sizes did not match those that maximized daily per capita food intake (Packer et al. 1990). In contrast, Etosha lions typically foraged in the group size that maximized food intake (Stander 1992a). For Serengeti cheetahs, changes in daily per capita food intake across group sizes were equivocal (Caro 1994). For one pack of Serengeti wild dogs, a meat-yield index was maximized at a group size of one for hunts of Thomson's gazelles (the most common prey), and at four for hunts of wildebeest (Fanshawe & Fitzgibbon 1993). (The meat yield index was calculated by dividing prey mass between those dogs who participated in a kill, although packmates often shared the meat, so it was not equivalent to daily per capita food

intake: Caro 1994.) For another pack of wild dogs in the north of the Serengeti ecosystem, daily per capita food intake did not decrease when pack size decreased from 29 to 19 (Fuller & Kat 1990, 1993).

Using the currency of daily per capita food intake, only Etosha lions have been shown to hunt preferentially in the predicted group size if communal hunting is the prime determinant of group size (Stander 1992a, b; Stander & Albon 1993). Although acknowledging that data are limited, recent summaries of communal hunting have argued that communal hunting has little power to explain grouping patterns in felids (Packer 1986; Packer et al. 1990; cf. Stander 1992a) and across social carnivores in general (Caro 1994).

The above discussion has addressed only the effects of group size on the payoff to hunting, however, disregarding costs. For example, if individuals in groups of all sizes hunted sufficiently often to meet their needs and no more, daily per capita food intake would not vary across group sizes. Groups of some sizes might work harder to attain this food intake, in terms of time or distance travelled, but this variation in hunting effort would not affect the results discussed above. Such results would be misleading.

METHODS

Study Area

The Selous Game Reserve occupies 43 000 km^2 in southern Tanzania. Our study area of 2600 km^2 in the northern sector of the reserve (7°35'S, 38°07'E) is a mosaic of miombo and chipya woodland (dominated by *Combretum, Brachystegia/ Julbernardia, Pteleopsis,* and *Terminalia sericea), Terminalia spinosa* woodland, thickets of *Acacia drepanolobium,* riverine thickets along seasonal rivers, long grass (dominated by *Andropogon, Sporobolus* and *Setaria)* and wooded short grass.

Study Population

African wild dogs are considered endangered (Ginsberg & Macdonald 1990) in part because they are rare under the best of conditions. Population density on our study site is one adult per 25 km^2, considerably above mean density in other

populations (Frame et al. 1979; Reich 1981; Fuller et al. 1992; Maddock & Mills 1994). When yearlings and pups are considered, density reaches one dog per 17 km^2 at its annual peak following the denning period of July–October (during the dry season). Pack size ranged from three to 20 adults ($\bar{X} \pm \text{SE} = 7.7 \pm 0.23$). Including yearlings and pups, pack size ranged from three to 44 (18.3 ± 0.67). The sex ratio was not significantly biased for pups or adults (Creel et al. 1995). Home range size averaged 438 ± 87 km^2 ($N=6$ restricted polygons).

Hunting Observations

Hunting data came from six wild dog packs observed between November 1991 and March 1994 (11 pack-years of observation). Two members of each pack were radio-collared. All individuals were identifiable by variations in the patchwork of their black, tan and white coats (Fig. 1). We collected hunting data by direct observation during periods lasting from 1 to 14 days. Radio-collared packs were initially located from a light plane or a hilltop. We observed 404 kills in 905 complete hunts. Of 310 observation days (2210 h), we restricted our analyses to 266 days on which we observed entire hunting periods (Mills 1992). Following Packer et al. (1990), our measures of hunting cost and benefit use daily means as data points, to remove a bias towards zeros that existed for some variables when expressed per hunt.

We observed wild dogs from a Land Rover at distances of 20–400 m using binoculars and night vision goggles. Most hunting occurred in two periods, 0500–0900 hours and 1730–1930 hours, as in other populations (Kuhme 1965; Estes & Goddard 1967; Fuller & Kat 1990). Probably because Selous is wooded, wild dogs rarely hunted at night (fewer than 10 kills, mostly during denning periods), although they often travelled slowly on moonlit nights. During each hunt, we attempted to record the habitat type, prey species, prey number and herd composition, distance chased (estimated using the vehicle odometer), individuals leading the chase, individuals initiating the kill, characteristics of kill site, estimated mass of prey killed, estimated mass of remains not eaten, time on kill, and interactions with other carnivores. In this paper we focus primarily on relationships between group size and the costs and benefits of hunting.

Definition of Terms

Owing to variation in hunting techniques (e.g. stalking versus coursing) no single definition of a hunt applies to all large carnivores (Kruuk 1972; Schaller 1972; Mills 1990; Stander 1992a). We defined a hunt as a pursuit of prey that either exceeded 50 m at a full run, ended with intense testing of prey at bay, or ended in a kill. In Selous, wild dogs travel 12.3 km ± 0.5 ($\bar{X} \pm \text{SE}$ throughout) daily, and often pass near groups of potential prey that are ignored or tested briefly and with low effort. Our definition excludes low cost and apparently casual interactions with prey.

We have defined hunting group size as adult pack size. A priori, yearlings could plausibly be considered either dependants or hunters. Yearlings (4.3 ± 0.3 per pack in the 266 days analysed) usually participate in hunts and sometimes provide obvious help, but sometimes cause obvious hindrance. The number of yearlings was not associated with hunting success (simple regression, $t=0.66$, $df=1,265$, $P=0.51$) or with mean kill mass ($t=0.22$, $P=0.83$), but had a significant association with increased chase distance ($t=2.55$, $P=0.012$). Together, these relationships suggest that on average, yearlings have slight negative effects on foraging success and should be considered dependents. When yearlings are considered part of the hunting force, noise is added to the analyses (i.e. r^2-values drop) but the slopes and shapes of curves are not substantially altered.

Although we measured hunting group size as the number of adults, daily mean food intake rates were estimated by dividing the mass of prey killed by total pack size, including yearlings and pups. Pups were weighted by a factor of 0.5 (following M. G. L. Mills & M. L. Gorman, unpublished data; see also Packer et al. 1990). This measure yielded an estimate of the food intake that a pack's hunting force provided for themselves and their dependants. We estimated mass of kills using published figures (Sachs 1967; Blumenschine & Caro 1986). Our analyses were based on prey mass killed (except where noted), which could be converted to edible mass using weighting factors, but similar percentages of the mass (60–80%) of most carcasses were edible.

Wild dog packs are highly cohesive, and all pack members normally moved together during morning and evening hunting periods. (An exception is the 2–3-month denning period, when the

dominant female usually does not hunt: Malcolm & Marten 1982.) When a chase began, all pack members normally pursued and harassed prey. Social rallies almost invariably preceded hunting, and appeared to excite and coordinate the pack for hunting (Kuhme 1965; Estes & Goddard 1967; Malcolm 1979). Excluding pack members from the hunting group based on behavioural data could be misleading for three reasons. (1) We often did not have all dogs continuously in view through an entire hunt. (2) Multiple kills were common, but we often detected multiple kills only after the hunt finished. Thus, dogs not in view at one kill were often pursuing another prey animal. (3) Participation in a hunt is difficult to define operationally because the simple presence of an additional hunter may affect the prey's behaviour or escape options (Reich 1981; Stander 1992a; see Results).

No measures of hunting success or effort were affected by the within-pack adult sex ratio, which ranged from 20 to 80% male.

Statistical Methods

Data points were calculated on a daily basis (e.g. daily mean mass of kills, daily mean chase distance) and variances were calculated using daily means ($N=266$ days) as data points (following Packer et al. 1990). We used temporal autocorrelation to determine that successive days provided statistically independent points.

Means are reported with standard errors throughout. Linear regressions were fitted by ordinary least squares, using residual plots to test assumptions (Snedecor & Cochran 1967; Draper & Smith 1981). For most regressions, overlapping and truncated points prevented clear display of scatter in the data, so 95% confidence limits on linear regressions are shown as dotted lines. For analyses of the relationship between foraging success and pack size, the form of the relationship was of particular interest. Therefore, where non-linear regression models fitted significantly better than linear models, we used polynomial regressions. All polynomial regressions included quadratic terms. No higher-order terms were significant. We fitted non-linear regressions with initial values of the Marquardt parameter set so that regression coefficients were estimated by a compromise between steepest-descent and Gauss–Newton linearization methods (Marquardt 1963;

Snedecor & Cochran 1967; Draper & Smith 1981).

RESULTS

Mean Hunting and Foraging Success

Selous wild dog packs made from 0 to 16 chases per day ($\bar{X} \pm \text{SE} = 4 \cdot 2 \pm 0 \cdot 2$, $N=266$ days), and killed from 0 to 10 animals per day ($1 \cdot 8 \pm 0 \cdot 1$, $N=266$). Hunting success (kills/hunt) was 44% (range 0–100%) when calculated using only data from complete days, and 45% (range 0–100%) using all observations. Estimated mass of prey ranged from 0·5 to 208 kg ($48 \cdot 5 \pm 2 \cdot 15$ kg, $N=384$). Feeding duration ranged from 1 to 312 min ($35 \cdot 3 \pm 2 \cdot 1$ min, $N=357$). Chase distances ranged from 50 m to 4·6 km ($0 \cdot 57 \pm 0 \cdot 03$ km, $N=775$). Successful chases also ranged from 50 m to 4·6 km, but were generally longer ($0 \cdot 84 \pm 0 \cdot 05$ km, $N=304$).

Packs killed $4 \cdot 0 \pm 0 \cdot 35$ kg/dog/day ($N=216$), with a range of 0–37·5 kg. Clearly, a wild dog cannot eat 37·5 kg in a day. Actual food consumption averaged between 2·0 and 2·5 kg/dog/day, based on two adjustments to the overall mass killed. First, mass of prey was devalued to reflect that 20–40% of it is usually not eaten (e.g. large bones, stomach contents). Second, observations of feeding by wild dogs known not to have eaten for several days suggest that adult stomach capacity is roughly 9 kg, so edible biomass in excess of 9 kg/dog was excluded.

Prey Selection and Hunting Success

In 817 hunts in which at least one prey species was identified, 17 species were hunted: impala, *Aepyceros melampus* ($N=293$ hunts), blue wildebeest ($N=266$), warthog ($N=88$), African hare, *Lepus capensis* ($N=32$), zebra ($N=30$), duiker, *Sylvicapra grimmia* ($N=27$), Lichtenstein's hartebeest, *Alcelaphus lichtensteini* ($N=17$), eland, *Taurotragus oryx*, common reedbuck, *Redunca arundinum*, buffalo, *Syncerus caffer*, greater kudu, *Tragelaphus strepsiceros*, bushbuck, *Tragelaphus scriptus*, sable antelope, *Hippotragus niger*, bushpig, *Potamochoerus porcus*, waterbuck, *Kobus ellipsiprymnus*, banded mongoose, *Mungos mungo*, and yellow baboon, *Papio cyanocephalus* ($N \leq 10$ hunts each). In a sample of 368 identified kills, 10 prey species were killed: impala ($N=188$ kills),

Table I. Profitability of common prey for African wild dogs in Selous

Species	Hunts	Kills	% Success	Mass (kg)	Chase (km)	Profitability	
						kg/hunt	kg/km chased
Impala	293	188	64	31·9	1·19	20·4	17·1
Wildebeest	266	100	38	92·7	0·69	35·2	51·0
Warthog	88	31	35	33·8	0·31	11·8	38·1
African hare	32	10	31	2·0	0·13	0·6	4·8
Zebra	30	2	7	157·5	1·70	11·0	—
Common duiker	27	16	59	17·6	0·53	10·4	19·6
Total	736	347					
Weighed mean*			47	48·8	0·88	22·9	29·8

*Means were weighted using number of kills or chases (as appropriate) for each species.

blue wildebeest (N=100), warthog (N=31), common duiker (N=16), Lichtenstein's hartebeest (N=15), African hare (N=10), common reedbuck (N=4), zebra (N=2), waterbuck (N=1) and bushbuck (N=1).

The four ungulate species that were hunted but not killed were either much larger than the range of normal prey (eland and buffalo), had unusually dangerous horns or were uncommon in Selous (greater kudu and especially sable). Mongooses and yellow baboons were also not killed, but appeared to be hunted in play.

Table I shows hunting success, chase distance and two measures of profitability (mass killed per hunt, and per km chased) for prey species hunted on more than 25 occasions. Impala were hunted most often (40% of the total), killed most often (54% of the total) and yielded the highest hunting success (64%). Zebra provided the most mass per kill, but were rarely killed, with a probability of killing (7%) far lower than other species (minimum of 31%). Excluding zebra, wildebeest were the heaviest prey killed (mean of 93 kg). African hares were killed with the shortest chases (mean of 130 m), but yielded little food (2 kg).

Combining these relationships shows that wildebeest yield the greatest food mass per hunt and the greatest food mass per km chased (Table I). Indeed, wildebeest were hunted three to 10 times more frequently than all prey species except impala (Table I). Impala were hunted most frequently of all, despite ranking second in mass/ hunt and fourth in mass per km chased (Table I). The apparently sub-optimal preference for impala is probably the result of different population densities of prey species (impala are common).

Also, seasonal patterns of prey species' reproduction create asynchronous peaks in the availability of vulnerable young (which are highly preferred by wild dogs). More 'detailed analysis of profit, prey availability and prey choice will be presented elsewhere.

Communal Hunting and Group Size

Cooperative hunting behaviour

Coordination between the members of an African wild dog pack is seen throughout a hunt (Fig. 1). At several stages, effectiveness appears to depend on the number of cooperating hunters.

Although its function for hunting is arguable, the members of a pack almost invariably go through an intense greeting ceremony or 'rally' just prior to a period of hunting. The rally appears to ensure that all pack members are awake, alert and ready to hunt simultaneously, prior to trotting in search of prey (Estes & Goddard 1967; Malcolm 1979). Once on the move, pack members trot or canter together at 10 km/h, usually spread over 10–100 m (Fig. 1a).

Upon sighting prey, a pack often does not hunt. If the pack hunts, small prey (e.g. impala or duiker) flee immediately, but large prey (e.g. wildebeest) often stand in a defensive 'pinwheel', facing outward, charging and using their horns to defend themselves (Fig. 1b). Juveniles keep to the centre of the pinwheel. Well-armed prey (e.g. warthog, greater kudu males) may also stand and defend themselves rather than fleeing, even when solitary. When faced with a defensive formation, wild dogs encircle the herd and simultaneously

attack from several directions (Fig. 1b). If the prey defend themselves well, the pack often departs after testing the prey for 10 s to 5 min. The apparent goal of testing and attack is to force some or all of the herd to run, thus increasing their vulnerability. Simultaneous attacks appear to be effective because one wild dog can incite a charge, then packmates rush behind the charging prey to separate it from the herd. Once one or a few prey begin running, the entire herd often bolts, and a full-speed chase (at 40–60 km/h) ensues (Fig. 1c).

Especially in woodland, prey do not run in a straight line. For example, they follow lines of low resistance through trees, uneven ground, and waterholes. Prey with territories that are small relative to the length of a chase (e.g. duiker) often attempt to circle. Individual wild dogs pursuing a prey animal do not all follow the same line (Fig. 1d). Together, these patterns often result in one or more wild dogs intercepting a prey animal after a shortcut, whether intentional or not (Estes & Goddard 1967; cf. Fanshawe & Fitzgibbon 1993).

Once a prey animal has been caught, pack members cooperate in pulling it to a halt, or in occupying the animal's attention by feinting from the front, while others attack from behind and begin disembowelling. Several dogs may attack and distract a female while packmates attack its dependent offspring (Fig. 1e). Cooperation is important in restraining the head of large prey (e.g. wildebeest) and dangerous prey (e.g. warthog: Fig. 1f). Because killing can take several minutes and prey remain dangerous, restraint of the head is important to protect the dogs involved in disembowelling from being hooked by horns or tusks. Deep cuts, broken teeth and injured limbs from tusks and horns are not unusual.

Although simultaneous chases and kills are not cooperative per se, larger packs often chased several prey animals from a single herd. Simultaneous chases resulted in simultaneous kills of up to six wildebeest and seven impala (see below). Multiple kills almost invariably included juveniles: either mother and young or several juveniles from one herd.

Finally, wild dogs cooperate in defence of their kills from other carnivores. In Selous, competition at kills was not intense, and came primarily from spotted hyaenas. Spotted hyaenas were present at 76 wild dog kills (18% of all kills), but appropriated only 14 kills (2%). These percentages form a
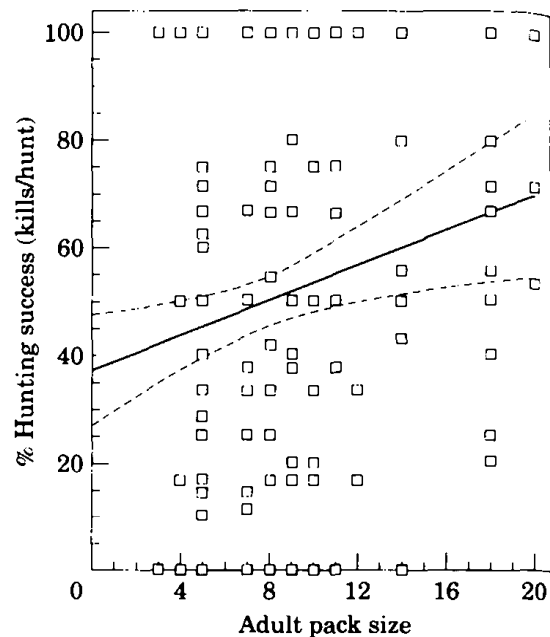

Figure 2. Hunting success (measured as kills/hunt) significantly increased as the number of adult wild dogs increased. Dotted lines are 95% confidence limits.

sharp contrast to those seen in Serengeti National Park, where hyaena group sizes are larger (Hofer & East 1993). There, hyaenas were present at 86% of wild dog kills (excluding gazelle fawns), and the duration that wild dogs retained their kills depended on the number of each species present (Fanshawe & Fitzgibbon 1993). In Selous, competition at wild dogs' kills also came occasionally from lions (four interactions, four kills lost; <1%), and other packs of wild dogs (two interactions, both kills lost to larger pack; <1%).

Wild dogs rarely scavenged. Three times, wild dog packs attacked adult leopards (two females and one male) until they fled into a tree, appropriating one impala carcass and one wildebeest carcass. One adult wildebeest was taken from a lion, and four kills were taken from spotted hyaenas (two impala, two of unknown species). Two additional kills were scavenged from unidentified carnivores, and three were scavenged from poachers' snares.
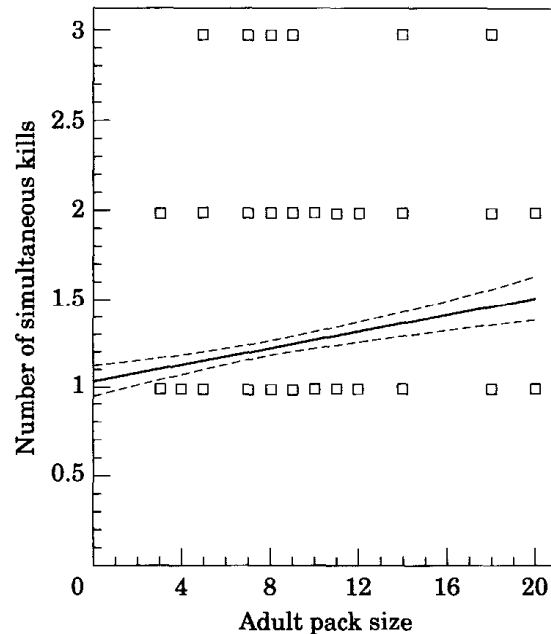
Quantitative effects of pack size on hunting

Hunting success significantly increased as adult pack size increased (Fig. 2), ranging from 42% in packs of three adults to 67% in packs of 20 adults ($b=1.64 \pm 0.61$, $r^2=0.16$, $t=2.70$, $P=0.007$). The mean mass of prey killed also significantly
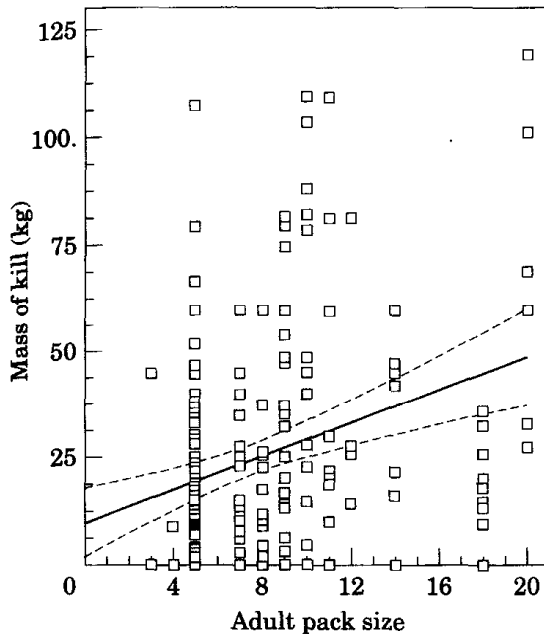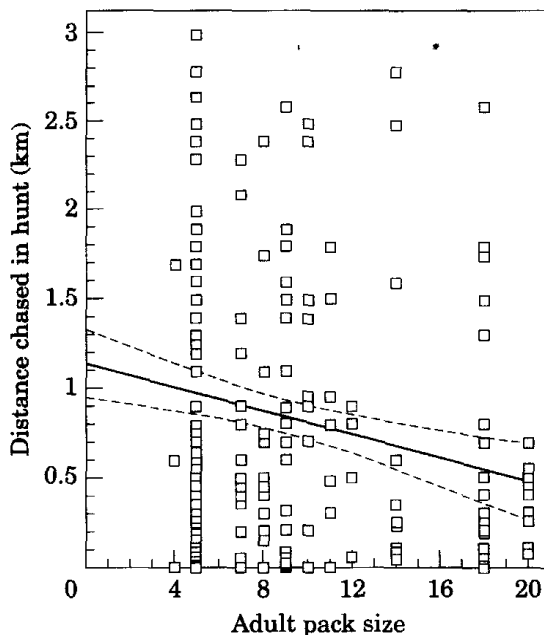
Figure 3. Mean mass of prey killed significantly increased as the number of adult wild dogs increased. Points are daily means. Dotted lines are 95% confidence limits.

Figure 4. Mean distance of successful chases significantly decreased as the number of adult wild dogs increased. Points are daily means. Dotted lines are 95% confidence limits.

increased with adult pack size (Fig. 3), from 16 kg in packs of three to 40 kg in packs of 20 (b=1·55 ± 0·28, r^2=0·19, t=5·59, P<0·001).

Figure 5. Mean number of prey killed simultaneously increased significantly as the number of adult wild dogs increased. Points are daily means. Dotted lines are 95% confidence limits.

The distance chased in a successful hunt significantly decreased as group size increased (Fig. 4), from 1·1 km in packs of three adults to 0·5 km in packs of 20 adults (b= − 33·7 ± 9·37, r^2=0·20, t=3·60, P<0·001). The number of animals simultaneously killed also increased with group size (Fig. 5; b=0·02 ± 0·005, r^2=0·24, t=4·80, P<0·001).

In summary, larger packs were more likely to kill in a given hunt, killed heavier prey with shorter chases, and killed more members of the herds they chased. None the less, larger packs made more chases per day (Fig. 6; b=0·23 ± 0·05, r^2=0·28, t=4·66, P<0·001), with the number of chases/day doubling over the observed range of adult pack sizes. Might larger groups be required to work harder to meet their greater absolute food needs, despite the advantages shown above? This question can be resolved only with data on per capita food intake.

Optimal hunting pack size

The standard measure of foraging success among large carnivores is kilograms eaten or killed per animal per day (Packer et al. 1990; Stander 1992a; Fanshawe & Fitzgibbon 1993; Stander & Albon 1993). Figure 7a shows the relationship of this measure of foraging success to
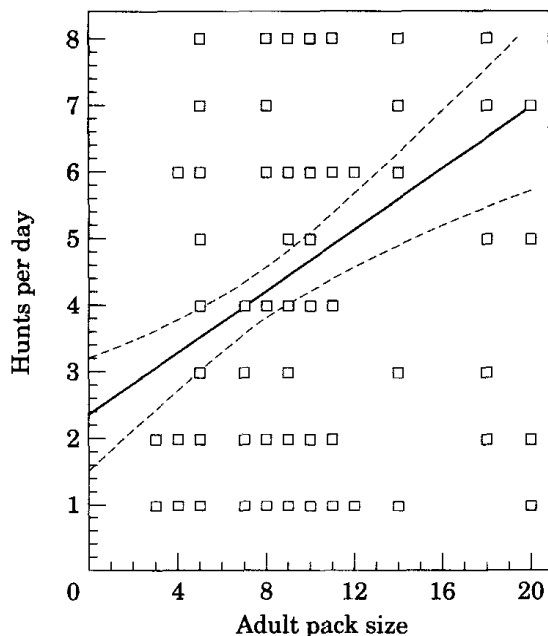
Figure 6. The number of hunts per day significantly increased as the number of adult wild dogs increased. Points are daily means. Dotted lines are 95% confidence limits.

pack size ($Y=6\cdot0-0\cdot6X+0\cdot04X^2$, $F_{3,246}=54\cdot4$, $P<0\cdot001$). As pack size increases, kg killed/dog/day initially decreases, reaches a minimum at eight to nine adults, and subsequently increases. To maximize kg killed/dog/day, selection would favour wild dogs that avoided adult pack sizes of seven to 11, particularly by forming packs larger than this range. But Selous wild dogs were most often found in packs of 10 adults ($\bar{X} \pm$ SD of normal approximation for frequency distribution $=9\cdot8 \pm 3\cdot9$; Fig. 8), diametrically opposing the predictions shown in Fig. 7a. Using this measure of foraging success, wild dog pack size appears unrelated to cooperative hunting.

Measuring foraging success as kg/dog/day does not incorporate variation in hunting effort. Hunting effort can be crudely incorporated by measuring foraging success as kg/dog/hunt. The relationship between kg/dog/hunt and pack size is shown in Fig. 7b ($Y=2\cdot1-0\cdot13X+0\cdot005X^2$, $F_{3,246}=34\cdot2$, $P<0\cdot001$). Similar to kg/dog/day, this measure of hunting success initially decreases as pack size increases. However, kg/dog/hunt does not reach its minimum until a pack size of 14, and maximal foraging success was obtained by dogs in the smallest packs observed. To maximize kg/dog/hunt, wild dogs would be selected to live in the smallest packs possible.

Hunting costs can be incorporated into foraging success in a more precise way by measuring kg/dog/km chased per day, or kg/dog/km travelled per day. Both of these measures improve on kg/dog/hunt by incorporating variation in effort expended in a hunting bout. 'Chasing' refers only to focused, high-speed pursuit of prey (Fig. 1c). 'Travelling' refers to all movement, including both chases and slow-paced searching (Fig. 1a). Kilograms/dog/km chased has the advantage of narrowly focusing on effort that is unequivocally directed to hunting. Kilograms/dog/km travelled has the advantage of being a more inclusive measure of cost, but it might include costs of travel that were in fact directed to another purpose. In practice, wild dog packs rarely travel without hunting, and we consider all movement to be hunting-related, although travel undoubtedly serves other functions simultaneously (e.g. territorial defence, assessing dispersal opportunities).

As adult pack size increases, kg killed/dog/km travelled also increases, throughout the observed range of pack sizes (Fig. 7c; $Y=0\cdot15+0\cdot06X-0\cdot001X^2$, $F_{3,244}=16\cdot3$, $P<0\cdot001$). Using this measure of foraging success, selection would favour wild dogs that foraged in packs as large as possible, with other factors setting an upper limit on pack size.

As adult pack size increases, kg killed/dog/km chased increases until reaching an intermediate optimum at 12–14 adults and subsequently decreasing (Fig. 7d; $Y=-1\cdot05+0\cdot99X-0\cdot04X^2$, $F_{3,194}=10\cdot57$, $P<0\cdot001$). By this measure of foraging success, selection acting on hunting alone would favour life in intermediate pack sizes. Optimal pack size is slightly higher than the observed peak in the pack size distribution (12–14 versus 10 adults: Figs 7d and 8).

Variance in foraging success

Risk-sensitive foragers should hunt in group sizes that depend both on mean foraging success and its variance, to minimize the risk that food intake will dip to starvation level (Pulliam & Caraco 1984; Houston et al. 1988; Mangel & Clark 1988). Stochastic models of risk-sensitive foraging and group size in large carnivores depend on estimates that are poorly known for wild dogs (e.g. daily requirements, toleration of starvation, stomach capacity), so we have not applied them. However, risk sensitivity will modify the optimal group size only if
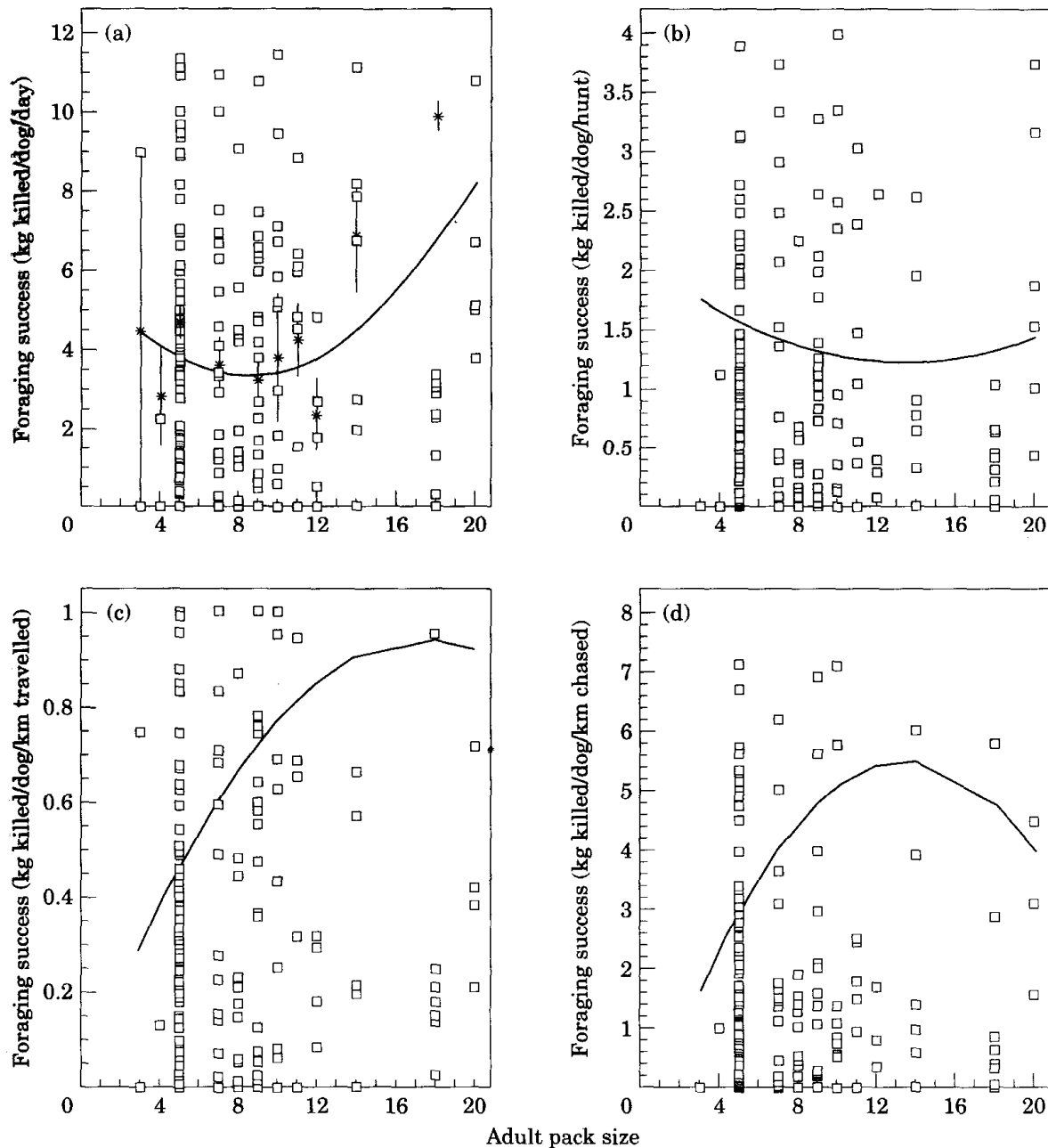
Figure 7. The relationship of foraging success to pack size, shown by non-linear regressions. Points are daily means. Four measures of foraging success are shown as the dependent variable: (a) kg killed/dog/day; (b) kg killed/dog/hunt; (c) kg killed/dog/km travelled, including search; (d) kg killed/dog/km chased in full-speed pursuits.

variance in foraging success is affected by group size (Pulliam & Caraco 1984). For Selous wild dogs, variance in foraging success did not correlate with group size (NS for all measures of foraging success; e.g. for kg/dog/km travelled, $r_S = 0.20$, $P = 0.69$), nor were non-linear associations apparent. Thus the results of simple optimality and stochastic models are likely to coincide reasonably (as in Serengeti lions: Packer et al. 1990).

DISCUSSION

Other Wild Dog Populations

Wild dogs are generally regarded as efficient hunters, and their high hunting success in Selous (44%) parallels that recorded in other populations, which ranges from 39 to 85% (Estes & Goddard 1967; Kruuk & Turner 1967; Schaller 1972;
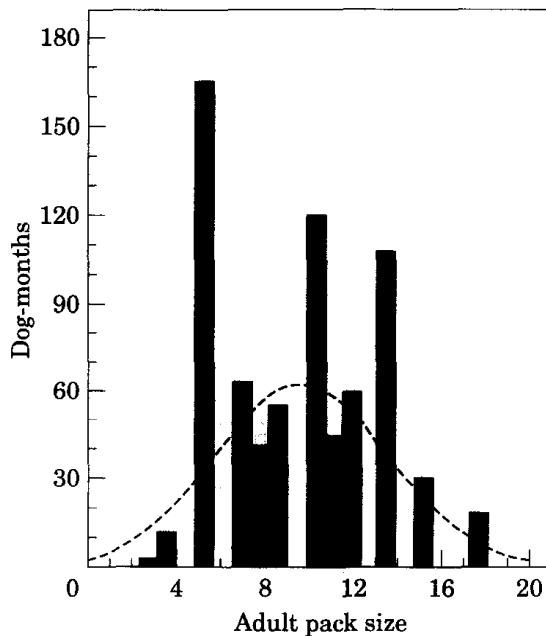
Figure 8. Frequency distribution of pack sizes in which Selous wild dogs lived, based on individual-months of observation (following Rodman 1981). Dashed line shows normal approximation.

Malcolm & van Lawick 1975; Fanshawe & Fitzgibbon 1993; Fuller & Kat 1993). Some of the variation in hunting success between studies is probably due to small sample sizes (the highest and lowest values reported were based on ≤30 hunts). Pooling data from four wild dog studies in the Serengeti ecosystem, hunting success was also 44% (*N*=666 hunts: Schaller 1972; Malcolm & van Lawick 1975; Fanshawe & Fitzgibbon 1993; Fuller & Kat 1993). The accord with Selous is somewhat striking, given substantial differences in the prey set available and the physical environment. None the less, energetic returns might differ substantially between populations, owing to variation in prey size or hunting effort.

The range of prey species hunted and killed is broader in Selous than has been reported for most other populations (e.g. Malcolm & van Lawick 1975; Fuller & Kat 1990, 1993). This difference is probably partly due to sample size differences. All of the prey species killed in Selous have been recorded in at least one other study (see especially de V. Pienaar 1969, who summarized results for 4406 carcasses eaten by wild dogs in Kruger National Park). Of the species hunted but not killed in Selous, three have not previously been reported (bushpig, baboon and banded mongoose).

Effects of Group Size Unrelated to Hunting

Our analyses of optimal group size address only the effects of communal hunting. Although our results confirm that communal hunting favours sociality in wild dogs, factors completely unrelated to hunting are also likely to affect pack size. We do not suggest that other group-level activities (e.g. group defence of territories or offspring: Packer et al. 1990) or patterns of relatedness (Rodman 1981; Giraldeau & Gillis 1988; Giraldeau & Caraco 1993) are unimportant.

Preliminary evidence suggests that there are other benefits of group living for Selous wild dogs. First, clashes between packs (which have included fatal fights) were won by the larger pack in 10 of 10 cases. In two clashes between packs of equal size, each retreated once. Second, large groups produce large same-sexed cohorts, which may confer advantages in dispersal. Groups of transient females can take over existing packs by evicting resident females, and numbers are likely to affect the outcome of take-over attempts. Finally, large packs may be better at defending their pups from predation. For example, a pack of 16 attacked an adult male lion that was stalking their pups, and drove it away without casualties. Systematic data are needed to test whether these and other potential benefits (and potential costs such as easier transmission of pathogens) are important. In addition, our data address only the energetics of hunting; selection on the risks of injury during hunting might not act in parallel.

Hunting and Group Size

Analyses of optimal hunting group size are strongly dependent on the currency of foraging success that is used (Fig. 7a–d). Hunting success (kills/hunt) and daily per capita food intake (kg/individual/day) have been widely used in analyses of optimal hunting group size in large carnivores (Mills 1985; Packer et al. 1990; Stander 1992a; Fanshawe & Fitzgibbon 1993; Stander & Albon 1993; Caro 1994). It is widely recognized that hunting success will rarely be an appropriate currency, because it does not account for covariation between group size and mass of prey (Caro 1994).

For wild dogs, daily per capita food intake is also inappropriate for analysis of optimal group size, because it fails to account for covariation

between hunting costs and pack size. Although kg/dog/day showed an intermediate minimum when regressed on pack size (Fig. 7a), kg/dog/km chased showed an intermediate maximum (Fig. 7d), and kg/dog/km travelled steadily increased (Fig. 7c). Thus, both measures of foraging success that incorporate variation in costs show that communal hunting favours sociality in wild dogs. The currency of kg/dog/km travelled suggests that communal hunting provides directional selection in favour of large groups, with other factors (e.g. parasite loads or intra-group aggression) setting an upper limit. The currency of kg/dog/km chased suggests that communal hunting provides stabilizing selection for packs slightly larger than the observed modal pack size.

These results may be of widespread importance when considering the role of communal hunting in the evolution of carnivore sociality. For example, lions in Serengeti National Park have been examined in an influential series of papers on optimal group size (Schaller 1972; Caraco & Wolf 1975; Rodman 1981; Packer 1986; Mangel & Clark 1988; Packer et al. 1990). Packer et al. (1990) showed that kg/lion/day was minimized at intermediate hunting group sizes. They concluded that 'group-size-specific foraging success is insufficient to account for the observed distribution of group sizes' (page 2). Incorporating the costs of hunting may alter this result (although lions in intermediate-sized hunting groups would still fail to meet their daily metabolic needs; the primary conclusion, that lions in small and intermediate-sized prides should hunt alone, should therefore remain true: C. Packer, personal communication).

Caro (1994) reviewed analyses of optimal hunting group size based on daily per capita foraging success, and concluded:

few studies report per capita foraging returns, but in the majority of those that do, per capita foraging success did not increase with group size. In populations in which it did, grouping patterns did not reflect optimal foraging group sizes. Though limited, current evidence therefore suggests that cooperative hunting is not responsible for group living in any carnivore. [page 342]

Until analyses of optimal hunting group size incorporate hunting costs, however, a broad rejection of the influence of communal hunting on sociality is premature. For stalkers, covariation between group size and the frequency of hunts should be tested. For coursers, both the frequency and length of chases should be considered. For both, the risks of injury should be assessed. Many large social carnivores display a range of costly cooperative hunting behaviour patterns that logic suggests would not be maintained without an offsetting benefit (Fig. 1; Mech 1970; Kruuk 1975; Mills 1990; Stander 1992b).

In principle, comparisons between species could be standardized by measuring both benefits and costs of hunting in kilojoules, rather than kilograms of meat or kilometres run. We did this using estimates of the energetic content of meat (6000 kJ/kg: Ulmer 1983), and an allometric regression of the costs of terrestrial locomotion (kJ/km = $10.7 \times$ body mass in kg$^{0.68}$: Tayler et al. 1982; Calder 1984). Because these relationships are not based on data specific to wild dogs, the results are speculative. None the less, it is interesting that kJ killed/dog/kJ in chase was maximized in packs of 12 adults, and kJ killed/dog/kJ in travel was maximized in packs of 18.

Finally, models of optimal group size often assume that individuals' fitness peaks at intermediate group sizes (Rodman 1981; Giraldeau & Caraco 1993; Higashi & Yamamura 1993). As Rannala & Brown (1994) noted, there is relatively little empirical support for this assumption. For Selous wild dogs, the fitness effects of cooperative hunting do peak at intermediate group sizes, using three of four logical currencies (kg killed/dog/km chased; kJ killed/dog/kJ in chase; and kJ killed/dog/kJ in travel; these currencies are collinear). Despite recent rejections of its importance, communal hunting may still prove to be a force in the evolution of sociality and group size.

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