

## Pack size and wolf pup survival: their relationship under varying ecological conditions

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**Summary.** The relationship between pack size and two parameters of reproductive success (litter size at 7–8 months and pup weights at 5–6 months) were determined for two wolf (*Canis lupus*) populations in northern Minnesota. Pup weights were not correlated with pack size for either population. Litter size, however, was correlated with pack size, but the direction of the relationship varied between the two study populations.

In the superior National Forest, where prey were scarce and the wolf population was declining from high densities, litter size and pack size were inversely related. Pairs produced more surviving pups than did larger packs with one or more potential helpers. In the Beltrami Island State Forest, where prey were relatively abundant and the wolf population was increasing, pack size and litter size were positively correlated. The results suggest that ecological factors, such as prey availability, affected the ability or willingness of various pack members to provide food or other care for the pups.

The lack of correlation between number of auxiliaries and number of pups in canid populations with low and declining prey densities may be explained on the basis of heterogeneous prey density resulting in drastic annual variation in litter production. No study to date has measured the actual benefit that pups derive from helping by auxiliaries, and the costs and benefits of it. The relationships discussed herein can be considered valid only after such research is completed.

### Introduction

‘Helping’ has been reported in an increasing number of birds and mammals. This is the phenomenon in which older, potentially reproductive offspring (‘auxiliaries’) help feed and/or protect their younger siblings. Because auxiliaries defer breeding, but foster the breeding success of relatives, altruism has been postulated, with kin selection the likely evolutionary pathway (Skutch 1961; Fry 1972; Brown 1974; Ricklefs 1975). Other explanations allege that auxiliaries may benefit more directly through increased personal fitness, while their effects on relatives’ fitness may be trivial, or even negative (Zahavi 1974). Thus the evolutionary pathway to helping may involve a complex interaction of individual and kin selection (Brown 1978; Emlen 1978).

Auxiliaries occur in a number of canids including blackbacked and golden jackals (*Canis mesomelas*, *C. aureus*), coyotes (*C. latrans*), wolves (*C. lupus*), red foxes (*Vulpes vulpes*), arctic foxes (*Alopex lagopus*), dholes (*Cuon alpinus*), and African wild dogs (*Lycaon pictus*) (Murie 1944; Ryden 1975; Camenzind 1978; Macdonald 1979, 1980; Moehlman 1979, 1981, 1983; Montgomerie 1981; Bekoff and Wells 1980, in press; Johnsingh 1980; Hersteinssen and Macdonald 1982; Malcolm and Marten 1982).

For only a few species, however, have the effects of auxiliaries on the pups, or parents (Brown et al. 1978), been assessed quantitatively. Moehlman (1979, 1983) showed that increased numbers of auxiliaries were associated with significantly greater pup survival through 14 weeks of age in blackbacked and golden jackals. For both species,

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prey appeared to be plentiful and relatively easy to acquire for both parents and auxiliaries. Malcolm and Marten (1982) found that the correlation between the number of adults in a pack and pup survival in African wild dogs was positive, but the correlation was not significant unless total breeding failures were eliminated from the analysis. The effect of yearlings on pup survival appeared to depend on food availability, being associated with increased pup survival under good food conditions but with decreased pup survival during food scarcity (Malcolm and Marten 1982). Throughout the study, the wild dog population was declining (Frame et al. 1979). These studies suggest that the effects of helping and/or the probability of its expression, depends on prevailing environmental conditions influencing food availability (Macdonald and Moehlman 1982).

Helping occurs in both wild (Murie 1944) and captive (Fentress and Ryon 1982) wolf packs. A wolf pack is a family usually derived from a single mated pair (Mech 1970). Young typically remain with their pack for at least 10 months and sometimes to 4 years without breeding (unpublished data). Generally, they associate closely with other pack members, and often spend more time with pups than do the parents, sometimes feeding and/or protecting them (Murie 1944; Haber 1977; Harrington and Mech 1982). In captivity, pup-care by non-parent wolves is common, although important individual differences may exist (Fentress and Ryon 1982). Thus the case for kin-selected helping in wolves appears strong despite a recent study questioning the role that auxiliaries play in pup survival during prey declines (Harrington and Mech 1982).

The objective of the present study was to determine the relationship between auxiliary presence and pup survival for two wolf populations in northern Minnesota. One population was expanding from a low density with abundant prey. There, auxiliaries may easily meet their own food needs and may be able to provide food to pups with relatively little cost to themselves, thereby increasing total food available to the litter. Thus we hypothesized that helping should be common in this population, and the effects of auxiliary presence should be positive. In the second population, wolf densities were declining following a drastic decrease of the major prey. Under such conditions, auxiliaries may have difficulty meeting their own food requirements and consequently be less able or willing to provide food to pups. In some cases, they may intercept food potentially available to pups. Thus we hypothesized that in the latter pop-

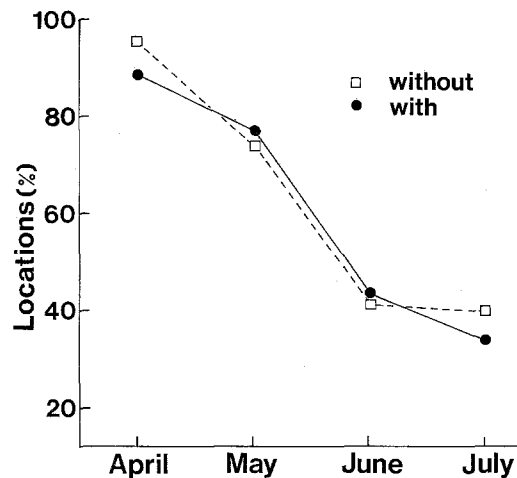


Fig. 1. Percentage of time that the Harris Lake pack breeding female was located at the den in relation to the number of auxiliaries in the pack. The pups were born in late April, and probably were weaned by early June. Years and monthly number of radio locations for determining percent time at den: with auxiliaries during 1973, 1976, 1977–46, 49, 32, 38; without auxiliaries during 1972 and 1975–25, 42, 17, 20

ulation helping should be less common and that the effects of auxiliary presence should be neutral or negative. If such relationships are found, this would tend to support the hypothesis that the expression of helping is dependent on its relative costs.

For both populations, the wolves could only be observed from an aircraft, and then primarily between early December and mid-April (Mech 1974). Thus we could not observe helping directly, but had to infer it from the presence of auxiliaries around summer homesites and with the pack. For this reason, we use the term 'auxiliary' rather than 'helper' throughout the paper.

## Study areas and methods

The study areas are located 250 km apart within 'primary' wolf range (Leirfallom 1970) in Minnesota. The increasing wolf population inhabited the Beltrami Island State Forest (BISF) in northwestern Minnesota (Fritts and Mech 1981), and the declining population inhabited the Superior National Forest (SNF) in northeastern Minnesota (Mech 1977a, 1980). The topography of both areas is generally characterized by low relief, with poorly-drained soils interspersed with drier ridges supporting mixed deciduous-coniferous forest. Percent forest cover and constituent species are similar between areas, and both have been heavily logged in recent decades, although some virgin boreal forest remains in the SNF. Both areas experience relatively cool summers, and long cold winters, but the SNF generally has longer and deeper snow accumulations.

Wolves have been live-trapped, radio-collared, and followed by light-aircraft in the SNF since 1968 (Mech and Frenzel 1971; Mech 1973; 1977a, b, 1980). Wolf densities there ap-

proached one wolf/26 km<sup>2</sup> in the early 1970's (Mech 1973), but then declined by over 40% (Mech 1977a) as the wolves' major prey, white-tailed deer (*Odocoileus virginianus*), declined drastically beginning in 1968 (Mech and Karns 1977). Deer densities prior to the decline were estimated at about 3.5/km<sup>2</sup> (Stenlund 1955) and by 1976, at less than 1 deer per km<sup>2</sup> (Floyd et al. 1979). During the pup-rearing season, moose (*Alces alces*) calves, and beaver (*Castor canadensis*) were alternate prey, but neither formed a high percentage of the wolf's diet (Van Ballenberghe et al. 1975, Frenzel 1974).

Wolves were radio-collared and aerially radio-tracked in the BISF between 1972 and 1977 (Fritts and Mech 1981), during which their densities doubled from one/77 km<sup>2</sup> to one/39 km<sup>2</sup>, apparently because of reduced human-related mortality following legal protection of the population. Deer densities were greater (4–6 deer/km<sup>2</sup>) than those in the SNF. Moose calves and beaver were also available as alternate summer prey.

During several weeks before parturition (April), we obtained pack-size data allowing us to determine the approximate number of auxiliaries. Because generally only one pair of animals breeds in each pack (Mech 1977a), the number of auxiliaries equals spring pack size minus two. Usually only one or a few pack members were radiocollared; thus we could not determine reliably the age or age-class (yearling or adult) of auxiliaries, especially for the larger packs. During the crucial pup-rearing period – May through September – emigration and mortality of auxiliaries was minimal (Mech 1977a; Fritts and Mech 1981). Immigration into packs during this period has not been documented, and rarely occurs at other times (Fritts and Mech 1981, Mech, unpublished observation).

Our data on pup survival and fitness had to be collected during fall live-trapping and winter aerial observations. Between parturition and early December, pup development is rapid, and virtually all natural pup mortality occurred then (Van Ballenberghe and Mech 1975; Mech 1977a). Most natural pup mortality was related to malnutrition (Seal et al. 1975), a factor likely to be affected by helping. After early December, most pup mortality was human-caused (Mech 1977a). Thus we used the first accurate pack-size data in December to estimate natural pup survival.

December pack size is a function of (1) April pack size, (2) emigration and mortality of auxiliaries and breeders, and (3) recruitment of pups. Because most emigration or mortality of older, non-radioed pack members was unknown, we could not determine exact litter size for all packs. Thus for 10 of 36 pack-years, we calculated minimum and maximum estimates for December litter size. Maximum litter size was determined under the assumption that all unknown pack members were pups (maximum litter size = December pack size minus breeding pair minus known auxiliaries). Minimum litter size was calculated assuming no emigration or mortality of breeders or auxiliaries between April and December (minimum litter size = December pack size minus April pack size).

Spearman rank correlation coefficients ( $r_s$ ) (Siegel 1956) were calculated using minimum and maximum estimates for both number of auxiliaries and size of litters in December. Because of the uncertainty in calculating the quantities, the four correlation coefficients calculated for each population should place approximate boundaries on the actual relationship between the variables.

An assumption of the above test is that initial litter size was sufficiently large to reveal significant changes by December. Litter sizes in other populations (Rausch 1967; Pimlott et al. 1969; Kuyt 1972), and earlier in ours (Stenlund 1955) were usually up to twice as large as our December litters were, suggesting that pup mortality was a significant factor in our study. However, the SNF population was food-stressed (Seal et al.

1975; Van Ballenberghe and Mech 1975; Mech 1977a, b). Abnormally small litters but high survival rates could have occurred there, making December litter size a poor index of the effects of auxiliaries. Thus we supplemented our measure of quantity with one of quality, as reflected by pup weight.

Pups were weighed during late summer and fall trapping, usually in September and October, when 5–6 months old. Their ages were estimated, assuming birth during April.

Parturition dates over a long period might vary by as much as 5 weeks in a given area (Mech and Knick 1978), but during a particular year, most wolves probably are born within a 7–10-day period (Mech 1970; J. Ryon, personal communication). Furthermore, pups from a single litter can vary considerably in weight (Van Ballenberghe and Mech 1975). Thus the ranges of pup weights noted within any year (Tables 1 and 2) cannot be accounted for solely by differences in the parturition dates. We compared pup weights with those of same-age, captive-reared pups as a standard (Kuyt 1972; Van Ballenberghe and Mech 1975) to allow comparison of pups of various ages. We then tried to correlate these relative weights (%) with both maximum and minimum number of auxiliaries.

Litter size at birth could influence pup weight; i.e., pups of large litters may be smaller than pups from small litters. Therefore, we used Spearman rank correlations to test the association between December litter size and pup relative weight. These correlations were initially attempted for data from packs for which December litter size was accurately known.

Because helpers may benefit parents more directly through foraging relief (Brown et al. 1978), we examined the relationship between the presence of auxiliaries and the attendance of a particular breeding female at her den. This female (wolf 2407) was radio-collared in 1971 and was radio-tracked through 1978 (Mech 1977b, 1980). An influence of the auxiliaries on the female's foraging budget might be indicated by a change in her attendance patterns at the den. We could not obtain similar data from any other females in either study area.

## Results

### Superior National Forest

Data were available for nine wolf packs (including pairs), for a total of 24 pack-years between 1970 and 1978 (Table 1). The Spearman correlations between litter size and number of auxiliaries (Table 3) demonstrated that increased numbers of auxiliaries were associated with smaller December litters. All four correlations were negative, and two were statistically significant. Overall, pairs without auxiliaries produced surviving litter sizes ( $n=9$ ) that were slightly larger than ( $\bar{x}=3.1$  vs 2.6;  $n=15$ ; Mann-Whitney  $U=76.5$ ,  $P>0.2$ ) or significantly larger than ( $\bar{x}=3.1$  vs 1.9;  $n=15$ ; Mann-Whitney  $U=96$ ,  $P=0.05$ ) pairs with varying numbers of auxiliaries, based on maximum and minimum litter size estimates. Similar trends were evident within the same pack over several years (Table 1). (The Harris Lake pack had the same breeding female from 1972 through 1978, suggesting that variation in surviving litter size was not systematically related to age of breeding female.) Thus any effect attrib-



**Table 1.** Number of auxiliaries and parameters of reproductive success of wolf packs or pairs in the Superior National Forest, Minnesota

Pack	Year	No. of auxiliaries	Surviving <sup>a</sup> litter size	Relative weights (%) of pups captured <sup>b</sup>
Harris Lake	1971	2-4	1	73
Harris Lake	1972	0	2	86, 106
Harris Lake	1973	1-2	0	—
Harris Lake	1975	0	3	—
Harris Lake	1976	2-3	2-3	110, 157
Harris Lake	1977	2-3	1-2	103, 118, 127
Perch Lake	1974	0	3	75, 89, 96
Perch Lake	1975	3	3	107
Perch Lake	1976	3-4	0	—
Perch Lake	1977	0	4	98, 103, 113, 113
Quadga Lake	1973	0	1	58, 66, 70
Quadga Lake	1974	1	3	92, 114
Quadga Lake	1975	3	1-3	76
Quadga Lake	1976	2-3	1	54
Jackpine	1970	2-3	3	59, 80, 84
Jackpine	1972	2	3	47, 62, 68, 88
Jackpine	1973	3	2	51, 59, 62, 69
Wood Lake	1976	0	7	—
Wood Lake	1977	3-6	1-5	—
Maniwaki Lake	1974	4-7	3-6	84, 97, 103
Argo Lake	1976	0	3	—
Argo Lake	1977	1-2	4	—
L. Gabbro Lake	1978	0	3	75
Dent Lake	1975	0	2	—

<sup>a</sup> At least to December (7 months of age)<sup>b</sup> Relative weight

$$= \frac{\text{weight of pup at capture}}{\text{weight of same-age captive-reared pups}} \times 100.$$

Includes pups captured in fall which perished prior to December

utable to the presence and number of auxiliaries was a decrease in the number of pups surviving to December.

Neither correlation between number of auxiliaries and pup weight was significant (Table 3). Overall, pairs without auxiliaries produced pups of similar weight to those of pairs with auxiliaries (Mann-Whitney  $U=183$ ,  $n=14$ ,  $25$ ,  $P>0.2$ ). Pup weights tended to vary among years (Kruskal-Wallis test,  $0.05 < P < 0.10$ ), perhaps reflecting yearly variation in parturition, but within a given year, packs with or without auxiliaries produced pups of similar relative weight (Table 1).

The relationship between litter size and pup relative weight, determined for packs with known litter size (Table 1), was positive and significant ( $r_s = 0.37$ ,  $n=29$ ,  $P<0.05$ ), indicating that larger litters tended to have larger pups. With the remainder of the data included, the correlation was weaker but still significant ( $r_s = 0.30$ ,  $n=39$ ,  $P<0.05$ ).

**Table 2.** Number of auxiliaries and parameters of reproductive success of wolf packs or pairs in the Beltrami Island State Forest, Minnesota

Pack	Year	No. of auxiliaries	Surviving <sup>a</sup> litter size	Relative weight (%) of pups captured <sup>b</sup>
Bankton	1975	0	2	105
Bankton	1976	2	3	—
Clear River	1973	2	4-5	120
Clear River	1974	3-4	4-5	86, 98, 122
Clear River	1975	2-4	0-1	—
Faunce	1973	1	3	71, 85
Faunce	1975	0	1	—
Faunce	1976	0	2	—
Peet's	1975	4	5	80, 98, 98, 114
Rapid River	1975	3	3-6	—
Vacuum	1975	3	4-6	—
Vacuum	1976	4	3	—

<sup>a</sup> At least to December (7 months of age)<sup>b</sup> Relative weight

$$= \frac{\text{weight of pup at capture}}{\text{weight of same-age captive-reared pups}} \times 100.$$

Includes pups captured in fall which perished prior to December

Breeding female 2407 of the Harris Lake pack was radio-tracked from fall 1971 through 1978. Her monthly pattern of den attendance did not vary with the absence or presence of auxiliaries (Fig. 1), which ranged from none to as many as 3 during 4 breeding seasons. (In 1974 and 1978, she apparently produced no pups.)

#### Beltrami Island State Forest

Data were obtained from 3 pairs and 9 larger packs (12 pack-years) in the BISF (Table 2). All four correlations between number of auxiliaries and December litter size were positive, and two were statistically significant (Table 2). Mean maximum and minimum December litter sizes for pairs with auxiliaries ( $\bar{x}=4.1$  and  $3.2$ ;  $n=9$ ) were significantly larger than litter sizes for pairs without auxiliaries ( $\bar{x}=1.7$ ;  $n=3$ ; Mann-Whitney  $U=24.5$  and  $24$ ;  $n=3.9$ ;  $P<0.05$ ).

The correlations between pup relative weight and number of auxiliaries were both positive but not significant (Table 3). No significant correlation was found between pup relative weight and December litter size ( $r_s=0.10$ ,  $n=11$ ,  $P>0.05$ ).

#### Comparisons between study areas

Both minimum and maximum estimates of December litter sizes were compared between study areas, but none of the 4 comparisons differed sig-

**Table 3.** Spearman rank correlation coefficients between number of auxiliaries and (a) December litter sizes and (b) pup relative weights for wolf packs in two areas of northern Minnesota

		Number of auxiliaries	
		Minimum	Maximum
<i>Superior National Forest</i>			
(a) December			
Litter	Minimum	-0.38 *	-0.45 *
Size (n=24)	Maximum	-0.01 (ns)	-0.07 (ns)
(b) Pup			
Relative			
Weight (n=39)		-0.15 (ns)	-0.03 (ns)
<i>Beltrami Island State Forest</i>			
(a) December			
Litter	Minimum	+0.69 *	+0.42 (ns)
Size (n=12)	Maximum	+0.68 *	+0.45 (ns)
(b) Pup			
Relative			
Weight (n=11)		+0.06 (ns)	+0.15 (ns)

\*  $P < 0.05$

nificantly (Mann-Whitney  $U$ -test). Mean litter sizes in the two areas did not appear to differ for pairs (3.1 vs 1.7) or for packs with 1–2 auxiliaries (2.3–3.0 and 1.8–2.7 vs 3.0 and 2.3–3.0). The major difference in mean litter size occurred for packs with 3 or more auxiliaries. In the SNF, mean litter sizes were 1.4–2.6 and 1.3–3.0 for packs with 3 and 4+ auxiliaries, whereas the corresponding figures for the BISF were 3.7–5.7 and 4.0.

Pup relative weights did not vary significantly between the study areas, either as a function of number of auxiliaries or of December litter size (cf. Tables 1 and 2).

## Discussion

The results support our original hypotheses. Where prey availability was high and the wolf population was increasing, the correlation between April pack size and December litter size was positive. Where prey were scarce and the wolf population was declining, the correlation between initial pack size and subsequent litter size was absent or negative. The correlations between pack size and pup weight were weak, but followed the same expected pattern. If April pack size reflected the number of helpers available during summer, prey availability may have influenced either the overall effectiveness, or the individual expression, of helping behaviors.

If decreasing prey availability diminishes an individual's ability to provision the pups, but not its willingness, we would expect a continued positive correlation between number of auxiliaries and amount of food provisioned, despite an overall reduction in food provided for the litter. On the other hand, if individual rates of provisioning differentially decline as prey declines, if some individuals stop provisioning and others begin to pilfer food intended or available for the pups, then we would expect to see an increasingly negative relationship between number of auxiliaries and litter size develop as prey availability declines. We found the latter, which suggests that the degree to which helping was expressed varied among individuals and was related to food availability, as found elsewhere for yearling African wild dogs (Malcolm and Marten 1982).

Previous studies have provided evidence that nonbreeding yearling and adult wolves could hinder pup survival. Auxiliaries are sometimes fed at the den by other individuals, or they may raid caches near the den (Murie 1944; Haber 1977), thus intercepting food potentially available for the pups. At dens of two packs in the SNF, patterns of den attendance suggested that auxiliaries were not actively foraging (Harrington and Mech 1982). In addition, these patterns did not support the hypothesis that auxiliaries provided protection for pups. Other studies have shown that auxiliaries are more reluctant to confront dangers at the den than are the parents (Murie 1944; Haber 1977; Harrington and Mech 1979). Auxiliaries in the SNF were more likely exploiting the den area as a center of food exchange, or because information about likely foraging areas was readily available there (Harrington and Mech 1982).

In captive wolves, similar individual differences in food provisioning and pup protection have been reported (Fentress and Ryon 1982; Zimen 1975, 1982). For example, yearlings will feed pups and are fed by adults, whereas adults will feed pups but are rarely if ever fed by others (Fentress and Ryon 1982). In the present study, we could not reliably distinguish adult from yearling auxiliaries. If these age classes differed in their effects on pup survival, especially in the SNF, these effects would vary with pack composition and could account for some of the variation noted in the correlation between the number of auxiliaries and both December litter size and relative weights of pups.

Auxiliaries remain associated with their natal pack, rather than emigrate and attempt to breed, for any number of reasons (see reviews by Brown 1978; Emlen 1978, 1982) that need not be asso-

**Table 4.** Relationships among pack size, pup survival and prey availability in the Canidae

Species	Correlation between pack size and surviving litter size <sup>a</sup>			Relative prey size	Relative prey density	Difficulty of prey capture <sup>b</sup>
	$r_s$	( $n$ )	$P$			
<i>Canis mesomelas</i> <sup>c</sup>	+0.61	(18)	<0.01	Small (medium)	Moderate to high	1, (2, 3)
<i>Canis aureus</i> <sup>c</sup>	+0.49	(13)	<0.05	Small	High	1, (2, 3)
<i>Canis latrans</i> <sup>d</sup>	+0.37	(7)	ns	Small	High	1
<i>Canis lupus</i> SNF	-0.01 to -0.45	(24)	ns <0.05	Medium to large	Low	2, (3)
BISF	+0.42 to +0.69	(12)	ns <0.05	Medium to large	Moderate	2, (3)
<i>Lycan pictus</i> <sup>e</sup>	+0.40	(17)	ns	Medium to large	Moderate to high	2, 3

<sup>a</sup> Ages at which pup survival was determined: *C. mesomelas*, *C. aureus* at 14 weeks; *C. lupus* at 7–8 months; *L. pictus* at 12 months, *C. latrans* at 5–6 months

<sup>b</sup> Difficulty of prey capture: 1 single animal is effective, experience of less importance; 2 single animal can be effective with adequate experience; 3 single animal relatively ineffective, with group hunting a usual requisite for success. Parentheses indicate options that are relatively uncommon during the pup-rearing season

<sup>c</sup> From Moehlman (1979, 1983) and Macdonald and Moehlman (1982)

<sup>d</sup> From Bekoff and Wells (in press)

<sup>e</sup> From Malcolm and Marten (1982)

ciated with helping. Because they remain, the auxiliaries have the opportunity to help, making helping an ontogenetic epiphenomenon of nondispersal and postponed breeding (Packard et al. 1983), based on more immediate circumstances.

A helping decision based on immediate conditions should involve considerable variation, both in the extent and manner of helping. Below we will consider how prey availability, probably among the most influential of factors, may influence the expression of helping.

The ability of individuals to provision both themselves and the pups would depend on the species, age, condition, and density of prey. Under prey conditions favorable to wolves, individual needs would be more easily met, permitting a greater average contribution to the young. As prey conditions decline, the costs of meeting individual needs would rise and eventually would not permit the provisioning of young. The point at which individuals cease to help should vary; younger animals or those in poor condition probably would be among the first to hesitate to feed the pups.

Helping costs and an individual's influence on pup fitness would change, however, as individuals acquire experience or as prey conditions change (see Malcolm and Marten 1982). Such variability would obscure the relationship between overall pack size and pup survival, not only on a population-wide basis, but also within a single pack during one breeding season.

The above considerations may help explain some of the variation in the relationships between pack size and pup survival in the various canids (Table 4). The prey size, density, and the difficulty of capture for the species varied considerably during the period of crucial pup development. For coyotes and both jackals, prey are relatively small, apparently plentiful during the denning season, and relatively easy to capture, especially for younger animals (Moehlman 1979, 1983; Macdonald and Moehlman 1982; Bekoff and Wells, in press). Thus all or most individuals should have been capable of provisioning pups, and individual differences in helping should have been slight, resulting in significant positive correlations between pack size and pup survival (Table 4).

For African wild dogs and wolves, on the other hand, prey are larger, more difficult to capture, and in many cases require extensive experience before individuals are proficient hunters (Mech 1970; Sullivan 1978, 1979; Haber 1977; Malcolm and Marten 1982). Therefore, the relationship between pack size and pup survival would be expected to vary relative to those parameters which most affect the availability of prey for individual animals, especially for those auxiliaries that may have less at stake in regard to pup survival. If prey availability is high, the relationship between pack size and pup survival should be positive and high; as prey availability declines, the relationship should weaken, vary, and eventually reverse. For both Af-

ican wild dogs and wolves, such changes have been noted (Malcolm and Marten 1982; this study) (see Table 4).

We believe that the relationships discussed above are real and significant in the lives of several canid species. Nevertheless, we must point out that the degree of actual benefit that pups derive from helping by auxiliaries has not been measured in any canid. Rather the alleged benefits of helping have been based either on correlations between number of auxiliaries and pup survival or on comparisons of relative differences in provisioning and protection provided by parents and auxiliaries. Zahavi (1974) has pointed out that the positive correlations between numbers of auxiliaries and survival of young in birds may be the result of food abundance in the parents' territory (but see Brown et al. (1982) for experimental verification of auxiliaries' effects for one bird species). With adequate or abundant food, the number of both auxiliaries (usually yearlings) and young should usually be high. Conversely, with less food, the numbers of both auxiliaries and young should be low. This would be true quite aside from any helping the auxiliaries might do.

Furthermore, a lack of correlation between number of auxiliaries and number of pups in canid populations with low and declining prey densities, including ours, can also be explained without resorting to the helping concept. In such low prey populations, prey density will often or usually be heterogeneous (Mech and Karns 1977, Peterson 1977). Thus some wolf packs will have more prey than others. Those having a certain prey density in such a declining population may be able to support a larger litter of offspring one year, some of which could become auxiliaries, but may then have so depleted their prey that they are unable to support pups the next year. Such a situation could lead to negative correlations between numbers of auxiliaries and numbers of pups, quite independent of any helping.

Therefore, the most important research remaining in the area of canid helping is to determine the actual amount of helping conducted by auxiliaries, and the costs and benefits of it. Only after such research is completed can we be certain that the relations discussed above are valid.

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