



## Raven scavenging favours group foraging in wolves

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Wolves, *Canis lupus*, routinely live in large packs that include unrelated individuals and mature offspring. Studies show that individual wolves that live in large packs suffer reduced foraging returns. Therefore, group hunting and group living (sociality) in wolves is generally thought to be favoured by indirect fitness gains accrued through kin-directed altruism. However, we show that kin-directed altruism cannot account for groups that include mature offspring or unrelated individuals. We also present an analysis that incorporates a previously ignored feature of wolf foraging ecology, namely the loss of food to scavenging ravens, *Corvus corax*. By accounting for this process, we show that individuals in large packs do indeed accrue foraging advantages. In the hypothetical absence of this scavenging pressure, an individual would maximize its rate of prey acquisition, and minimize its risk of energetic shortfall, by foraging with just one other individual. However, incorporating the effect of scavenging by ravens leads to a dramatic increase in the predicted group size. Our analysis indicates that per capita gains are highest in the largest observed packs. The greater food-sharing costs in a larger pack are more than offset by smaller losses to scavengers and increased rates of prey acquisition. Thus, in contrast with previous interpretations, the selfish benefits of social foraging appear to contribute to the maintenance of sociality in wolves after all. We explore whether such benefits favour group living in various social carnivores that hunt large prey and are thus vulnerable to scavenging.

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Most carnivore species (85–90%) are solitary (Gittleman 1989). Because of this and their folkloric reputation as solitaires, an enduring question in the study of social behaviour is why the remaining carnivore species are social (group living). Many social animals are known to live in a so-called aggregation economy, in which individuals experience higher foraging payoffs in the group, at least for some group sizes, than they would as solitaires (reviewed by Giraldeau & Caraco 2000). Thus, a common view is that sociality, particularly in large carnivores, is favoured by benefits accruing to individuals that forage socially rather than solitarily (e.g. Schaller 1972; Kruuk 1975; Nudds 1978; Gittleman 1989; Fuller & Kat 1990; Packer et al. 1990; Fanshawe & Fitzgibbons 1993; Stander & Albon 1993; Thurber & Peterson 1993; Caro 1994; Creel & Creel 1995; Schmidt & Mech 1997; Hayes et al. 2000). Attempts to test this hypothesis have led to considerable confusion and debate.

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In an aggregation economy, the per capita intake rate increases initially with increasing group size. But because interference between group members increases with group size, intake rate reaches a peak, at  $G^*$ , and then falls with further increases in group size. Eventually, beyond  $\hat{G}$ , the intake rate falls below the rate for a solitary forager. Group foraging is clearly favoured in such an economy, but what is the expected group size? Superficially, it seems plausible that  $G$  should equilibrate around the optimal size  $G^*$ , at which each group member would maximize its fitness gain. Most studies to date, however, suggest that social carnivores routinely forage in groups exceeding  $G^*$  (Fuller & Kat 1990; Packer et al. 1990; Fanshawe & Fitzgibbons 1993; Thurber & Peterson 1993; Caro 1994; Schmidt & Mech 1997; Hayes et al. 2000; reviewed by Giraldeau & Caraco 2000; for an exception see Baird & Dill 1996). These findings have led some workers to doubt the role of foraging economics in the evolutionary maintenance of sociality in large carnivores (Packer et al. 1990; Caro 1994; Packer & Caro 1997; but see Creel 1997).

However, it is important to recognize that these findings do not necessarily contradict the theory on group foraging (reviewed by Giraldeau & Caraco 2000; see also Waite & Field, in press). Indeed, the optimal group size  $G^*$  is expected to be unstable because any solitary individual has

a strong incentive to join the group. Thus, a group of  $G^*$  individuals may continue to grow, but it should not exceed  $\hat{G}$ , because a solitary individual would do better to remain as such than to join a group that already has  $\hat{G}$  members. Depending in subtle ways on whether the potential joiner or the group controls entry and on the degree of genetic relatedness between individuals, the equilibrium group size may be as small as  $G^*$  or as large as  $\hat{G}$  (see below).

Even though, based on this logic, it is no longer considered paradoxical to find free-ranging animals in groups larger than  $G^*$ , the role of foraging payoffs in the maintenance of group living in large carnivores remains contentious (e.g. Packer et al. 1990; Caro 1994; Creel 1997). The paradox we attempt to resolve here is not why group size in wolves, *Canis lupus*, often exceeds  $G^*$ , but why, according to conventional foraging models, group size often appears to exceed  $\hat{G}$  (Thurber & Peterson 1993; Schmidt & Mech 1997; Hayes et al. 2000). We begin by showing that conventional hypotheses and models of group foraging (i.e. need for territorial defence, maximization of net intake rate, minimization of risk of energetic shortfall, and kin-directed altruism) predict values of  $\hat{G}$  that are substantially less than observed pack sizes. We then incorporate into the analysis a previously overlooked yet conspicuous feature of wolf foraging ecology, namely loss of food to scavenging ravens, *Corvus corax*. By taking scavenging into consideration, we show that  $\hat{G}$  increases to correspond with pack sizes that are routinely observed in nature. Thus, we provide the first evidence that foraging economics favour large group size in wolves after all.

### Behavioural Interactions Between Wolves and Ravens

Ravens are ubiquitously present at carcasses of wolf-killed prey throughout North America (e.g. Crisler 1956; Mech 1966, 1970; Bruggers 1988; Heinrich 1989; Paquet 1991; Promberger 1992; Carbyn et al. 1993; Mech et al. 1998; Hayes et al. 2000; Drummer et al. 2002; Stahler et al. 2002; see also Bjarvall & Isakson 1982). Numbers of ravens per carcass typically range from 6 to 25 (e.g. Promberger 1992; Heinrich 1999; Drummer et al. 2002; Stahler et al. 2002), but sometimes as many as 50 (Promberger 1992), 80 (Carbyn et al. 1993), or more than 100 (Drummer et al. 2002) ravens have been observed at sites where wolves have killed prey. On Isle Royale, ravens (typically 5–15) have been present at virtually every wolf-killed moose, *Alces alces*, carcass documented over the past 32 years.

Ravens also routinely associate with wolves away from carcasses (Mech 1966, 1970; Peterson 1977; Harrington 1978; Allen 1979; Bjarvall & Isakson 1982; Carbyn et al. 1993). In some locations where ravens and wolves co-occur, ravens are rarely found except in the presence of wolves (e.g. Stahler et al. 2002). This close association is thought to represent an adaptive foraging tactic for ravens because in winter they depend on carrion, which may be difficult to find.

Beyond simply associating with wolves, ravens scavenge substantial amounts of wolf-killed prey. An individual

raven can ingest and hoard 0.5–2 kg of food per day from the carcass of a large prey (Heinrich & Pepper 1999; see also Magoun 1976). On a per capita basis, wolves have been estimated to lose 2–4 kg of food per day to scavenging ravens (Hayes et al. 2000). In one case, ravens removed approximately half of a 300-kg moose carcass (Hayes et al. 2000). In another study, groups of ravens removed an estimated 37 kg of food per day from carcasses of wolf-killed prey (Promberger 1992). These observations provide the basis for our conservative assumption that while wolves are feeding on a carcass, they routinely lose 2–20 kg of food per day to ravens.

The detailed circumstances in which wolves lose food to ravens vary. For example, wolves lose limited amounts of food when they actively feed or rest in the immediate vicinity of their carcass. Food loss is limited because wolves frequently chase ravens away from their carcass. However, in several common circumstances, wolves do not effectively repel ravens. Such circumstances include when ravens are numerous, wolves are engorged, and when wolves rest near, but not immediately next to, their partially consumed carcass. Apparently, under conditions such as these, the net energetic costs of trying to repel all ravens routinely exceed the net energetic benefits. Notably, the cost and the risk of injury to the raven appear to be minimal, given their relative mobility. Finally, wolves also lose food to ravens when they temporarily leave an unfinished carcass to, for example, maintain and defend the boundaries of their territory against other wolves. Apparently, the net benefit of territorial defence exceeds the net benefit of further limiting rates of food loss to ravens and other scavengers. The explanation for why wolves do not invest more energy to repel scavenging ravens awaits a game theoretic analysis.

Despite the limited effectiveness and expression of agonistic behaviour towards ravens, the loss to scavengers would seem to be a significant selective pressure. Accounting for the losses to scavenging ravens, the expected rate of ingestion is very close to the wolf's minimal metabolic requirement (see below), so the expected risk of starvation is high. In fact, annual mortality rates in naturally regulated wolf populations are typically on the order of 20–30% (e.g. Parker & Luttich 1986; Fuller 1989; Wydeven et al. 1995; Mech et al. 1998; Peterson et al. 1998; Boyd & Pletscher 1999; Hefner & Geffen 1999; Hayes & Harestad 2000; Drummer et al. 2002) and most mortality is associated with starvation and intraspecific competition for food (e.g. Mech 1970; Peterson & Page 1988; Mech et al. 1998). The increased starvation risk attributable to losses to ravens may induce wolves to compensate by killing approximately twice as many large prey as would be needed in the absence of ravens (see Figure 3 in Hayes et al. 2000). The costs of this extra hunting may be substantial. Hunting is dangerous and energetically expensive: wolves routinely receive serious injuries (e.g. cracked ribs and skulls) from being kicked and thrown by large prey (e.g. Rausch 1967; Mech 1970; Weaver et al. 1992; Mech et al. 1998), and the instantaneous rate of energy expenditure for a canid hunting large prey may be extraordinary (~25 times the basal metabolic rate; Gorman et al. 1998). Thus, scavenging by

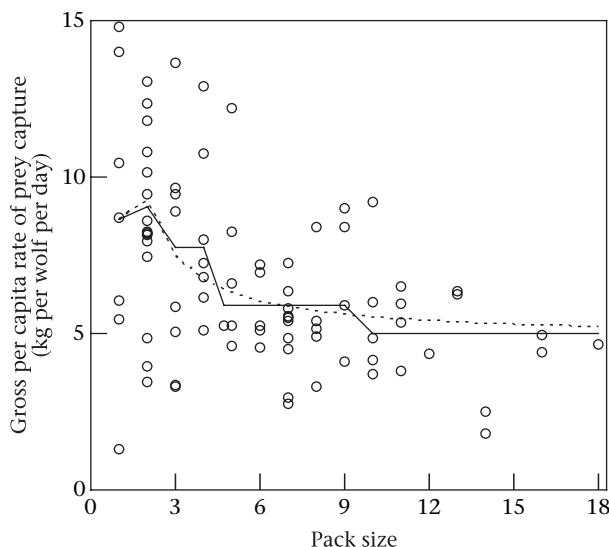
ravens, a previously ignored aspect in economic analyses of wolf foraging, appears to be a strong selective agent. We will show that wolves reduce these losses when they live in groups, regardless of the extent to which agonistic behaviour limits food losses.

## FIELD METHODS

Data were collected in Isle Royale National Park, U.S.A., an island (544 km<sup>2</sup>) in Lake Superior, where wolves and moose interact virtually in a single-predator–single-prey system (Peterson & Page 1988). Other species capable of preying upon moose are absent, hunting is prohibited on the island, and moose are the only significant source of food for Isle Royale wolves during winter (Peterson & Page 1988). During winter, wolves hunt and travel in family-based groups called packs (Olson 1938; Murie 1944).

Our observations permit estimation of pack size, per capita rate of prey acquisition (kills per wolf per day) for each pack, and abundance of moose in each pack's territory. Data were collected during January and February, 1971–1998. The size of each pack was determined using fixed-wing aircraft. Confidence in the accuracy of pack size estimates is based on: (1) frequent simultaneous visibility of entire wolf packs, and (2) repeated censuses during each winter survey. During the study period, median observed pack size was five wolves (interquartile range 2–5; Fig. 1).

In our analysis of foraging economics, we operationally treated these estimates of pack size as estimates of group size. This is justifiable because on Isle Royale (and elsewhere) all members of the pack are routinely present



**Figure 1.** Relationship between pack size and mean daily per capita gross rate of prey capture (kg). Means were taken over 44-day periods in January and February of each year, 1971–1998. The dashed line connects the mean rate for lone wolves and rates for other pack sizes as predicted by a reciprocal exponential model. The solid line connects the mean rate for pack size categories: 1, 2, 3–4, 5–9 and  $\geq 10$ . The group size that maximizes per capita rate of intake ( $G^*$ ) is two. At larger group sizes, per capita rate of intake falls below that of a solitary forager (i.e.  $\hat{G}=2$ ).

during hunting, all members consume each moose captured by the pack, and nonmembers are excluded (e.g. Mech 1966; Peterson 1977; Peterson et al. 1998; see also Mech 1970; Carbyn et al. 1993; Mech et al. 1998; Hayes et al. 2000; Drummer et al. 2002). Thus, the size of the foraging group is equal to the size of the pack. Our analysis, therefore, investigates not just whether foraging economics may favour large foraging groups but also whether they may favour sociality (pack living).

Kill rate was calculated for each wolf pack during each winter. Each estimate was based on daily travel routes (median = 44 routes, interquartile range 38–47) documented by aerial survey. Along these routes, wolf-killed moose were detected by following tracks left by the wolves in the snow. The chance of missing any particular carcass was low because: (1) highly visible remnants (e.g. hair mat, stomach contents, and bloodied bones) persist for days (regardless of pack size) and (2) wolves often revisit old carcasses. Snowfall occasionally prevented us from documenting some intervals of travel, which were not included in our calculations. This method and other comparable methods are routinely used to estimate kill rate (e.g. Mech 1966; Peterson 1977; Peterson et al. 1984; Ballard et al. 1987; Thurber & Peterson 1993; Dale et al. 1995; Schmidt & Mech 1997; Hayes et al. 2000).

Following detection from the aircraft, we examined each wolf-killed moose from the ground to determine the sex and age of the carcass. Estimates of per capita rate of prey acquisition were based on average masses of the edible portion of moose carcasses (330 kg for adult males, 261 kg for adult females and 114 kg for calves). These masses represent means of whole carcasses weighed by Peterson (1977), and are similar to masses of Isle Royale moose reported by Murie (1934) and Kellum (1941). During the 27-year period of our study, we detected and investigated 558 wolf-killed moose carcasses.

We calculated per capita kill rate as the number of kills made by a pack divided by the number of wolves in the pack divided by the number of days that the pack was observed. In aggregate, over the 27-year study and with the population typically comprising three packs (range 2–5), we obtained 85 pack-specific estimates of per capita kill rate. The overall average kill rate was 0.88 moose per wolf per month (= 4.5 moose per pack per month), where month equals 365/12 (for a discussion of the ecological determinants and consequences of these kill rates, see Vucetich et al. 2002).

Finally, we estimated the density of moose within each pack's territory annually using an aerial-survey method described elsewhere (Peterson & Page 1993; see also Peterson et al. 1998), and estimated the boundary of each pack's territory from the travel routes documented by aerial tracking.

## ANALYSIS AND RESULTS

### Territorial Defence

Group living may be maintained in some carnivores (Packer et al. 1990), including wolves (Schmidt & Mech 1997), by the need to defend territories that are large

enough to contain adequate foraging resources. However, in 14 (54%) of the years between 1971 and 1996, the smallest pack on Isle Royale defended a territory with the highest per capita availability of moose. Moreover, in 6 of 8 years in which any pack comprised just a pair of wolves, the pair defended the territory with the highest per capita availability of moose. Our records thus suggest that larger packs defended less adequate territories than did smaller packs. Because we found no evidence that the per capita abundance of prey was higher for larger packs, territorial defence does not seem to be important for the maintenance of group living in Isle Royale wolves.

### Rate Maximization

To re-evaluate the potential role of social foraging advantages in the maintenance of group living in wolves, we first describe the relationship between group size and foraging rate. Field studies show that wolves commonly forage in packs of six or more individuals (Mech 1970), even though the per capita rate of prey acquisition is higher in smaller packs (Thurber & Peterson 1993; Schmidt & Mech 1997; Hayes et al. 2000). For example, data from Isle Royale National Park indicate that the per capita rate of prey acquisition is maximal for wolves hunting in pairs and declines with increasing pack size (Fig. 1). However, these data, like those used in almost all previous studies of large social carnivores (e.g. Fuller & Kat 1990; Packer et al. 1990; Fanshawe & Fitzgibbons 1993; Stander & Albon 1993; Thurber & Peterson 1993; Caro 1994; Schmidt & Mech 1997; Hayes et al. 2000; see also Creel & Creel 1995), are estimates of gross rate of prey acquisition. Natural selection is expected to favour individuals that forage in ways that tend to maximize net, rather than gross, rate of intake (Giraldeau & Caraco 2000). Thus, the cost of foraging must be incorporated to generate meaningful predictions of  $G^*$  and  $\hat{G}$ .

To incorporate the cost of foraging, we calculated average per capita daily energy expenditure (DEE) for wolves in different-sized packs:

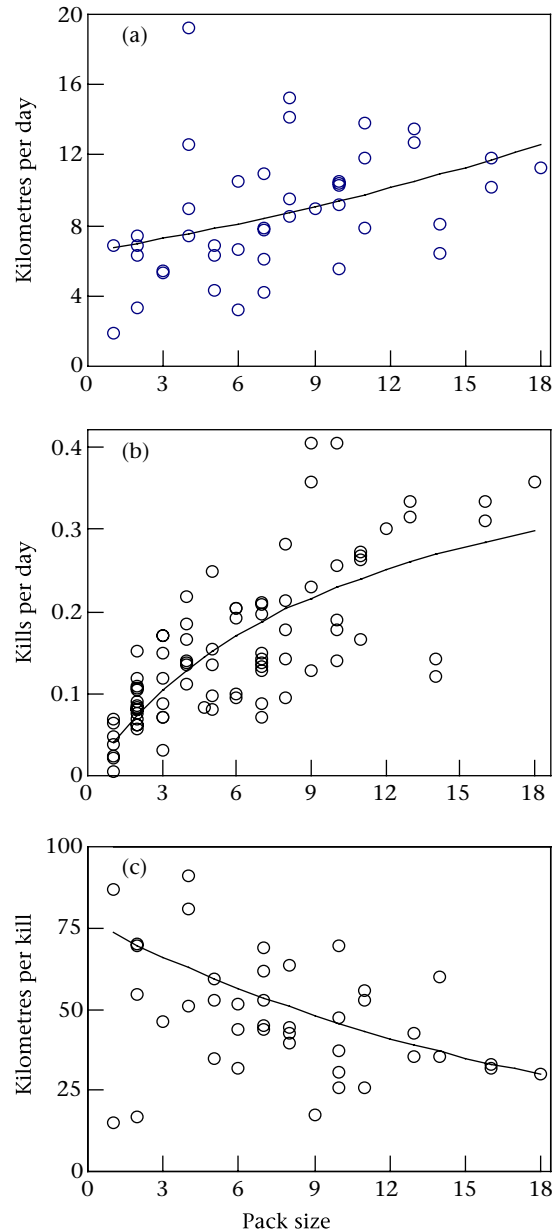
$$\text{DEE} = (\text{MR}_{\text{walking}} \times T_{\text{walking}}) + (\text{MR}_{\text{chasing}} \times T_{\text{chasing}}) + (\text{MR}_{\text{other}} \times T_{\text{other}}), \quad (1)$$

where MR is the metabolic rate associated with walking, chasing and other activities (e.g. resting), expressed as multiples of basal metabolic rate (BMR).  $T$  is time spent walking, chasing and engaging in other activities. (We calculated  $T_{\text{other}}$  as the portion of a day (24 h) not spent walking or chasing.) Observations from Isle Royale indicate that  $T_{\text{walking}}$ , and hence the expected distance walked daily (by all members of a pack), increases with pack size,  $x$  (Fig. 2a):

$$\text{km/day} = \exp(1.87 + 0.037x). \quad (2)$$

We estimated  $T_{\text{walking}}$  as km/day divided by the average observed speed of travel for Isle Royale wolves (i.e. 4 km/h; Mech 1966).

We calculated  $T_{\text{chasing}}$  as  $d \times c/\text{day}$ , where  $d$  is the duration of a chase and  $c/\text{day}$  is the number of chases per



**Figure 2.** Relationships between pack size and (a) distance travelled per day, (b) number of kills per day, and (c) distance travelled between kills. Lines are best-fit curves: (a) equation (2) ( $P=0.002$ ), (b) equation (3) ( $P<0.001$ ) and (c) equation (4) ( $P<0.001$ ). In panel (c), two data points (3,175; 4,155) are not shown, but are accounted for by the best-fit curve.

day, and  $c/\text{day} = c/\text{kill} \times \text{kills}/\text{day}$ . Observations from Isle Royale indicate that the expected number of kills/day increased with pack size (Fig. 2b):

$$\text{kills}/\text{day} = (0.479x)/(10.91 + x). \quad (3)$$

Calculating  $T_{\text{chasing}}$  also requires an estimate of  $c/\text{kill}$ . For large packs of Isle Royale wolves, an estimated 5.6% of the moose that are chased are killed (7 of 124; Peterson 1977), which corresponds to 17.9  $c/\text{kill}$ . This estimate is based on observations of packs ranging in size from 10 to 16 wolves (median = 16); estimates for smaller packs were unavailable. Information was available, however, for another

relationship that may indicate how success rate varies with pack size. Specifically, that the expected kilometres travelled per kill decreased with pack size (Fig. 2c):

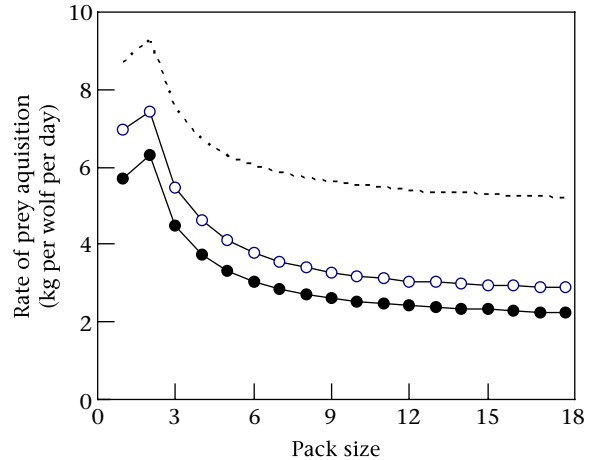
$$\text{km/kill} = \exp(4.35 - 0.053x). \quad (4)$$

If encounter rate is independent of pack size (see below),  $c/\text{kill}$  is estimated by multiplying the right side of equation (4) by 0.54, which yields an expression for which packs with 16 wolves chase 17.9 moose per successful kill, and thus converts the observed relationship between pack size and  $\text{km}/\text{kill}$  into a relationship between pack size and  $c/\text{kill}$ .

We estimated that a wolf's daily BMR is 3724 kJ. This estimate was based on a mammal-specific allometric relationship (Kleiber 1947) and the assumption that an average Isle Royale wolf weighs 31.5 kg (Peterson 1977). Observations of free-ranging canids suggest that the metabolic rate associated with walking falls between three and eight times the BMR (Gorman et al. 1998; R. Peterson, unpublished data), the metabolic rate associated with chasing prey could be as high as 25 times the BMR (Gorman et al. 1998), and the metabolic rate associated with other activities of free-ranging vertebrates falls between 1.5 and 3.5 times the BMR (Gorman et al. 1998). Observations from Isle Royale indicate that chases typically last between 1 and 10 min (Peterson 1977). Based on these observations and estimates, we conducted a sensitivity analysis on DEE by assuming various values of  $\text{MR}_{\text{walking}}$ ,  $\text{MR}_{\text{chasing}}$ ,  $\text{MR}_{\text{other}}$  and  $d$  (i.e.  $\text{MR}_{\text{walking}} = (3, 8)$ ;  $\text{MR}_{\text{chasing}} = (8, 25)$ ;  $\text{MR}_{\text{other}} = (1.5, 3.5)$ ; and  $d = (1, 10)$ ). DEE was also restricted by assuming that, on average, no wolf expends less than three times or more than five times the BMR (Gorman et al. 1998).

To permit direct comparison between DEE and the gross rate of prey acquisition, we converted DEE from units of BMR into kilograms of ungulate prey (i.e. 6862 kJ per kg of ungulate prey; Creel 1997). To obtain relationships between pack size and net rate of acquisition, we then subtracted DEE for each pack size (equation (1)) from the average gross rate of acquisition for each pack size (Fig. 1). For the entire range over which we conducted the sensitivity analysis, foraging rate was maximized for individual wolves that foraged in pairs (i.e.  $G^* = 2$ ; Fig. 3). Because the average foraging rate for individuals in a trio fell below that for a solitary individual (i.e.  $\hat{G} = 2$ ), the predicted stable group size was two. Hence, this initial analysis failed to explain why wolves forage in packs of three or more individuals.

Does this conclusion hold if we revise our assumption (equation (4) and associated text) about the relationship between prey encounter rate and pack size? If we were to assume that encounter rate increases with pack size (rather than varies independently), we would expect to observe the following cascading effects. First, equation (2) (Fig. 2a) would reflect the positive relationship between encounter rate and pack size. Consequently, the relationship between  $x$  and  $c/\text{kill}$  would be less negative than shown in Fig. 2a. In turn, the relationship between  $x$  and  $(\text{MR}_{\text{chasing}} \times T_{\text{chasing}})$  would be less negative than we calculated (see equation (1)). Consequently, the relationship between pack



**Figure 3.** Relationship between pack size and mean daily per capita net rate of energy acquisition (expressed in terms of kilograms of prey). The net rate is the gross rate (dashed line; see also Fig. 1) minus the per capita daily energy expenditure (DEE) expressed in terms of kilograms of prey (equation (1)). The most extreme relationships are shown for all combinations of values considered in the sensitivity analysis. The curve with open symbols has the greatest values and the steepest slope. The curve with the closed symbols has the lowest values and the shallowest slope. Thus, in the absence of scavenging, rate maximization failed to predict group sizes exceeding two.

size and DEE would be less negative than we calculated. Finally, the slope of the relationship between  $x$  (for  $x > 1$ ) and net rate of acquisition would be more negative than we calculated (Fig. 3). Thus, if encounter rate increases with pack size, our conclusion that  $G^* = \hat{G} = 2$  would only be reinforced.

### Risk-sensitive Foraging

Here, we consider whether an alternative foraging currency could account for large pack size. Specifically, it remains possible that the trend towards lower variation in per capita prey acquisition rates in larger groups (Fig. 1) translates into reduced risk of energetic shortfall. To calculate the risk of energetic shortfall based on risk-sensitive foraging theory (Stephens 1981), we estimated the minimum rate of per capita consumption required to avoid energetic shortfall ( $R$ ), and for each pack size category  $i$ , the average ( $\mu_i$ ) and standard deviation ( $\sigma_i$ ) of net per capita consumption rate. Based on these estimates and the assumption that average consumption during the period of data collection (typically  $\sim 44$  days) is normally distributed, we calculated the probability ( $P$ ) that wolves in pack size category  $i$  will fail to consume prey at a rate that exceeds their minimum daily requirements:

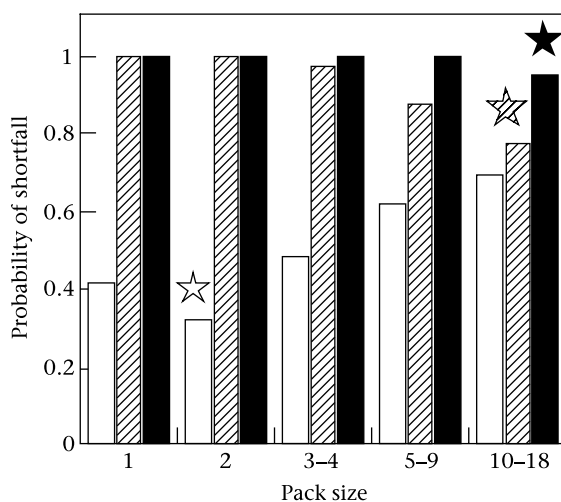
$$P_i = \Phi[(R - \mu_i)/\sigma_i], \quad (5)$$

where  $\Phi$  is the cumulative normal distribution. Our estimate of  $R$  was based on the assumption that a wolf's daily BMR is 3724 kJ (see previous section). By further assuming that a wolf expends energy at a daily rate falling between three times and five times the BMR (Gorman et al. 1998), and that the consumable portion of ungulate prey contains 6800 kJ/kg (Creel 1997),  $R$  lies between 2.55 and 4.25 kg of prey per day.

The predicted risk of shortfall was high for all pack sizes (Fig. 4). Unless competition between pack members for food consists of pure scramble competition, and does not include elements of contest competition (*sensu* Nicholson 1955; see also Hassell 1975), the actual risk of shortfall may be less than we predict. However, high risk of shortfall is consistent with the relatively high annual mortality observed for Isle Royale wolves. For the years between 1971 and 2001, the median annual mortality rate was 0.22 (interquartile range 0.12–0.42) (Peterson et al. 1998, unpublished data).

Notwithstanding any potential for overestimating risk of shortfall, our primary interest was in making comparisons of the relative risk among pack size categories. In this regard, our analysis indicated that a wolf is most likely to meet its energetic requirement if it forages with just one other wolf (Fig. 4). Moreover, its risk of shortfall would be higher in a group of three or more than as a solitary individual. This analysis contradicts the hypothesis that wolves forage in packs because solitary individuals would be unable to reliably capture their usually large prey (Mech 1970). Indeed, our analysis suggests that a solitary wolf preying upon moose would be more likely to meet its energetic demands than if it foraged in a pack comprising three or more individuals (Fig. 4). Because a solitary individual would be better off remaining as such rather than joining a pair, foraging in groups of three or more does not appear to be a risk-averse foraging strategy.

These inferences apply if  $R$  lies between 2 and 10.5 kg. Figure 4 is based on mean net rates of acquisition for an assumed average per capita metabolic cost of three times the BMR for wolves in a pack of any size. However, the pattern depicted in Fig. 4 is qualitatively unaffected by any combination of costs generated by the sensitivity analysis (described above).



**Figure 4.** The probability (equation (5)) of failing to acquire adequate food (over a 50-day period) when the loss to scavengers equals 0 kg/day (□), 2 kg/day (▨) and 10 kg/day (■). Methods and assumptions are based on risk-sensitive foraging theory (see text for details). Stars indicate predicted group size for each level of scavenging. In the absence of scavenging, risk-sensitive foraging theory failed to predict group sizes exceeding two.

## Genetic Relatedness and Group Size

Under some but not all conditions, larger groups are predicted by social foraging theory when the influence of genetic relatedness is considered (Giraldeau & Caraco 1993; reviewed by Giraldeau & Caraco 2000). Larger groups arise because the direct fitness cost of reduced per capita foraging rate incurred by group members could be offset by an indirect fitness benefit, provided group members are genetically related. That is, an individual's group membership can be determined by applying Hamilton's rule:

$$rE_R + E_S < 0, \quad (6)$$

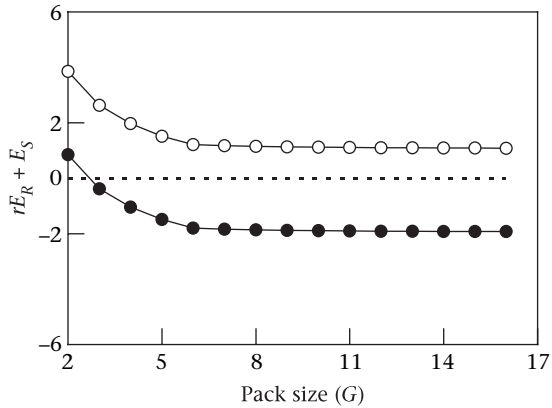
where  $r$  is the relatedness between individuals,  $E_R$  is the fitness consequence for an individual not in a group, and  $E_S$  is the fitness consequences for other group members (Giraldeau & Caraco 1993). The calculation of  $E_R$  and  $E_S$  and thus the determination of membership depend on whether group membership is free or controlled by the group (Giraldeau & Caraco 1993).

For wolves, the operative process is group-controlled eviction, rather than group-controlled entry, because close relatives of pack members are born into the pack. For these circumstances,  $E_R$  is  $\Omega_1 - \Omega_G$  and  $E_S$  is  $(G - 1)(\Omega_{G-1} - \Omega_G)$ , where  $\Omega_i$  is the fitness of individuals in a group of size  $i$ , and pack members should allow an individual to remain in the pack if  $rE_R + E_S$  is less than zero. By letting  $\Omega_i$  represent per capita rate of net prey acquisition, a surrogate of fitness, we applied our data (Fig. 3) to this inequality. The data indicate that a related individual should be evicted from a pack containing two or more other individuals (open symbols in Fig. 5), provided the evictee has already developed hunting skills and would be able to achieve the average net rate of intake of a solitary individual (i.e. the observed rate of intake for  $G = 1$  in Fig. 3). This result is expected because, although relatedness can lead to group sizes exceeding  $G^*$  (i.e. group size for which per capita intake is maximized), it cannot lead to group sizes exceeding  $\hat{G}$  (i.e. smallest group size for which intake rate falls below that of a solitary forager; Giraldeau & Caraco 1993).

However, packs with more than two other individuals should not evict immature offspring with undeveloped hunting skills (closed symbols in Fig. 5). Thus, although we can invoke kin selection to account for packs containing parents and their dependent young, we cannot account for packs (of up to 18 individuals) containing mature wolves other than parents. Although kin-directed altruism (parental nepotism) certainly favours sociality among wolves, it seems unable to explain the full range of sizes and compositions of wolf packs observed in nature (Fig. 1).

## Effect of Scavenging

Although the preceding analyses fail to explain why packs often contain more than two mature individuals, they overlook a key feature of wolf foraging ecology: loss of food to scavengers. To assess how raven scavenging might affect the predicted relationship between pack size



**Figure 5.** Application of Hamilton's rule (equation (6)) to predict whether individual mature (○) and individual immature (●) wolves should be evicted (or excluded) from various-sized packs comprising first-order relatives ( $r=0.5$ ). According to the theory of group-controlled membership, a pack should evict an individual when  $rE_R + E_S > 0$ , where  $E_R$  would be the fitness effect on the evicted individual, and  $E_S$  is the fitness effect of eviction on the current pack members. Mature individuals, with developed hunting skills, are assumed to achieve the average net rate of intake of a solitary individual (specifically, the gross intake for a solitaire indicated in Fig. 1 minus 1.6 kg/day; i.e. three times the basal metabolic rate) should they be evicted. Immature individuals, with undeveloped hunting skills, are assumed to be unable to obtain prey and would expend energy at three times the daily basal metabolic rate ( $(3 \times 3724 \text{ kJ/day}) / (6800 \text{ kJ/kg}) = -1.6 \text{ kg/day}$ ), should they be evicted. The value of  $G$  does not include the individual whose eviction is being considered. The net rate of prey (energy) acquisition (kg/day) is used as a surrogate for fitness (see curve with open symbols in Fig. 3).

and rate of foraging, we first calculated the number of days required for ravens and wolves to consume a carcass of a specified mass (i.e. 295 kg represents a typical adult moose carcass; Peterson 1977). The longevity of a carcass as a food source depends on pack size, daily rate of loss to scavengers, and daily consumption rate by a wolf when a carcass is available (assumed to be 20% of a wolf's body weight (Mech 1970) or 6.3 kg/day for Isle Royale wolves). We then calculated the number of kilograms consumed per wolf per kill based on the longevity of the carcass and the assumed per-wolf consumption rate. To obtain kilograms per wolf per day as a function of pack size and rate of loss to scavengers (Fig. 6), we multiplied kg per wolf per kill by kills/day, which also depends on pack size (Fig. 2b; equation (3)). Predictions (Fig. 6) are based on the reciprocal exponential curve (Fig. 1). Although Fig. 6 is based on mean net rate of acquisition for an assumed average per capita metabolic cost of three times the BMR for wolves (independent of pack size), the qualitative pattern depicted is unaffected by any of the patterns of costs described above for rate maximization.

Our calculations indicate that, by incorporating the effect of scavenging, foraging economics (i.e. both rate maximization (Fig. 6a) and shortfall minimization (Fig. 4)) favour the formation of large packs. More specifically, in the absence of scavenging,  $\hat{G} = G^*$  and wolves would be expected to hunt in pairs. However, as scavenging rates

increase,  $\hat{G}$  increases to substantially larger values (Fig. 6). Because the average net rate of intake varies little across a range of group size (Fig. 6), our analysis offers a foraging-based explanation not only for why wolves form large packs but also for why observed pack size varies so widely (Fig. 1).

Our analysis suggests that the cost of reduced per capita rate of consumption in larger packs (Fig. 1) is offset by the benefit of increased frequency of prey capture (Fig. 2b; see also Thurber & Peterson 1993; Hayes et al. 2000) and reduced loss of food to scavengers. By extension, if the potential loss to scavengers increases with prey size, then wolves that consistently hunt large prey (e.g. moose) should do so in large packs (Fig. 6a), but wolves that consistently hunt smaller prey (e.g. white-tailed deer, *Odocoileus virginianus*, ~88 kg) should do so in smaller packs (Fig. 6b). As predicted, field studies have found a positive association between prey size and pack size (Nudds 1978; C. Schiffer, T. A. Waite & J. A. Vucetich unpublished data).

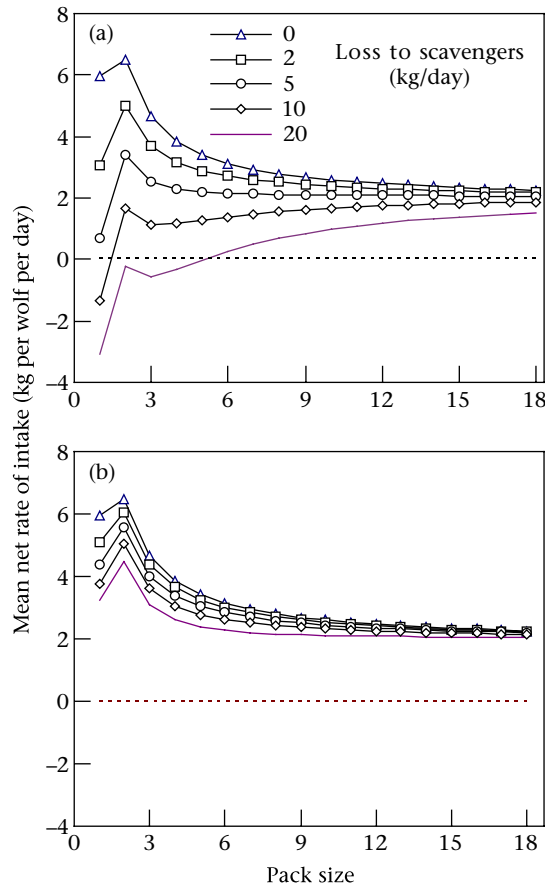
## GENERAL DISCUSSION

Individual wolves appear to maximize their foraging returns by foraging in large packs (Fig. 6a), particularly when prey are large (cf. Fig. 6a, b) and thus, vulnerability to scavenging losses is high. Sociality appears to be favoured because the benefits of reduced losses to scavengers outweigh the costs of increased food sharing among group members and increased hunting efforts. These conclusions contrast with prior claims that per capita rate of prey acquisition declines with pack size (Thurber & Peterson 1993; Schmidt & Mech 1997; Hayes et al. 2000).

Our analysis focuses on ravens because they are the most significant scavenger of wolf-killed prey throughout the geographical range of wolves and because losses to ravens (but not other species) have been quantified. However, to the extent that other scavengers (e.g. coyotes, foxes, eagles, etc.) contribute to substantial food losses that are not effectively minimized by agonistic behaviour, it may be said that wolves reduce losses to such scavengers by group living.

After accounting for pack size, wolves that prey upon moose kill substantially more prey (in biomass) than do wolves that prey upon white-tailed deer (Schmidt & Mech 1997). For example, a pack of four wolves that prey upon moose is estimated to capture 10 kg per wolf per day more than a pack of four wolves that prey upon deer (from equations reported in Schmidt & Mech 1997). Moose-eating wolves may capture more biomass of prey per capita, yet more of each carcass is lost to scavengers. Even when the difference in weight of each prey is considered, moose-eating wolves consume between 60 and 200% more individuals than deer-eating wolves. Thus, the total predation rate of a wolf population may depend on the interaction between prey size and kleptoparasitism.

Studies of kleptoparasitism have focused on assessing rates (e.g. Tuckwell & Nol 1997; Morissette & Himmelman 2000), negative impacts on host species (e.g. Finney et al.



**Figure 6.** Relationship between pack size and mean daily per capita net consumption for several hypothetical rates of daily loss to scavenging, where prey is either (a) moose-sized or (b) deer-sized (see text for details). Consistent with observed group sizes (Nudds 1978), wolves foraging on large prey (a) must do so in larger groups than wolves foraging on small prey (b) to achieve positive mean net rates of intake.

2001), host mechanisms for reducing these impacts (e.g. Lahti et al. 1998; Goss-Custard et al. 1999; Stienen & Brenninkmeijer 1999), and fitness trade-offs associated with being a kleptoparasite (e.g. Whitehouse 1997; Broom & Ruxton 1998; Goss-Custard et al. 1998; Ruxton & Broom 1999). Most studies of kleptoparasitism have focused on bird and spider species (Higgins & Buskirk 1998; Stienen & Brenninkmeijer 1999). Our analysis complements this rich and growing literature of kleptoparasitism by highlighting the influence of scavenging on a behaviour as conspicuous as sociality.

Wolf–raven interactions may be relevant for understanding interactions between other scavengers and social carnivores. For example, social carnivores of Africa may lose substantial amounts of food to vultures (the dominant avian scavenger in Africa), and benefit from group living in a similar fashion to that shown here for group-living wolves. However, it may also be that vultures are more effectively repelled because they are larger and less mobile than ravens. Using a modelling approach similar to ours, Carbone et al. (1997) concluded that the cost of

increased food sharing in larger packs did not outweigh the benefits associated with reduced kleptoparasitism. However, this conclusion may be inaccurate because it fails to account for increases in hunting frequency and success known to occur with increasing pack size (Creel & Creel 1995). Regardless, kleptoparasitism results in extremely high energy expenditure in African wild dogs, *Lycaon pictus*, and would seem to be an important selective force in that species (Gorman et al. 1998).

If losses to scavengers represent a general selective pressure for large carnivores, then a fuller understanding of the evolutionary basis of sociality and asociality in carnivores may be emerging. Small carnivores that forage in groups tend to eat small prey that are spatially clumped throughout the environment. In these species, group foraging may increase foraging proficiency, provide antipredator defence, or both (Clutton-Brock et al. 1999). Small and medium-sized carnivores that forage singly but eat prey as large as themselves (e.g. some mustelids and vivrids) may not attract scavengers simply because their prey are so small. Some large carnivores that tend to eat large prey and are thus vulnerable to scavenging may minimize losses by foraging socially (e.g. African wild dogs, lions, *Panthero leo*, hyaenas, *Crocuta* spp., and coyotes, *Canis latrans*, that hunt deer). Other large carnivores that forage solitarily may rely on small prey that are not exploited by scavengers (e.g. maned wolves, *Chrysocyon brachyurus*, coyotes and wolves that feed on small prey; Peterson et al. 1984; Schaller 2000), or may eat large prey and reduce scavenger losses by alternative mechanisms. For example, solitary felids may avoid excessive scavenging by exploiting the cover of dense jungle vegetation or by caching prey in trees or under debris.

To conclude, the influence of raven scavenging appears to favour the evolutionary maintenance of wolf sociality. We have no doubt that the maintenance of sociality in wolves and other large carnivores is complex, and may often involve kin selection (Schmidt & Mech 1997) and/or better defence of carcasses from kleptoparasites (Caraco & Wolf 1975; Cooper 1991; Fanshawe & Fitzgibbons 1993). Nevertheless, the foraging economics examined here also seem to contribute to the maintenance of sociality in wolves and possibly other large carnivores, particularly those that hunt large prey and are thus vulnerable to scavenging losses.

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