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Plural breeding in Gray Wolf (*Canis lupus*) packs: how often?

L. David Mech

U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401 USA; email: mechx002@umn.edu

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Abstract

The occurrence of more than a single female breeder in North American Gray Wolf (*Canis lupus*) packs, i.e., plural breeding, is well known, but its incidence has not been estimated since 1982. Using winter pack size as an index to plural breeding in wolves, I reviewed the literature from North American populations least exploited by humans to assess the general incidence of plural breeding. Generally winter packs >15 were associated with incidents of plural breeding. Wolf packs preying primarily on White-tailed Deer (*Odocoileus virginianus*) and in locations south of 52°N latitude seldom exceeded 10–15. Plural breeding occurred in packs preying primarily on larger ungulates in areas mostly above 52°N. The estimated incidence of plural breeding in the overall wolf population was <15% and perhaps <10%, which is lower than a 1982 estimate of at least 20–40%. I discuss reasons why plural breeding is associated with larger prey.

Key words: *Canis lupus*; Gray Wolf; multiple breeding; pack size; plural breeding; reproduction; Yellowstone

Introduction

Gray Wolf (*Canis lupus*) restoration to Yellowstone National Park (YNP), USA, has raised awareness of the occurrence of a considerable amount of plural breeding in some of the park's wolf packs. Plural breeding has long been documented (Murie 1944), and Harrington *et al.* (1982) concluded that it might occur in 20–40% of wolf packs or more. However, that assessment was based on data from only 27 free-ranging wolf-pack years and only from Bathurst Island, Canada; Denali National Park in Alaska; and five dissected breeding-season reproductive tracts in Alaska. (Note: Harrington *et al.* only provide data in terms of pack years without division into years and packs.) It included no packs from areas where plural breeding had not been reported. Thus, the estimate is highly upwardly biased and not necessarily applicable to wolves at lower latitudes.

The necessary condition for plural breeding is thought to be a surfeit of food, which would allow maturing females to remain in their natal pack longer instead of dispersing (Mech *et al.* 1998; Mech and Boitani 2003). Much of the literature on wolf-pack social structure indicates that the usual basic pack includes a single mated pair and their immature offspring, which disperse as they mature (Mech 1970; Harrington *et al.* 1982; Mech and Boitani 2003). In packs with plural breeding, however, maturing daughters that remain with their natal pack mate with stepfathers, immigrant males, or rarely with fathers and produce their own litters (vonHoldt *et al.* 2008). In the most extreme case, in 2008, one YNP pack included six pregnant females, producing at least four litters (Smith *et al.* 2020a).

Yellowstone's wolf population and the associated research has fostered some of the most notable scientific and popular literature on plural-breeding wolf packs. *Yellowstone Wolves: Science and Discovery in the World's First National Park* (Smith *et al.* 2020b) synthesizes the scientific literature about YNP wolves, and McIntyre's (2019, 2020, 2021, 2022) popular accounts have enlightened the public about them.

It is only natural then that questions should arise about just how common plural breeding is in wolf packs. The apparent novelty of such cases has encouraged researchers to report them, and several besides those mentioned above have done so (see Mech and Boitani 2003 for a summary). However, no one since Harrington *et al.* (1982) has attempted to estimate the incidence of this phenomenon in the wolf population at large. My objective was to determine what proportion of breeding in North American wolf packs involves plural breeding by examining data from a wide variety of locations in North America.

Methods

Despite several reports of plural breeding, most studies are not extensive enough or long enough to

assess the proportion of plural breeding accurately. However, a large enough sample can be studied to allow a general estimate by using an index of the proportion of successful plural-breeding packs. A convenient index is winter pack size, a commonly reported feature of most wolf studies and meta-analyses (Mech 1970; Ballard *et al.* 1987; Mech and Boitani 2003; Wydeven *et al.* 2009; Smith *et al.* 2020b).

Pack size is a suitable indicator of plural breeding because, with mean wolf litter sizes of five to six (Mech 1970), winter pack size would usually include more than about 10 if many pups of more than a single female survive. For example, in YNP, plural-breeding packs have numbered up to 37 members (Stahler *et al.* 2020). The distinction between packs larger and smaller than 10 would not always indicate plural breeding or the lack thereof. Large packs sometimes split into subgroups, and sometimes both pup and yearling survival is high and yearlings fail to disperse, making such packs larger than usual. In addition, pup survival in a plural-breeding pack could be unusually low, leaving that pack with fewer than 10. For example, three YNP packs included plural breeding in 1997, but only one of them contained more than 10 wolves by midwinter (Smith 1998).

I strived for a general gross estimate of plural breeding by examining pack-size data from as many published studies as possible from least-exploited wolf populations (Table 1), that is, those from parks or other areas where wolves are legally protected or, in one case, where the study area had low human use.

Results and Discussion

Over the long term, some 25% of YNP packs included plural breeders (Smith *et al.* 2020b); in 39% of pack years, packs had more than 10 members and in 16% more than 15 members (Table 1; one pack breeding for one year is one pack year, one pack breeding for two years is two pack years, four packs breeding for two years is eight pack years, etc.). Similarly, six (19%) of Denali's 32 packs produced multiple litters, and, during 29% of Denali pack years, pack sizes exceeded 10 individuals and 11% exceeded 15 (Mech *et al.* 1998). Thus, although pack size is not a perfect index, it is a reasonable indicator of populations that include plural breeding and it provides a general estimate of the proportion of such packs.

Plural breeding has also been reported from several other areas where wolf populations were being exploited or where insufficient data on pack sizes were available (Table 2). Although these reports provide useful relevant information, the populations studied were subject to anthropogenic disruption. Thus, pack size data could have been compromised,

TABLE 1. Proportion of Gray Wolf (*Canis lupus*) mean pack sizes >10 or >15, as a general estimate of plural breeding. Bold type indicates locations where plural breeding has been documented. One pack breeding for one year is one pack year, one pack breeding for two years is two pack years, four packs breeding for two years is eight pack years, etc.

Location (N latitude) years of study	Pack years	Primary prey	% pack years >10 (>15)	Reference
Superior National Forest (48°), 1966–67 to 1984–85	78	Deer	2 (0)	Mech 1986
Superior National Forest (48°), 1985–86 to 2006–07	315	Deer	7 (0)	Mech 2009
Superior National Forest east (48°), 1971–72 to 1972–73	13	Deer	0	Van Ballenberghe 1972
Wisconsin (46°), 1980–2007	1092	Deer	11 (0)*	Wydeven *et al.* 2009
Northwestern Minnesota (48°), 1972–73 to 1976–77	24	Deer	7 (0)	Fritts and Mech 1981
Voyageurs National Park (48°), 1987–88 to 1990–91	23	Deer	4 (0)	Gogan *et al.* 2004
Denali National Park (63°), 1986–94	106	Moose/Caribou	29 (11)	Mech *et al.* 1998
Yellowstone National Park (45°)†, 1998–2021	282	Elk	39 (16)	YNP Wolf Project 1995–2021
Isle Royale National Park (48°), 1971–91	50	Moose	24 (6)	Thurber and Peterson 1993
North-central Minnesota (48°) 1980–86	35	Deer	14 (0)	Fuller 1989
Algonquin Park (46°), 2002	14	Deer/Moose	0	Patterson *et al.* 2004
Northern Ontario (52°), 2009–10 to 2011–12	42	Moose	2 (0)	Kittle *et al.* 2015

*Based on proportion of years in which pack sizes exceeded 10; all entries except this one are based on the percent of pack years. This entry had to be based only on the percent of years (not pack years) because of the way the authors provided their data.
†Wolf founders transplanted from 52° and 56°N.

TABLE 2. Miscellaneous evidence of plural breeding in Gray Wolf (*Canis lupus*) packs.

Area (N latitude)	Primary prey	Proportion of plural breeding	Remarks	Reference
Baffin Island, Canada (69°)	Muskoxen, Caribou	1 (9%) of 11 pack years		Clark 1971
Kenai, Alaska (61°)	Moose	1 (20%) of 5 packs	50% of pack years >10; 22% >15	Peterson *et al.* 1984
South-central Alaska (63°)	Moose/Caribou	7–10% of 13 packs	Largest pack = 20 (fall)	Ballard *et al.* 1987
South-central Alaska (63°)	Moose/Caribou	1 pack	20	Van Ballenberghe 1983
Northwest Territories, Canada (63°)	Caribou	At least 1 pack of several during 4 or 5 years		Frame *et al.* 2004
Ellesmere Island, Canada (80°)	Muskoxen	2 (9%) of 22 pack years	Largest pack = 20	Anderson *et al.* 2019
Idaho (45°)	Elk	2 (3%) of 70 pack years	Population founders transplanted from 52° and 56°N	Ausband 2018

and I assessed those studies separately. I include the percentage of packs larger than 10 in Table 1 only as a one-way assessment of the maximum percentage of plural breeding. That is, given that packs of >10 could represent multiple breeders—even though they might consist of a single breeder with high pup and/or yearling survival—they still do not show a high rate of plural breeding.

Of the sites listed in Table 1, plural breeding has been documented only in Yellowstone and Denali National Parks, which host relatively large proportions of packs >15. They also include the most packs >10. The only other location in Table 1 that included any packs >15 was Isle Royale National Park. However, despite >60 years of studies there (Mech 1966; Peterson *et al.* 1984; Hedrick *et al.* 2019), plural breeding has not been documented. Based on the lack of large packs at locations listed in Table 1, it is reasonable to conclude that none hosted plural-breeding packs, which accords with the lack of documented plural breeding in those areas.

Plural breeding has been documented in five other locations (Table 2) where such information on pack sizes was not available. In none of those locations did evidence indicate that the incidence of plural breeding was more than 20%. That information, combined with the known 19% incidence in Denali (Mech *et al.* 1998), the known 25% incidence in Yellowstone, the complete lack of known plural breeding in the other areas listed in Table 1, and the low percentage of possible plural breeding in packs of >10 or >15 in Table 1 strongly counters the Harrington *et al.* (1982) conclusion. Rather, in the overall wolf population, I conclude that the rough incidence of plural breeding appears to be <15% and perhaps <10%.

It is also apparent from the existing data that wolf packs that include plural breeders tend to live in areas where their main prey is large, i.e., Elk *(Cervus canadensis*), Caribou (*Rangifer tarandus*), Moose (*Alces amerianus*), and Muskoxen (*Ovibos moschatus*), rather than White-tailed Deer (*Odocoileus virginianus*).

The reason plural-breeding packs tend to be much larger than those with single breeders may be twofold. First, the additional breeders are usually daughters of the original breeding female that have failed to disperse (vonHoldt *et al.* 2008). In those cases, the reason offspring remained with the pack instead of dispersing is thought to be because of a surfeit of food, resulting in less competition for food (Mech *et al.* 1998; Mech and Boitani 2003). An alternative explanation is that pack members might be more likely to remain with their natal packs as habitat becomes saturated (Sells *et al.* 2022). However, surplus food would seem to better explain the existence of Yellowstone's large packs within three years of reintroduction when the population was not yet saturated (Smith *et al.* 1999).

Just because prey are larger where packs might include plural breeders, however, does not necessarily mean that food supply is greater. Also, wolves do not fail to disperse in all places or times of larger prey. For example, in Denali, plural breeding was only found when food supply increased (Mech *et al.* 1998), and on Isle Royale where the only major prey is Moose, there is no documentation of plural breeding (Table 1).

Prey size might be a factor in plural breeding, though, through social competition. Murie (1944: 45) suggested the following about pack-size limitation:

> a pack might be so large that, after the strongest members had finished feeding on a kill,

> there would be little or nothing left for the rest. In such a situation, hungry ones would go off to hunt again, and the strong ones, already fed, would remain where they were. There, thus, might result a natural division of a band which was too large to function advantageously for all its members.

In other words, prey size might dictate pack size, such that with larger prey, more wolves can feed at individual kills concurrently with less competition than with smaller carcasses. About 13 wolves can simultaneously fit around an adult cow-Moose carcass (Mech 1966), but much fewer around a deer.

Not only would competition be reduced around larger carcasses, but another consideration about carcass size might come into play. Generally, wolves do not have to hunt as often for large prey as for smaller prey. For a given amount of food, wolves must find, catch, and kill more deer, for example, than Moose. The extra striving in packs that must hunt smaller prey might require more time and energy expenditure depending on the degree of tradeoff with the lower density of, and greater defense by, larger prey. If so, the greater effort required could lead to increased competitiveness among the pack members for the resulting benefits. The converse of this pattern might be that larger prey, then, translates into less competition, which in turn leads to decreased social pressure to disperse.

One other association with plural breeding that bears mention is that instances of plural breeding occurred at latitudes at 61°N or higher, except those in Yellowstone and Idaho (45°N), but those wolves were descendants from those translocated from 52° to 56°N (Fritts *et al.* 2020). No instance of plural breeding was found in latitudes from 46° to 52°N. This latitudinal association might just reflect areas with larger prey.

In summary, it appears that plural breeding occurs in <15% and perhaps <10% of North American wolf packs (a smaller proportion than previously reported) and that the phenomenon is associated with larger packs, larger prey, and higher latitudes.

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