

Original Research

Gray Wolf (*Canis lupus*) Dyad Monthly Association Rates by Demographic Group

Shannon BARBER-MEYER¹ and L. David MECH²

¹U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 – 37th St., SE, Jamestown, North Dakota, USA 58401-7317. Postal address: USGS, 1393 Hwy 169, Ely, Minnesota, USA 55731. Email: sbarber-meyer@usgs.gov

²U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 – 37th St., SE, Jamestown, North Dakota, USA 58401-7317. Postal address: USGS, The Raptor Center, University of Minnesota, 1920 Fitch Ave., St. Paul, Minnesota, USA 55731. Email address: david_mech@usgs.gov

Abstract

Preliminary data from GPS-collared wolves (*Canis lupus*) in the Superior National Forest of northeastern Minnesota indicated wolves had low association rates with packmates during summer. However, aerial-telemetry locations of very high frequency (VHF)-radioed wolves in this same area showed high associations among packmates during winter. We analyzed aerial-telemetry-location data from VHF-collared wolves in several packs ($n=18$ dyads) in this same area from 1994-2012 by month, and found lowest association rates occurred during June. While other studies have found low association among wolf packmates during summer, information on differences in association patterns depending on the wolf associates' demographics is sparse. During May-July, association rates were greatest for breeding pairs, followed by sibling dyads, and lowest for parent-offspring dyads. Our findings improve our understanding of how individual wolf relationships affect monthly association rates. We highlight some important remaining questions regarding wolf packmate associations.

Key Words: *Canis lupus*, Dyad Associations, Minnesota, Gray Wolf, VHF collars, Wolf Pack Cohesion.

INTRODUCTION

Although gray wolves (*Canis lupus*) generally travel as a pack during winter (summarized by Mech 1970), in summer they often forage individually, and generally each pack wolf returns to the pack's den or rendezvous site each day or so (Murie 1944; Harrington and Mech 1982; Ballard *et al.* 1991; Mech and Merrill 1998). In Denali National Park, Alaska, some 78% of 275 observations of wolves away from dens during summer were of

single wolves (Mech *et al.* 1998), and on Ellesmere Island, Canada, wolves often returned singly to dens (Mech and Merrill 1998). In the Superior National Forest (SNF) of northeastern Minnesota, 3 packmates were >100 m apart in 94% of ~1,000 locations/wolf during summer (Demma *et al.* 2007), and in another study 2 packmates were >50 m apart in ~99% of >12,000 summer locations (Palacios and Mech 2010).

Although coarse seasonal differences in wolf pack cohesion when away from dens appear well known, finer-scale association rates and

the factors influencing them need further study. In southwestern Québec, Canada, yearling and adult females spent more time separated from their packs and alone than males, and yearlings were the most loosely associated pack members (Messier 1985). Prey size significantly influenced pack association around carcasses during summer, and age class and pack size were important variables during winter (Metz *et al.* 2011). These findings do not necessarily reflect wolf associations during travel because once a wolf makes a kill, other packmates may join them there (Palacios and Mech 2010; Mech, unpublished data). Similar to Messier (1985), the highest association rates of 6 canid dyads (including *C. lupus*, *C. lycaon* and *C. latrans* and some hybrids) during winter were between 2 males, but 2 other packs with similarly high cohesion included females (Benson and Patterson 2015). Winter association rates were highest among packs with larger prey, similar to Metz *et al.* (2011), but in contrast, pack size was not correlated with cohesion (although this finding could have been because of a small sample). Benson and Patterson (2015:39) stated, “Investigating how sex, age, and breeding status influences the degree to which individuals associate with other wolves in the pack will be a valuable next step for achieving a better understanding of pack cohesion.”

Because most wolf studies suffer from small samples (few wolf dyads to analyze), information on how demographics influence pack-member association remains sparse. Thus we analyzed location data from very high frequency (VHF)-collared wolves in the SNF from 1994–2012 by month and dyad demographics to determine (1) whether the observed lower summer association rates among packmates in the 2 earlier SNF studies were typical of SNF wolves; (2) when SNF packmate associations increase and decrease during the annual cycle; and (3) how association rates differ depending on wolf demographics.

MATERIAL AND METHODS

As part of a long-term wolf research project (Mech 2009), our study area comprised 2,060 km² in the SNF, Minnesota, USA (48° N, 92° W - see Nelson and Mech 1981 for a detailed description). Vegetation was predominately conifers, e.g., jack pine (*Pinus banksiana*), white pine (*P. strobus*), red pine (*P. resinosa*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*) in the forest overstory, which was interspersed with white birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) (Heinselman 1996). Elevations ranged from 325 to 700 m above sea level and included swamps, uneven upland, and rocky ridges. Temperatures rarely exceeded 35°C and average monthly temperatures ranged from approximately 4 to 18°C during May – October and approximately -18 to 2°C during November – April (Heinselman 1996). Snowfall averaged 150 cm during mid-

November through mid-April (Nelson and Mech 2006).

During 1988–2011, mean wolf density was 31/1,000 km² (Mech 2009, and authors' unpublished data). Generally, in the northeastern portion of our study area, the wolf's primary prey was moose (*Alces alces*) and in the southwestern portion, white-tailed deer (*Odocoileus virginianus*) (Frenzel 1974; Mech 2009).

We captured wolves with modified foot-hold traps (either Newhouse 14 or Livestock Protection Company's EZ Grip 7) (Mech 2009) following guidelines of the American Society of Mammalogists (Gannon and Sikes 2007) during capture and processing (see Barber-Meyer and Mech 2014 for details). We anesthetized trapped wolves with a standard dose of 250 mg ketamine (Ketaset®, ketamine hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) (1988–1991) or 250 mg telazol® (tiletamine hydrochloride and zolazepam hydrochloride, Pfizer and Fort Dodge Animal Health, Fort Dodge, IA, USA) (1992–2011) and 37 mg xylazine (Anased®, Llyod Laboratories, Shendandoah, IA, USA) given intramuscularly. We recorded standard morphological measurements, collected specimens, applied ear tags and a VHF radiocollar (Telonics, Inc., Mesa, AZ). Beginning in 2000, we estimated wolf age by tooth wear comparing with the chart in Gipson *et al.* (2000). Prior to 2000, unless the age of the wolf was known (i.e., captured as a pup), we assigned a known-minimum age of 1 year and updated it if a wolf was recaptured. We generally did not collar pups until they were ~5-months old. We administered antibiotics and an antagonist to the anesthetic, and handled wolves for approximately 1 h. We located wolves approximately weekly via aerial radio-telemetry, and we considered locations accurate within 400 m. We calculated winter pack counts as the maximum pack size observed during weekly locations during December–March each year.

We analyzed locations of wolf dyads (2 VHF-collared wolves from the same pack) from 1994 to 2012. Because we were interested in seasonal comparisons, we only included dyads where we had at least some association data from May – August and also from December – March. We categorized dyads as breeders, siblings, or parent–offspring. Assumed breeding pairs included males that were older than 1 yr old and whose testis length measured at least 2.5 cm (Gese and Mech 1991), and females whose teats were not “inconspicuous” (Barber-Meyer and Mech, in press). Sibling dyads included 2 immature (i.e., not assumed breeders) wolves from the same pack. Parent–offspring dyads included 1 assumed breeder and 1 immature wolf. In addition, at least some of our radioed-wolf dyads could sometimes have represented more than a dyad, because, as with earlier studies, not all members of each pack were radiocollared.

We recorded the percent-together locations for each month for each dyad and averaged these for each month within each type of demographic pair. Once a particular dyad association dissolved (e.g., one wolf dispersed or died), we no longer included their data

in the monthly summaries.

RESULTS

We considered more than 45 radio-collared wolf dyads for analysis. However, because of lack of complete data or because we could not assign them definitively to a demographic group, we analyzed 18 (3 breeding pair, 6 sibling, and 9 parent–offspring dyads) (Table 1). The 6 sibling dyads consisted of 3 male dyads and 3 male–female dyads (Table 1). The parent–offspring dyads included 4 dyads with a male adult (3 with a female offspring), and 5 with a female adult (3 with a male offspring) (Table 1). Eleven of the dyads lived in the primarily “deer economy” area of our study area, whereas 7 lived in the primarily “moose economy” area (Table 1).

Mean wolf packmate association rates by month were lowest in summer (Figure. 1). During May – July, association rates were highest for breeding pairs, followed by siblings, and lowest for parent–offspring dyads (Figure 1). Mean association rates for breeder pairs ranged from 34% in June to 95% in January; for sibling dyads, from 26% in June to 87% in December; and for parent–offspring dyads, from 11% in June to 91% in January. Average association rates among demographic groups generally declined gradually from winter to summer (Figure 1). Due to data limitations, we were unable to statistically compare the effects of gender, age, pack size and prey type on association rates but we report summary association rates in June and January for each dyad to illustrate the variability even within a particular wolf pair (Table 1). We also found wide variation in monthly mean association rates within demographic groups (average SD of annual mean wolf-association rates among siblings=32.9, parent–offspring=30.5, and breeders=31.5) that we suspect may be driven partly by the timing of individual dyad dissolutions (Table 1) that larger samples might resolve. Notwithstanding the variation, within particular dyads, the annual trend of greater association rates within the winter versus summer held.

DISCUSSION

Our findings confirmed the more-limited GPS-data from the same area (Demma *et al.* 2007; Palacios and Mech 2011) that wolf packmate foraging associations are lowest in summer. During summer, young prey are smallest, most numerous, and easier to catch than when they are older and more mobile (Mech *et al.* 2015). Thus it would be more efficient for wolves to hunt singly or in smaller groups in summer than in winter when all these factors are the opposite. In addition, wolves may also travel together more often during winter because it is more efficient to travel single-file in a group through deep snow than for each wolf to have to “break trail” individually (Mech 1966). Also, larger prey can be more efficiently consumed (rather than lost to scavengers) by several wolves than by an individual (Vucetich *et al.* 2004). Furthermore,

larger prey tend to be riskier for wolves to hunt (Murie 1944; Mech *et al.* 2015), and we hypothesize that – up to a point – having more wolves to potentially join in the attack (MacNulty *et al.* 2012, 2014) may reduce the probability of injury per wolf and/or allow for pack persistence and provisioning even when one wolf is severely injured and cannot hunt (in support of this hypothesis, see Almborg *et al.* 2015 for evidence that group living in wolves mitigates the impacts of chronic disease). Due to data limitations we could not test whether association rates differed among demographic dyads that primarily preyed on deer (smaller prey) versus moose (larger prey).

A number of important spatial questions remain regarding wolf association rates during summer when association is lowest. How is the pack’s territory used by each type of wolf? Do breeders use the entire territory separately? Do juveniles use separate core sections? Also, general rotational-use (Jedrzejewski *et al.* 2001) questions persist regarding territory use by individuals throughout the year (Demma *et al.* 2007; Demma and Mech 2009). Depending on wolf demographics, how does summer territory use compare with winter use? How do association rates differ in warmer climates without snow? Unfortunately, we did not have enough data with our VHF- locations to construct meaningful individual ranges between or among dyads. Additional data from GPS-studies similar to those of Benson and Patterson (2015) but expanded and deploying several collars/pack would best resolve these kinds of questions.

Our association rates were generally higher than those of GPS-based studies, at least partly because our study relied on VHF location data that were accurate only to within 400 m. In addition, at least some of our radioed-wolf dyads could sometimes have represented more than a dyad because, as with earlier studies, not all members of each pack were radiocollared. Nevertheless, our results basically support earlier findings that wolves tend to travel singly during summer. Our findings better quantify the seasonal-association history of wolf-pack members throughout the year, and represent the first categorization of average monthly dyad association rates by demographic group. Because these types of data are rare in most studies, even these results add new information to our understanding of factors related to wolf association rates as Benson and Patterson (2015) suggested.

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Table 1. Demographics, winter pack count, main prey, and June and January association rates of the VHF-radioed-wolf dyads in the Superior National Forest, Minnesota, USA, 1994-2012.

Wolf1	Sex & age ^a at collaring	Yr collared	Wolf2	Sex & age ^a at collaring	Yr collared	Inclusive period of association ^b	Winter pack count ^c	Prey	% associated ^d in Jun.	% associated ^d in Jan.
Breeders										
7057	F/3yr	2008	7063	M/2yr	2009	2009-2011	X,2,4	Deer	X,0,0	X,83,86
7098	M/5yr	2009	7109	F/2yr	2009	2009-2012	X,X,5,4	Moose	X,0,100,X	X,X,100,100
879	F/4yr	2002	881	M/8yr	2002	2002-2004	X,3 ^e ,7	Deer	X,80,25	X,100,100
Siblings										
7153	M/pup	2010	7159	M/pup	2010	2010-2011	X,11	Moose	X,0	X,100
663	F/1yr/5yr	1997, 2001	645	M/pup	1997	1997-1999	X,9,9	Deer	X,0,33	X,33,80
567	M/pup	1995	569	M/pup/2yr	1995, 1997	1995-1996	X,9	Deer	X,X	X,50
701	M/pup	1997	743	F/pup	1998	1999-2002	X,3,6,4	Moose	X,25,100,X	X,100,25,100
705	M/pup	1997	713	F/pup	1997	1997-1998	X,7	Deer	X,0	X,60
11	M/pup/1yr	1987, 1988	107	M/pup	1998	1988-1989	X,12	Moose	X,25	X,20
Parent-offspring										
897	F/2yr/7yr	2003, 2008	7141	M/pup	2010	2010-2011	X,11	Moose	X,X	X,100
877	M/1-2yr/5-6yr	2002, 2006	911	F/2yr/7yr	2003, 2008	2004-2005	X,12	Deer	X,33	X,80
893	F/2yr/4yr	2003, 2004	963	F/3yr/7yr	2005, 2009	2005-2007	X,6,11	Deer	X,0, no data	X,100,100
879	F/4-6yr	2002	889	M/1yr	2003	2003-2004	X,7	Deer	X,X	X,100
881	M/8yr	2002	889	M/1yr	2003	2003-2004	X,7	Deer	X,X	X,100
891	M/7-9yr	2002	939	F/1yr/4yr	2004, 2007	2004-2005	X,8	Moose	X,X	X,100
911	F/2yr/7yr	2003, 2008	7069	M/1yr	2009	2009-2010	X,8	Deer	X,X	X,100
905	F/4yr	2003	971	F/3yr	2005	2005-2006	X,11,7 ^f	Moose	X, no data	X,100
877	M/1-2yr/5-6yr	2002, 2006	7067	F/2yr	2009	2009-2010	X,6	Deer	X,X	X,33

^a Beginning in 2000, we estimated wolf age by tooth wear comparing with the chart in Gipson *et al.* (2000). Prior to 2000, unless the wolf was known-age (i.e., captured as a pup), we assigned a known-minimum age of 1 year to wolves and updated each wolf's known-minimum age if that wolf was later recaptured.

^b Period of association includes years when the wolves were radiocollared and associated. In some cases, some months within these years lack data.

^c Maximum number of wolves observed, December - March. Entries included for each potential year in the "period of association"; X = not during the period analyzed because the wolves were not radiocollared or associating yet, or the dyad had dissolved.

^d Entries included for each potential year in the "period of association"; X = not during the period analyzed because the wolves were not radiocollared or associating yet, or the dyad had dissolved; no data = during period analyzed for association but data were not available; 0 = not located together but during period of association.

^e Three days before the winter census period.

^f This count was obtained 4 December 2006 which is a "winter 2007 pack count" but the wolves were never associated after this - so there are no association data for 2007.

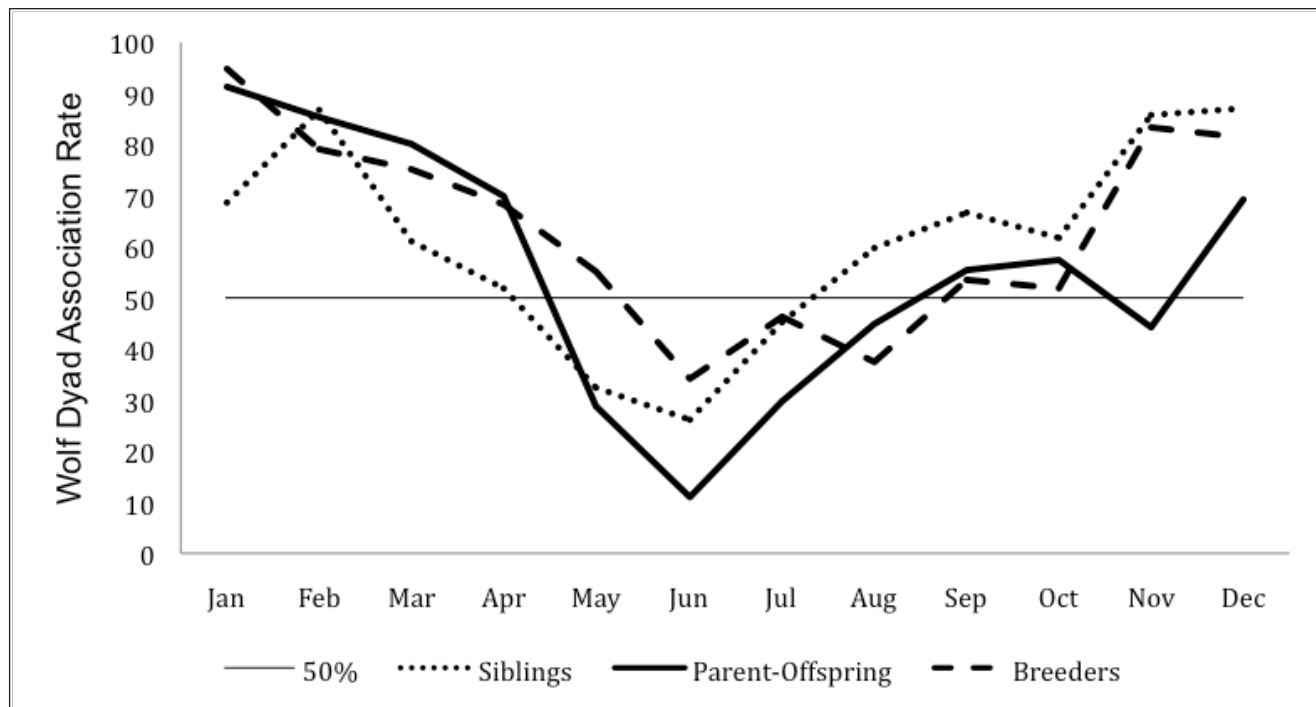


Figure 1. Wolf dyad mean association rates by month among differing demographic groups (siblings, $n=6$; parent-offspring pairs, $n=9$; breeders, $n=3$) in the Superior National Forest, Minnesota, USA, 1994-2012.

LITERATURE CITED

- Almberg, E. S., P. C. Cross, A. P. Dobson, D. W. Smith, M. C. Metz, D. R. Stahler, and P. J. Hudson. 2015. Social living mitigates the costs of chronic illness in a cooperative carnivore. *Ecology Letters* doi: 10.1111/ele.12444.
- Ballard, W. B., L. A. Ayres, C. L. Gardner, and J. W. Foster. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in southcentral Alaska. *Canadian Field-Naturalist* 105:497-504.
- Barber-Meyer, S.M. and L.D. Mech. 2014. How hot is too hot? Live-trapped gray wolf rectal temperatures and 1-year survival. *Wildlife Society Bulletin*. 38: 767-772.
- Barber-Meyer, S.M., and L.D. Mech. *In press*. Evaluation of a formula that categorizes female gray wolf breeding status by nipple size. *Northeast Naturalist*.
- Benson, J. F., and B. R. Patterson. 2015. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. *Wildlife Society Bulletin* 39: 31-40.
- Demma, D. J., S. M. Barber-Meyer, and L. D. Mech. 2007. Testing global positioning system telemetry to study wolf predation on deer fawns. *Journal of Wildlife Management* 71: 2767-2775.
- Demma, D. J., and L. D. Mech. 2009. Wolf, *Canis lupus*, visits to white-tailed deer, *Odocoileus virginianus*, summer ranges: optimal Foraging? *Canadian Field-Naturalist* 123: 299-303.
- Frenzel, L. D. 1974. Occurrence of moose in food of wolves as revealed by scat analyses: a review of North American studies. *Naturaliste Canadien* 101: 467-479.
- Gannon, W. L., and R. S. Sikes. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88: 809-823.
- Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969-1989. *Canadian Journal of Zoology* 69: 2946-2955.
- Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. *Journal of Wildlife Management* 64: 752-758.
- Harrington, F. H., and L. D. Mech. 1982. Patterns of domicile attendance in two Minnesota wolf packs. Pages 81-105 in F. H. Harrington and P. C. Paquet, editors. *Wolves of the world*. Noyes Publishing, Park Ridge, New Jersey, USA.
- Heinselman, M. L. 1996. *The boundary waters wilderness ecosystem*. University of Minnesota Press, Minneapolis, MN, USA.
- Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewski, and H. Okarma. 2001. Daily movements and territory

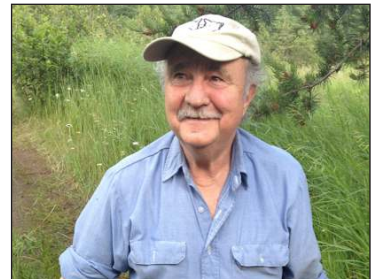
- use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest (Poland). *Canadian Journal of Zoology* 79: 1993-2004.
- MacNulty, D. R., D. W. Smith, L. D. Mech, J. A. Vucetich, and C. Packer. 2012. Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology* 23: 75-82.
- MacNulty, D. R., A. Tallian, D. R. Stahler, and D. W. Smith. 2014. Influence of group size on the success of wolves hunting bison. *PloS One* 9(11): e112884.
- Mech, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States. Fauna Series No. 7.
- Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press. Doubleday Publishing Co., New York, New York, USA.
- Mech, L. D. 2009. Long-term research on wolves in the Superior National Forest. Pages 15-34 in A. P. Wydeven, T. R. VanDeelen, and E. J. Heske, editors. Recovery of gray wolf in the Great Lakes Region of the United States: an endangered species success story. Springer, New York, New York, USA.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Mech, L. D., and S. B. Merrill. 1998. Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80° N latitude. *Canadian Field Naturalist* 112: 515-517.
- Mech, L. D., D. W. Smith, and D. R. MacNulty. 2015. Wolves on the hunt. University of Chicago Press, Chicago, Illinois, USA.
- Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Canadian Journal of Zoology* 63: 239-245.
- Metz, M. C., J. A. Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PloS One* 6(3): e17332.
- Murie, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Series No. 5.
- Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs* 77: 3-53.
- Nelson, M. E., and L. D. Mech. 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. *American Midland Naturalist* 155: 373-382.
- Palacios, V., and L. D. Mech. 2010. Problems with studying wolf predation on small prey in summer via global positioning system collars. *European Journal of Wildlife Research* 57: 149-156.
- Vucetich, J. A., P. O. Peterson, and T. A. Waite. 2004. Raven scavenging favours group foraging in wolves. *Animal Behaviour* 67: 1117-1126.

ABOUT THE AUTHORS

Shannon Barber-Meyer holds a BSc in biology from Eckerd College and a PhD in wildlife conservation from the University of Minnesota, and was a postdoctoral scholar at Scripps Institution of Oceanography. She is the US Geological Survey (USGS) wildlife biologist implementing the Superior National Forest Wolf and Deer Project under the direction of Dr. David Mech. Prior to joining the USGS, she taught graduate students in Grand Teton National Park, researched tiger (*Panthera tigris*) conservation in Asia, emperor penguin (*Aptenodytes forsteri*) populations in Antarctica, and elk (*Cervus elaphus*) calf mortality in Yellowstone National Park, and helped reintroduce Mexican gray wolves (*Canis lupus baileyi*) into the southwestern United States. Shannon is a member of the IUCN SSC Canid Specialist Group. She lives in Ely, Minnesota, USA with her husband John and their two daughters, Sova and Etta.



L. David Mech is a Senior Scientist with the U.S. Geological Survey and an Adjunct Professor in the Department of Fisheries, Wildlife and Conservation Biology at the University of Minnesota. He received his BSc degree from Cornell University and a PhD degree and an honorary doctorate from Purdue University. He has studied wolves since 1958 in places such as Isle Royale, Minnesota, Italy, Alaska, Yellowstone National Park, and Ellesmere Island, Canada.



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