

WOLF PACK SIZE AND FOOD ACQUISITION

PAUL A. SCHMIDT¹ AND L. DAVID MECH^{2,*}¹Department of Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55108;²Patuxent Wildlife Research Center, National Biological Service, Laurel, Maryland 20708

Submitted September 18, 1996; Revised March 21, 1997; Accepted March 31, 1997

*

Many workers have proposed or accepted the idea that the reason gray wolves (*Canis lupus*) live in groups, or packs, is because group hunting facilitates their acquisition of large prey (Murie 1944; Mech 1970; Zimen 1976; Nudds 1978; Pulliam and Caraco 1978; Bekoff and Wells 1980; Rodman 1981). In other words, a pack of eight wolves, for example, would be more than twice as successful as a pack of four. If this proposal is valid, then the amount of food acquired per individual should increase as pack size increases, at least to some optimal size (Nudds 1978).

Nudds (1978) utilized sparse data from the literature and detected an apparent relationship between wolf pack size and food acquired per wolf that implied that packs smaller than optimal size acquired substantially less food per wolf than those of optimal size. He also speculated that there were different optimal pack sizes for wolves preying on moose (*Alces alces*) and other large prey than for those preying principally on deer (*Odocoileus virginianus*), by analogy to the situation described by Caraco and Wolf (1975) for lions (*Panthera leo*).

However, Thurber and Peterson (1993) used considerably more data and demonstrated that for wolves preying primarily on moose on Isle Royale, food acquisition per wolf decreased with increased pack size. Hayes (1995) found the same for wolves preying on moose and caribou (*Rangifer tarandus*), and Dale et al. (1995) concluded that the larger packs they observed killing moose, caribou, and Dall sheep (*Ovis dalli*) acquired no more food per wolf than did the smaller packs. Their findings not only contradicted Nudds's (1978) notion of optimal pack size but also tended to refute the claim that wolves live in packs in order to facilitate the killing of larger prey. The relationship that Thurber and Peterson (1993) found implied that, for example, each member of packs of six to 12 gained only 60%–70% of the food that single wolves or pairs acquired. Hayes's (1995) figures indicated that each member of packs of six to 12 acquired only 35%–60% of the food that individual pair members did. In neither

* Address for correspondence and reprints; current address: North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, Minnesota 55108; E-mail: Mechx002@tc.umn.edu.

TABLE 1
SYNOPSIS OF INFORMATION ON WHICH ANALYSES AND FIGURES ARE BASED

Prey and Pack Size	<i>N</i>	Food Acquired (kg/wolf/d)	Reference
White-tailed deer:			
3	1	4.5	Stenlund 1955
5	1	.6	Mech and Frenzel 1971
8	1	3.7	Kolenosky 1972
2-9	4	1.6-3.6	Mech 1977
2-7	20	.5-6.8	Fritts and Mech 1981
Moose:			
4	1	1.8	Mech 1977
6-11	6	4.1-12.1	Fuller and Keith 1980
2-9	8	3.5-19.9	Ballard et al. 1987
2-17	5	5.5-14.6	Peterson et al. 1984
4-11	5	8.7-24.8	Dale et al. 1994
Moose/caribou, 2-20	45	2.5-45.2	Hayes 1995*
Caribou:			
4-8	3	5.7-10.2	Ballard et al. 1987
2-15	13	8.6-24.8	Dale et al. 1994
Dall sheep, 6-13	3	8.7-17.9	Dale et al. 1994
Bison, 7-13	8	3.5-7.4	Carbyn et al. 1993
Total	124		

NOTE.—Complete table of data for each data point on figures is available from L. D. Mech.

* Only combined data for moose and caribou were presented.

study was there evidence that packs of three to five obtained more food per wolf than pairs did, contrary to Nudds's (1978) preliminary finding.

Thurber and Peterson's (1993) study involved a single population of wolves and a single prey animal; Hayes's (1995) investigation included two prey species. Here we examine the literature based on wolf populations in many areas and involving several prey species to better evaluate the relationship between wolf pack size and food acquisition and its implications for the optimal pack size hypothesis or the hypothesis that wolves live in groups to facilitate killing larger prey.

We examined predation rates from 11 studies completed between 1971 and 1989 involving the following prey species: white-tailed deer, moose, sheep, caribou, and bison (*Bison bison*) (table 1). We converted reported predation rates to kilograms per wolf per day using two approaches. Either weight estimates of kills were already provided in the individual studies or the consumable weights of prey were based on conversion units outlined by Mech (1966).

We used logarithmic regression analysis (Microsoft 1995) to calculate the least-squares fit between pack size and kilograms per wolf per day. Analyses were completed using the individual prey species and also the aggregate data set. Because wolves preying on deer acquired considerably less food (0.5-6.8 kg/wolf/d) than wolves preying on moose and other species (2.5-45.2 kg/wolf/d), we also analyzed the data separately by deer and moose. Data for other prey species were too sparse to analyze separately.

The pack sizes in our review varied from two to 20 wolves, and the calculated

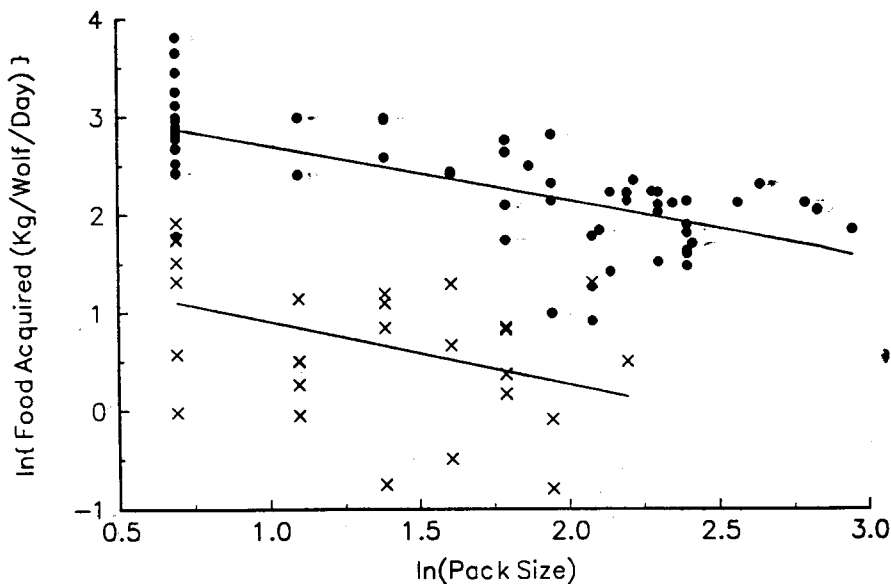


FIG. 1.—Relationship between amount of food acquired per wolf and wolf pack size for wolves preying on whitetailed deer (*crosses*) and on moose (*dots*). For deer, $\ln(y) = 1.5490 - 0.6438 \ln(x)$; $r^2 = 0.19$. For moose, $\ln(y) = 3.25494 - 0.5587 \ln(x)$; $r^2 = 0.47$ (table 1). Data for other prey species (table 1) not shown. For all data combined, $\ln(y) = -2.9973 \ln(x) + 14.202$; $r^2 = 0.07$.

number of kilograms of food acquired per wolf per day ranged from 0.5 to 45.2. The total data set, including wolves that preyed on more than one species, showed a negative curvilinear relationship between pack size and amount of food acquired ($y = -2.9973 \ln(x) + 14.202$; $r^2 = 0.07$). We found similar but stronger relationships when the data were examined separately for deer and for moose (fig. 1). No analysis showed an increase in food acquired per wolf with an increase in pack size.

We found no evidence that increased pack size resulted in increased food acquired per wolf. In fact, regardless of how the data were examined—using all data, using data by prey species, or using data by study area (Thurber and Peterson 1993; Hayes 1995)—the relationship indicated less food per wolf as pack size increased.

The relationship we found was weakest for the total data set. However, this was a result of a difference in scale between the data for wolves killing deer versus those killing other prey. Conceivably, the data for wolves killing deer represent underestimates (Fritts and Mech 1981; Fuller 1989). In any case, the individual analyses by prey species showed stronger relationships (fig. 1), similar to those for wolves preying on moose on Isle Royale ($r^2 = 0.30$; Thurber and Peterson 1993) and on moose and caribou in the Yukon ($r^2 = 0.40$; Hayes 1995).

This review includes data from wolves preying on several prey species in several areas, and they consistently show a negative relationship between pack size

and food acquisition per wolf, as does the other literature on the subject (Thurber and Peterson 1993; Hayes 1995). Taken together, these studies and our analysis provide strong evidence against the hypothesis that the reason wolves live in packs is to facilitate their predation on large prey.

We propose a kin-selection hypothesis to explain why wolves live in packs, as Schoener (1971), Rodman (1981), and Hayes (1995) also did, but for a slightly different reason. Most wolf packs consist of a pair of adults and their maturing offspring (Mech 1970). Almost all offspring disperse before 3 yr of age (Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987; Fuller 1989; Gese and Mech 1991). We believe that wolves live in packs primarily because adult pairs can then efficiently share with their offspring the surplus of food resulting from the pair's predation on large mammals. Single wolves can kill even their largest prey such as moose (Thurber and Peterson 1993) and bison (Carbyn et al. 1993), and even with large packs it is the adult pair that press the attack (Mech 1966, 1988).

The clearest support for our hypothesis comes from the fact that it is pairs of wolves, rather than, for example, packs of three or four, that acquire more food per wolf than does each member of larger packs on average (fig. 1). Furthermore, scavengers can usurp a high percentage of uneaten food (Promberger et al. 1993), so much of a pair's energetic profit could be lost. By bringing their young with them on hunts, pairs invest their energetic profit in their genetic heritage and maximize their energetic efficiency. Until they gain physical maturity and sufficient experience, the young likely obtain more food by remaining with their parents than by hunting on their own. In addition, they gain the hunting and killing experience that will further their survival after dispersal.

Evidence for a similar hypothesis for lion grouping was presented by Packer and Ruttan (1988) in contrast to earlier proposals emphasizing optimal foraging group size for that social species as well (Caraco and Wolf 1975).

ACKNOWLEDGMENTS

This study was supported by the U.S. National Biological Service and the U.S. National Forest Service North Central Forest Experiment Station. We thank R. E. McRoberts, T. D. Nudds, R. O. Peterson, and two anonymous reviewers for helpful suggestions for improving this note.

LITERATURE CITED

- Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monograph* 98. Wildlife Society, Washington, D.C.
- Bekoff, M., and M. C. Wells. 1980. The social ecology of coyotes. *Scientific American* 242:130-148.
- Caraco, T., and L. L. Wolf. 1975. Ecological determinants of group sizes of foraging lions. *American Naturalist* 109:343-352.
- Carbyn, L. N., S. M. Oosenbrug, and D. W. Anions. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute, Edmonton, Alberta.
- Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology* 63:644-652.

- . 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. Pages 223–230 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds. *Ecology and conservation of wolves in a changing world*. Occasional Publication No. 35. Canadian Circumpolar Institute, Edmonton, Alberta.
- Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monograph* 79. Wildlife Society, Washington, D.C.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monograph* 105. Wildlife Society, Washington, D.C.
- Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management* 44:583–602.
- Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota. *Canadian Journal of Zoology* 69:2946–2955.
- Hayes, R. D. 1995. Numerical and functional responses of wolves and regulation of moose in the Yukon. Master's thesis. Simon Fraser University, Burnaby, British Columbia.
- Kolenosky, G. B. 1972. Wolf predation on wintering deer in east-central Ontario. *Journal of Wildlife Management* 36:357–369.
- Mech, L. D. 1966. The wolves of Isle Royale. U.S. National Parks Fauna Series No. 7. Government Printing Office, Washington, D.C.
- . 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, New York.
- . 1977. Population trend and winter deer consumption in a Minnesota wolf pack. Pages 55–83 in R. L. Phillips and C. Jonkel, eds. *Proceedings of the 1975 Predator Symposium*. Montana Forest and Conservation Experiment Station, University of Montana, Missoula.
- . 1988. The arctic wolf: living with the pack. *Voyageur*, Stillwater, Minn.
- Mech, L. D., and L. D. Frenzel, eds. 1971. *Ecological studies of the timber wolf in northeastern Minnesota*. North Central Forest Experiment Station, USDA Forest Service Research Paper NC-52. St. Paul, Minn.
- Microsoft. 1995. Microsoft Excel for Windows '95, version 7.0. Microsoft Corp., Redmond, Wash.
- Murie, A. 1944. The wolves of Mount McKinley. U.S. National Park Service Fauna Series No. 5. Government Printing Office, Washington, D.C.
- Nudds, T. D. 1978. Convergence of group size strategies by mammalian social carnivores. *American Naturalist* 112:957–960.
- Packer, C., and L. Rutman. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monograph* 88. Wildlife Society, Washington, D.C.
- Promberger, C., R. D. Hayes, and P. Kaczensky. 1993. Interspecific competition between ravens and wolves in the boreal forest. Pages 52–53 in C. Vila and J. Castroviejo, eds. *Simposio Internacional sobre el Lobo*, León, Spain. Consejería de Medio Ambiente y Ordenación del Territorio, León.
- Pulliam, H. R., and T. Caraco. 1978. Living in groups: is there an optimal group size? Pages 122–147 in J. T. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Sinauer, Sunderland, Mass.
- Rodman, P. S. 1981. Inclusive fitness and group size with a reconsideration of group size in lions and wolves. *American Naturalist* 118:275.
- Schoener, T. 1971. Theory of feeding strategies. *Annual Review of Ecology Systematics* 2:369–404.
- Stenlund, M. H. 1955. A field study of the timber wolf (*Canis lupus*) on the Superior National Forest, Minnesota. Technical Bulletin Number 4. Minnesota Department of Conservation, St. Paul.
- Thurber, J. M., and R. O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* 74:879–889.
- Zimen, E. 1976. On the regulation of pack size in wolves. *Zeitschrift für Tierpsychologie* 40:300–341.

Associate Editor: Robert E. Ricklefs