Research Note

Multistage, Long-Range Natal Dispersal by a Global Positioning System–Collared Scandinavian Wolf

PETTER WABAKKEN,[1] *Hedmark University College, Faculty of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, Norway*

HÅKAN SAND, *Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Department of Conservation Biology, SE-73091 Riddarhyttan, Sweden*

ILPO KOJOLA, *Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2 A, FIN-90570 Oulu, Finland*

BARBARA ZIMMERMANN, *Hedmark University College, Faculty of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, Norway*

JON M. ARNEMO, *Norwegian School of Veterinary Science, Section of Arctic Veterinary Medicine, Department of Food Safety and Infection Biology, NO-9292 Tromsø, Norway, and Hedmark University College, Faculty of Forestry and Wildlife Management, Evenstad, N-2480 Koppang, Norway*

HANS C. PEDERSEN, *Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway*

OLOF LIBERG, *Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Department of Conservation Biology, SE-73091 Riddarhyttan, Sweden*

ABSTRACT We document a new record dispersal for wolves worldwide. The natal straight-line dispersal distance of a Global Positioning System–collared female wolf from the Scandinavian population was 1,092 km from southeast Norway to northeast Finland, with a multistage actual travel distance of >10,000 km. Natural gene flow to the isolated, inbred Scandinavian wolf population may occur if survival of dispersers is improved. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1631–1634; 2007)

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KEY WORDS *Canis lupus* L., Fennoscandia, Global Positioning System collar, long-range movement, multistage dispersal, natal dispersal, Scandinavia, wolf.

Dispersal influences animal population regulation, recolonization, social organization, spatial distribution, gene flow, and longevity (Shields 1987, Lande 1988, Gese and Mech 1991, Stenseth and Lidicker 1992). Canids may disperse far from their natal home range, with straight-line distances of 1,530 km having been recorded for the arctic fox (*Alopex lagopus*; Wrigley and Hatch 1976) and over 800 km for both sexes of wolves (*Canis lupus*; Fritts 1983, Ream et al. 1991). Long-range movements by wolves have rarely been studied in detail for financial and technological reasons (Merrill and Mech 2000, Frame et al. 2004), and published carnivore dispersal distances are biased towards short-distance movements (Linnell et al. 2005). However, new and improved Global Positioning System (GPS) technology has made such studies possible (Merrill et al. 1998, Zimmermann et al. 2001, Kojola et al. 2006). Herein, we present details of a case of multistage, long-range natal dispersal by a female wolf in Fennoscandia, the first GPS-collared wolf pup in Europe. The dispersal distance documented is a new record for wolves worldwide.

STUDY AREA

The 3 bordering countries Norway, Sweden, and Finland together constitute Fennoscandia (area 1,175,000 km^2; 55°–72°N, 5°–31°E; Fig. 1), including the Scandinavian Peninsula (Sweden and Norway). Fennoscandia was mostly covered by boreal coniferous forest and alpine areas. Human population density averaged 15/km^2, but in most areas including the main wolf ranges it was <1/km^2. Within the breeding range of wolves in all 3 countries, moose (*Alces alces*) was the main prey species, but roe deer (*Capreolus capreolus*) and wild forest reindeer (*Rangifer tarandus*) could be locally important to wolves (Olsson et al. 1997, Kojola et al. 2004, Sand et al. 2005). Two separate wolf populations inhabited Fennoscandia; the Finnish-Russian and the south-central Scandinavian (Fig. 1). Except for the Gulf of Bothnia when not covered with sea ice, there were few geographical barriers to wolf dispersal and exchange between the 2 populations (Fig. 1).

METHODS

We immobilized a female wolf (0301) from a helicopter and ear tagged and equipped her with a 675-g GPS neck collar (Simplex, Televilt International, Lindesberg, Sweden) by methods described by Sand et al. (2005). We determined her age by a combination of standard methods (Sand et al. 2005), known pack history (Wabakken et al. 2004), and DNA analysis (Liberg et al. 2005). We made the capture, handling, and collaring of the wolf with permission from the national management authority, the Directorate for Nature Management, and evaluation and approval by the Norwegian Agency of Animal Welfare. The GPS collar stored data, including latitude and longitude (WGS 84), date, time, and 2 estimates of position quality (2-dimensional–3-dimensional, dilution of position value; Sand et al. 2005) on the internal memory, which could be downloaded remotely at predetermined intervals (Zimmermann et al. 2001). We programmed the GPS collar to acquire positions at 4-hour intervals (0000 hr, 0400 hr, etc.), and additional hourly positions (0030 hr, 0130 hr, etc.) during certain weeks planned for detailed predation studies (weeks 8–16, 19–20, and 23–28). During the predispersal period (i.e., inside her

[1] *E-mail: petter.wabakken@hihm.no*

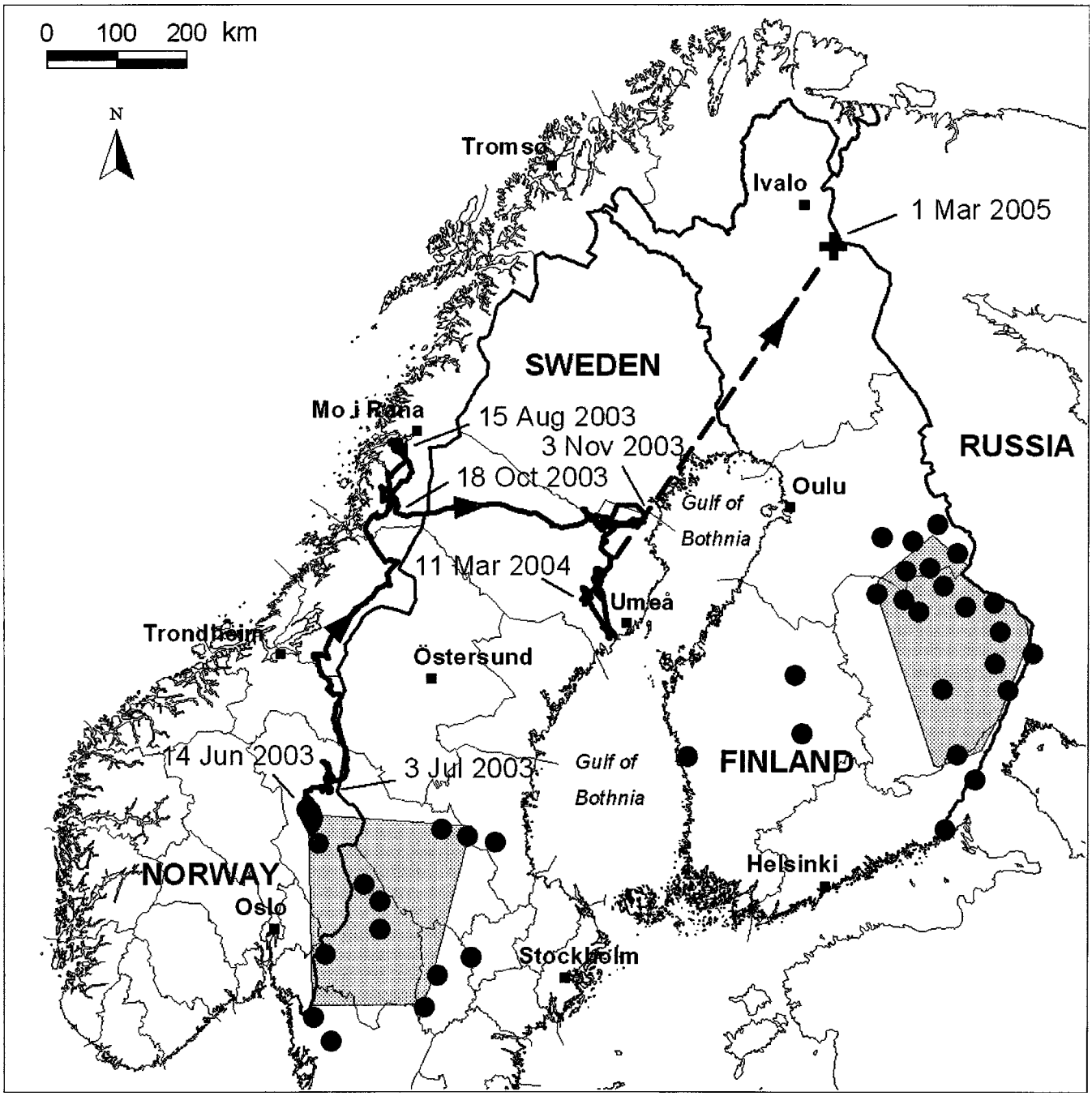

Figure 1. Dispersal of female wolf 0301 from her natal territory (black polygon) in southern Norway, 14 June 2003, and movements mapped in detail (solid line), until her Global Positioning System collar failed 11 March 2004 in northern Sweden. Almost a year later, 613 km further to the northeast (dashed line), the female was killed (cross) on 1 March 2005 in northeastern Finland, close to the Russian border. Wolf packs in winter 2004–2005 (black dots), and the 2 main wolf breeding areas in Fennoscandia (hatched), with reproductions in each of the 5 years 2000–2004 (Wabakken et al. 2004, 2005) are also shown.

natal territory) we downloaded positions stored in the GPS in the field. During her dispersal phase, we did not download data in the field, but dispersal data stored in the GPS became available to us when we retrieved the GPS collar from the dead wolf. We plotted and analyzed location data in ArcView 3.2. We defined natal dispersal as dispersal from the birth site to that of first reproduction or potential reproduction (Greenwood 1980). We visually defined directional and nondirectional dispersal as long-distance movement in more or less a single direction (Mech and Boitani 2003) and short-distance movement in a zigzag pattern, respectively.

RESULTS

Female 0301, born in the Gråfjell wolf territory in Norway (61°30′N, 11°15′E), was immobilized and marked 8.1 km from her natal den, on 6 December 2002 (Fig. 1). Female 0301 was 7 months old and weighed 30.5 kg at the time of capture. During the 2002–2003 winter, female 0301 was 1 of 4 GPS-collared wolves in a pack of 6 (Wabakken et al.

Table 1. Dispersal distances, number of days, average travel rate (km/d), and average travel speed (km/4 hr and km/1 hr; $\bar{x} \pm$ SD, resting included) for periods of directional and nondirectional, multistage dispersal by a female wolf in Fennoscandia (14 Jun 2003–11 Mar 2004).

Dispersal	Period (2003–2004)	D (*n*)	Straight-line distance (km)	Travel rate[a] (km/d)	Travel speed (km/4 hr)			Travel speed (km/1 hr)		
					$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Nondirectional	14 Jun–3 Jul	19	35	1.8	2.9	4.3	62	0.9	2.0	209
Directional	3 Jul–15 Aug	42.5	498	11.7	3.9	4.4	120	1.5	1.5	115
Nondirectional	15 Aug–18 Oct	64.5	95	1.5	1.7	2.0	169			
Directional	18 Oct–3 Nov	16	340	21.2	3.5	5.2	45			
Nondirectional	3 Nov–11 Mar	129	124	1.0	1.8	2.3	368	0.6	1.0	238
Total	14 Jun–11 Mar	271	486	1.8	2.3	3.2	764	0.9	1.4	562

[a] Straight-line distance divided by the no. of d.

2004). Her GPS-collared parents were territory holders and bred every year from 2001 until their death in early 2005, while her GPS-collared female sibling dispersed a straight-line distance of 233 km eastwards into Sweden before she was killed, in December 2003.

During 26 April to 10 June 2003, female 0301 made 3 short predispersal forays (3.5–10.8 km, 10–22 hr) before she left her natal territory on 14 June 2003, heading northeast (Fig. 1). Nineteen days later (3 July 2003), the last very high frequency signals from her GPS collar were heard at the Norwegian–Swedish border. On 1 March 2005, 626 days after the dispersal date, the female was legally shot by a reindeer owner in northeastern Finland (68°10′N, 28°24′E), 10 km from the Russian border (Fig. 1). Until 5 days earlier, when her mate was killed, female 0301 was a resident pair member, observed and tracked on snow in the area since November 2004. She may have arrived earlier because reindeer owners reported 72 semidomestic reindeer wolf-killed in the area during June 2004 to February 2005. When shot, the female weighed 34 kg, and she had not reproduced (no placental scars). The straight-line natal dispersal distance, between her natal den and the kill site, was 1,092 km.

On 11 March 2004, 9 months after dispersal, the GPS battery expired approximately 100 km northwest of Umeå, northeast in Sweden (Fig. 1). During these first 271 days of dispersal (14 Jun 2003–11 Mar 2004), the collar collected 1,997 locations, and had an overall GPS success rate of 68%. Multistage dispersal was noted, shifting between nondirectional and directional dispersal phases with different travel rates, speeds, and distances (Table 1). Hourly directional dispersal travel speed during summer was significantly greater than nondirectional dispersal, during both summer and winter ($t_{summer} = 2.86$, $P = 0.004$, and $t_{winter} = 4.94$, $P < 0.001$; Table 1). The straight-line distance between the first and the last stored GPS location of dispersal was 486 km (14 Jun 2003–11 Mar 2004; Table 1), and the minimum distance travelled (sum of line segments) was 3,471 km. Provided that the average 1-hour movements could be extrapolated to days with no such data (directional and nondirectional averages, respectively; Table 1), and multiplying all 1-hour line segments by a correction factor of 1.3 for actual movement distances (Musiani et al. 1998), an actual travel distance of 6,882 km was estimated for these first 9 months of dispersal. Thereafter, female 0301 dispersed an additional straight-line distance of 613 km to northeastern Finland (Fig. 1). Assuming a similar movement pattern to that of the first 9 months, the overall distance travelled during natal dispersal would rise to 15,557 km, or a conservatively evaluated actual travel distance of >10,000 km.

DISCUSSION

The historical Scandinavian wolf population became functionally extinct by the late 1960s, but during 1983–1991, a new Scandinavian wolf population was founded by 3 wolves from the Finnish-Russian population (Wabakken et al. 2001, Vilà et al. 2003, Liberg et al. 2005). There has been public debate about the origin of these wolves, and whether they arrived naturally, as the founders may have dispersed distances above or at the extreme limit (1,080–1,120 km) of previously confirmed dispersal distances (Linnell et al. 2005). Our reported straight-line distance of 1,092 km is within this range, the farthest dispersal distance documented for a wolf.

In areas of low wolf density, wolves may travel excessive distances to find suitable habitat, prey, or mates (Boyd and Pletscher 1999). Record average dispersal distance and presaturation dispersal have been described earlier for wolves on the Scandinavian Peninsula, where food or suitable habitat is not considered as a limiting factor to wolf settling and distribution (Wabakken et al. 2001). This may indicate that, in low density wolf populations, with a disjunct pack distribution as in Montana, USA (Boyd et al. 1995) and Scandinavia (Fig. 1), the ultimate factor for long-range dispersals is social (i.e., to find a mate).

As dispersal particularly affects the level of inbreeding in populations with a small effective population size (McNutt 1996), long distance movements may be of critical importance to the genetic health of low-density, recolonizing populations such as the present wolf populations in Montana and Scandinavia (Boyd et al. 1995, Vilà et al. 2003, Liberg et al. 2005). Long-range dispersing wolves have appeared in areas far from their source population on many occasions (review; Linnell et al. 2005) and are probably crucial to the wolf as a successful and widely distributed species, as well as of considerable importance to further recolonization in Eurasia and North America.

In Fennoscandia, wolf management is based on zoning. Between the isolated and severely inbred wolf population in

Scandinavia (Liberg et al. 2005) and the Finnish-Russian population, there are large land areas where wolf establishment is unwanted due to Fennoscandian reindeer husbandry and Norwegian sheep farming. A challenge for Fennoscandian wolf management will be to balance an increasing number of dispersers into areas where they are unwanted against the need for natural immigration from the Finnish-Russian to the Scandinavian wolf population.

MANAGEMENT IMPLICATIONS

A zoning management that excludes any presence of individuals outside reproduction zones contradicts natural gene flow by dispersing individuals. Our study has indicated that wolves are capable of long-range dispersal of more than 1 year. Because their survival when crossing the non-wolf areas between zones is of special importance, we recommend transboundary management focus on better protection of floaters that might be Finnish-Russian dispersers on the Scandinavian peninsula. If dispersers are monitored, they should be fitted GPS collars that last for $\geq$ 2 years.

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LITERATURE CITED

Boyd, D. K., P. C. Paquet, S. Donelon, R. R. Ream, D. H. Pletscher, and C. C. White. 1995. Transboundary movements of a recolonizing wolf population in the Rocky Mountains. Pages 135–140 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Boyd, D. K., and D. H. Pletscher. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management 63:1094–1108.

Frame, P. F., D. S. Hik, H. D. Cluff, and P. C. Paquet. 2004. Long foraging movement of a denning tundra wolf. Arctic 57:196–203.

Fritts, S. 1983. Record dispersal by a wolf from Minnesota. Journal of Mammalogy 64:166–167.

Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves in northeastern Minnesota, 1969–1989. Canadian Journal of Zoology 69:2946–2955.

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Kojola, I., J. Aspi, A. Hakala, S. Heikkinen, C. Ilmoni, and S. Ronkainen. 2006. Dispersal in an expanding wolf population in Finland. Journal of Mammalogy 87:281–286.

Kojola, I., O. Huitu, K. Toppinen, S. Heikkinen, K. Heikura, and S. Ronkainen. 2004. Predation by wolves (*Canis lupus*) on European wild forest reindeer in east-central Finland. Journal of Zoology (London) 263: 219–228.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1459.

Liberg, O., H. Andrén, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson, and S. Bensch. 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. Biology Letters (London) 1:17–20.

Linnell, J. D. C., H. Brøseth, E. J. Solberg, and S. Brainerd. 2005. The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. Wildlife Biology 11:383–391.

McNutt, J. W. 1996. Sex-biased dispersal in African wild dogs, *Lycaon pictus*. Animal Behaviour 52:1067–1077.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 *in* L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. Chicago University Press, Chicago, Illinois, USA.

Merrill, S. B., L. G. Adams, M. E. Nelson, and L. D. Mech. 1998. Testing releasable GPS collars on wolves and white-tailed deer. Wildlife Society Bulletin 26:830–835.

Merrill, S. B., and L. D. Mech. 2000. Details of extensive movements by Minnesota wolves (*Canis lupus*). American Midland Naturalist 144:428–433.

Musiani, M., H. Okarma, and W. Jedrzejewski. 1998. Speed and actual distances travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). Acta Theriologica 43:409–416.

Olsson, O., J. Wirtberg, M. Andersson, and I. Wirtberg. 1997. Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. Wildlife Biology 3:13–25.

Ream, R. R., M. W. Fairchild, D. K. Boyd, and D. H. Pletscher. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349–366 *in* M. Boyce and R. Keiter, editors. The Greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Heaven, Connecticut, USA.

Sand, H., B. Zimmerman, P. Wabakken, H. Andrén, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914–925.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pages 3–24 *in* B. D. Chepko-Sade and Z. T. Halpin, editors. Mammalian dispersal patterns: the effects and social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

Stenseth, N. C., and W. Z. Lidicker. 1992. Animal dispersal: small mammals as a model. Chapman and Hall, London, United Kingdom.

Vilà, C., A.-K. Sundqvist, Ø. Flagstad, J. Seddon, S. Bjöörnerfeldt, I. Kojola, A. Casulli, H. Sand, P. Wabakken, and H. Ellegren. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. Proceedings of the Royal Society London B 270:91–97.

Wabakken, P., Å. Aronson, H. Sand, H. Rønning, and I. Kojola. 2004. Ulv I Skandinavia: statusrapport for vinteren 2002–2003. Report no. 2. Hedmark University College, Elverum, Norway. [In Norwegian, with English summary.]

Wabakken, P., Å. Aronson, T. H. Strømseth, H. Sand, and I. Kojola. 2005. Ulv I Skandinavia: statusrapport for vinteren 2004–2005. Report no. 6 Hedmark University College, Elverum, Norway. [In Norwegian, with English summary.]

Wabakken, P., H. Sand, O. Liberg, and A. Bjärvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Canadian Journal of Zoology 79:710–725.

Wrigley, R. E., and D. R. M. Hatch. 1976. Arctic fox migrations in Manitoba. Arctic 29:147–158.

Zimmermann, B., T. Storaas, P. Wabakken, K. Nicolaysen, O. K Steinset, M. Döötterer, H. Gundersen, and H. P. Andreassen. 2001. GPS collars with remote download facilities, for studying the economics of moose hunting and moose-wolf interactions. Pages 33–38 *in* A. M. Sibbald and I. J. Gordon, editors. Proceedings of Conference on Tracking Animals with GPS, 12–13 March 2001, Aberdeen, United Kingdom.

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