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Comparison of VHF and satellite telemetry for estimating sizes of wolf territories in northwest Alaska

Warren B. Ballard, Mark Edwards, Steven G. Fancy, Sue Boe, and Paul R. Krausman

Abstract During 1987–1991 we deployed 23 satellite transmitters (PTTs) on wolves (*Canis lupus*) in northwest Alaska, and compared seasonal and annual estimates of territory size with those calculated from VHF telemetry data. Area-observation curves indicated that an average of 123, 73, and 98 locations were necessary to describe 90% of annual, summer, and winter territories, respectively. Estimates of annual, summer, and winter territories from PTT data averaged 3,375; 1,040; and 3,444 km², respectively, whereas estimates from VHF-equipped wolves averaged 1,430; 530; and 980 km², respectively. Annual and seasonal territory sizes for PTTs were not correlated with pack size or number of locations. We attributed the larger estimates of territory size provided by satellite telemetry to more frequent locations, greater numbers of locations, acquisition of locations when it was impractical to obtain VHF locations, and location error.

Key words Alaska, *Canis lupus*, satellite telemetry, territory size, VHF telemetry, wolf

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Radiotelemetry allows biologists to locate wolf dens, which are the focal point of pack activities during late spring and early summer. Photo by J. Foster.

Accurate determination of wolf territory size is important for managers attempting to census large areas (Fuller and Snow 1988). Estimates of wolf territory size frequently depend on the number of locations used, and territory size has been associated with pack size and prey availability and distribution (Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987, 1997). Several authors have investigated the number of VHF telemetry locations necessary to adequately estimate wolf territory size. Fritts and Mech (1981) suggested that approximately 79 relocations were necessary for packs followed >1.5 years. Messier (1985) suggested that 40–80 locations were required to estimate annual territories, whereas Fuller and Snow (1988) indicated that 30–35 locations were needed to estimate 85–90% of winter territory size. Wolf territory sizes in these studies were <650 km².

In Alaska, wolf territory sizes are commonly >1,500 km², but the numbers of locations necessary to accurately describe annual and seasonal territory sizes have not been described. Ballard et al. (1987) determined that approximately 60 locations were necessary to define total territory size over 8 years.

During 1987–1990 we equipped several wolf packs in northwest Alaska with conventional VHF transmitters and satellite transmitters (i.e., platform transmitter terminals or [PTTs]) that transmit to receivers on satellites. Objectives of our study were to compare estimates of territory size calculated from VHF telemetry with those obtained from satellite telemetry, and to determine the optimum number of PTT locations necessary to accurately define 90% of wolf territory size.

Study area

We conducted the study in northwest Alaska. Topography of the area ranged from broad, flat plains

along major rivers to rolling hills and steep, mountainous terrain. Elevations ranged from sea level to 1,168 m. A detailed description of the study area was provided by Ballard et al. (1995, 1997).

Methods

During April 1987 through April 1991 we immobilized 86 wolves in 19 packs by darting from a helicopter (Ballard et al. 1982, 1991). Twenty-three wolves were equipped with PTTs, and the remainder were equipped with VHF transmitters (both manufactured by Telonics Inc., Mesa, Ariz.). Each pack contained ≥ 1 wolf fitted with a PTT and 1–5 wolves fitted with conventional VHF transmitters.

Fancy et al. (1988) and Harris et al. (1990) provided detailed accounts of the history and use of the Argos Data Collection and Location System that we used. Physical description, accuracy and precision of locations, performance, and costs associated with the use of PTTs in this study were described by Ballard et al. (1995). Each PTT weighed from 1.1 to 1.2 kg, and none of the wolves we studied were adversely affected by the size or weight of the PTTs (Ballard et al. 1995). Each satellite location is accompanied by a location quality index (NQ) provided by Argos indicating its expected accuracy. We used NQs 1–3 which were reported to have the following accuracies (Service Argos 1989): NQ 1, 68% of relocations within 1,000 m; NQ 2, 68% of locations within 350 m; and NQ 3, 68% of locations within 150 m. However, location error varies with a number of factors (Fancy et al. 1988, Harris et al. 1990), such as elevation. The designated elevation for this study was sea level. Wolf packs occurred from sea level to about 1,000 m elevation (Ballard et al. 1997). Ballard et al. (1995) tested location accuracy of the PTTs used in this study and found average location errors of 728 ± 757 m for NQ 1s, $551 \pm$



Wolf recently fitted with VHF transmitter. Photo by W. Ballard.

528 m for NQ 2s, and 336 ± 220 m for NQ 3s. Mean location error for PTTs was 577 ± 610 m (Ballard et al. 1995). PTT locations used in this study contained directional error biases to the south and west (Ballard et al. 1995). Also, by using software packages designed to identify erroneous locations, we deleted outliers from the data sets (Fancy et al. 1988, Harris et al. 1990).

We included data for 15 packs with >30 locations in our analysis. Accuracy of aerial VHF locations was not determined, but most pack members were observed during fixed-wing flights, and locations were plotted as accurately as possible in relation to topographic features. However, VHF locations plotted on topographic maps also are subject to errors ranging from 16 to 175 m (Carrel et al. 1997) or more.

The 13 PTTs deployed in 1988 and 1989 transmitted 6 hours daily through the first 30 days, then 6 hours every 2 days until battery exhaustion. Ten PTTs deployed in 1987 and 1990 transmitted 6 hours every 2 days until batteries were exhausted. Average life span of PTTs was 181 days (range = 50–366 days) (Ballard et al. 1995). On average, each radiomarked pack was relocated and visually observed from fixed-wing aircraft once every 22 days throughout the study (Ballard et al. 1997). However, daily locations were obtained during March and April each year (Ballard et al. 1997).

Both PTT and VHF locations were converted to Universal Transverse Mercator (UTM) coordinates that were entered into ARC/INFO® (Environ. Sys. Res. Inst., Inc., Redlands, Calif.) geographic information system (GIS) for plotting annual and seasonal territories. We estimated annual and seasonal territory sizes from all locations, except from obvious extraterritorial forays, dispersals, and migratory movements (Ballard et al. 1997). Only VHF locations obtained while PTTs were functional were used to compare estimates of territory size. We defined seasons based upon a biological year; winter from 1 October through 30 April, and summer from 1 May through 30 September (Ballard et al. 1997). We estimated annual and seasonal territory sizes using the minimum convex polygon (MCP) method (Mohr 1947) and a modification of the McPAAL software package (M. Stuwe and C. E. Blohowiak, unpubl. rep., Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Va., 1985). We modified the McPAAL software by developing a Pascal program that allowed simulation of effects of sample size on estimates of territory size. For each wolf we randomly selected 3, 5, 7, ..., n locations and calculated the MCP; we repeated this process 5 times for each wolf and sample size, then calculated a mean

MCP and its standard error. We used least squares regression (Neter et al. 1989) to compare number of locations and estimates of territory size for each pack for seasonal and annual locations. When area-observation curves (Odum and Kuenzler 1955) reached an asymptote, we considered the territory fully defined, and then calculated the number of locations needed to estimate 90% of that territory size. Territory sizes for packs that did not reach an asymptote were considered undefined. We analyzed correlations between numbers of locations and pack sizes with estimates of territory size, using Spearman's rank correlation r_s (Conover 1971). Comparisons of estimates of territory sizes were conducted by Kruskal-Wallis analysis of variance (ANOVA, Ott 1988). We also calculated PTT estimates of territory size based upon the numbers of VHF locations and compared the PTT and VHF estimates by Wilcoxon matched pairs tests. We present parameter estimates as means \pm 1 SE.

Results

Based upon area-observation curves, annual territory sizes were fully estimated for 8 (wolf nos. 00, 01, 03, 05, 06, 08, 09, and 14) of 22 wolves equipped with PTTs (Fig. 1). One PTT failed shortly after deployment. Territory sizes of 13 other packs had not yet reached an asymptote when radio failure occurred. An average of 123 ± 53 (range = 55–179) locations were necessary to explain 90% of annual territory size that averaged $3,375 \pm 1,973$ (range = 1,414–7,271) km² (Table 1). Total annual territory sizes averaged $3,750 \pm 2,193$ (range = 1,572–8,079) km² (Table 1).

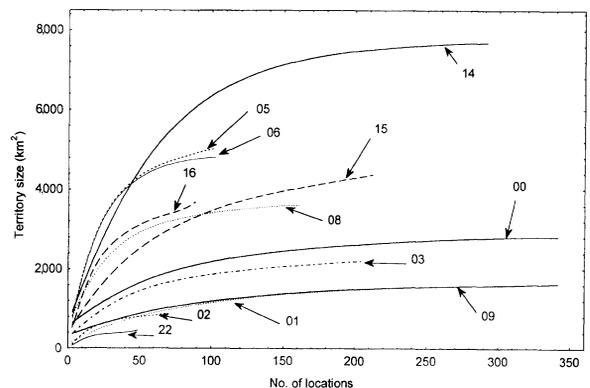


Fig. 1. Relationship between number of randomly selected locations and estimates of annual territory size for wolf packs equipped with 1 PTT during 1987 through 1991 in northwest Alaska. Numbers with arrows correspond to wolf packs listed in Table 1.

Table 1. Comparison of seasonal and annual sizes of wolf territories estimated by VHF versus satellite telemetry (PTT) in northwest Alaska, 1987–1991.

Year	Wolf No.	Pack name	Pack size	Summer			Winter			Annual							
				VHF		PTT	VHF		PTT	VHF		PTT					
				km ²	n	km ²	n	km ²	n	km ²	n	km ²	n				
1987	00	Rabbit Mt.	3	468	13	1,260	164	7	1,243	38	2,823	180	5	1,581	51	3,269	344
1988	01	Jade Mt.	1			536	83	2			1,670	123	1.5			2,024	206
	02	Ingruksukruk	10	900	29	968	67	14	1,252	30	2,294	125	15.5	1,821	43	1,015	69
03	Purcell Mt.	11	234	8	516	80	20	20	579	32	2,294	125	15.5	993	40	2,514	205
04	Nuna Creek	7	300	22	741	59	11	15	791	32	1,125	59	11	838	58	1,200	118
05	Pick River					741	59	15			1,125	59	11			1,200	118
06	Rabbit Mt.	2	296	16	876	58	8	8	1,099	12	1,127	20	5	2,334	50	1,617	79
1989	08	Rabbit Mt.	3			1,322	73	1			3,941	91	2			4,078	164
	09	Dunes	2	120	11	504	109	5	431	28	1,475	60	3.5	551	39	1,508	331
12	Ingruksukruk	9	900	29	5,008	63	7	7	1,316	30	2,674	36	8	1,991	59	6,327	99
14	Upper Tag	4			690	94	9	9			8,010	199	6.5			8,384	293
15	Dunes	5	393	9	680	106	6	6	514	29	4,645	107	5.5	745	38	5,124	213
16	Purcell Mt.	12	1,159	13	3,797	74	19	19	1,592	24	1,038	15	15.5	2,013	37	4,229	89
Pooled	\bar{x}		5.8	530	16.7	1,408	85.8	9.3	980	28.3	3,056	93	7.4	1,430	46	3,636	178
	SE		1.1	121.0	2.7	418	8.6	1.7	137	2.4	630	17.0	1.3	218	2.9	635	26.8

More locations were obtained during summer than winter because all except 1 PTT were deployed during spring and most PTTs were not functional for an entire winter season. Area-observation curves suggested that wolf territory sizes for ≥ 8 wolves (Nos. 00, 01, 03, 14, 15, 16, and 17) reached an asymptote (Fig. 2). Summer territories averaged $1,040 \pm 1,000$ (range = 511–3,258) km² (Table 1). An average of 73 ± 25 (range = 39–105) locations was necessary to explain 90% of summer territory size. Winter territory sizes were fully explained for only 4 wolves (Nos. 00, 01, 03, and 14) of 22 PTTs (Fig. 3). Total winter territory size averaged $3,444 \pm 2,843$ (range = 1,312–7,634) km² (Table 1). An average of 98 ± 11 (range = 87–113) locations were necessary to explain 90% of winter territory size.

Annual ($H = 8.1, P = 0.005$), summer ($H = 14.3, P = 0.0002$), and winter ($H = 5.2, P = 0.023$) territory sizes estimated from PTT data were larger than those estimated by VHF telemetry during the same periods. Furthermore, area-observation curves indicated that for many PTTs territory size had not been fully estimated (see Figs. 1–3 and Table 1). PTT estimates of territory size also were larger (annual, $H = 4.0, P = 0.047$; summer, $H = 6.2, P = 0.013$; and winter, $H = 4.7, P = 0.031$) than those previously reported and thought to be fully described according to available literature by Ballard et al. (1997).

We also compared estimates of territory size using identical numbers of locations between PTT- and VHF-equipped packs. We found no differences between estimates for summer ($Z = 0.8, P = 0.37, n = 9$), winter ($Z = 1.8, P = 0.07, n = 6$), or annual ($Z = 1.4, P = 0.17, n = 9$) territory sizes, suggesting that location error was not responsible for the large differences in estimates of territory size when all locations were used.

We found no significant correlations between pack size and annual ($r_s = 0.17, P = 0.86$), summer ($r_s = 0.35, P = 0.27$), or winter ($r_s = -0.26, P = 0.41$) territory sizes (Table 1), as estimated by PTTs. Also, we found no significant correlations between numbers of locations and annual ($r_s = 0.18, P = 0.55$) and summer ($r_s = -0.43, P = 0.16$) territory sizes from PTTs. However, we found a correlation between numbers of locations and winter ($r_s = 0.68, P = 0.02$) territory sizes. Winter territories were larger ($H = 18.3, P = 0.001$) than summer territories.

The larger estimates of territory size from PTTs resulted from more continuous contact, contact during periods when VHF transmitters were not lo-

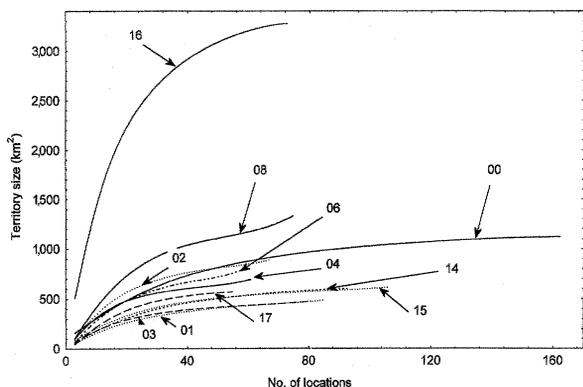


Fig. 2. Relationship between number of randomly selected locations and estimates of summer territory size for wolf packs equipped with 1 PTT during 1987 through 1991 in northwest Alaska. Numbers with arrows correspond to wolf packs listed in Table 1.

cated, and a greater number of locations per pack for wolves equipped with PTTs (Figs. 4, 5). Approximately 52% of the additional locations were obtained during October through January, when severe weather and short daylight prevented us from obtaining an adequate number of VHF locations. Also, 21% of the additional locations were obtained during June and July, when VHF transmitters were infrequently located because estimation of summer territory size was not a priority.

Discussion

Peterson et al. (1984), Ballard et al. (1987), Fuller (1989), and Hayes et al. (1991) found correlations between pack size and territory size. Ballard et al. (1997) also found a significant relationship between territory size, pack size, and number of locations. However, the Ballard et al. (1997) findings were

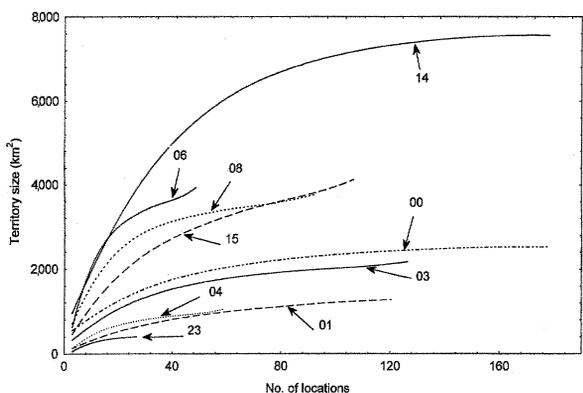


Fig. 3. Relationship between number of randomly selected locations and estimates of winter territory size for wolf packs equipped with 1 PTT during 1987 through 1991 in northwest Alaska. Numbers with arrows correspond to wolf packs listed in Table 1.

based on results of VHF telemetry for many of the same packs presented here. We found no relationship between pack size and territory size or between numbers of locations and territory size except for number of locations and winter territory size. The larger PTT territory sizes presented here suggest that Ballard et al. (1997) did not fully describe seasonal or annual territories in this study area. Because we found no correlations between pack size and number of locations with territory size, we suggest that differences among individual pack territory sizes may be more reflective of habitat quality and quantity (i.e., prey densities and distribution) than were previous estimates. Although territory sizes were not fully described with VHF telemetry, VHF data provided conclusions similar to Ballard et al. (1997) regarding differences in seasonal territories. Both data sets indicated that winter territory sizes were significantly larger than summer territories.

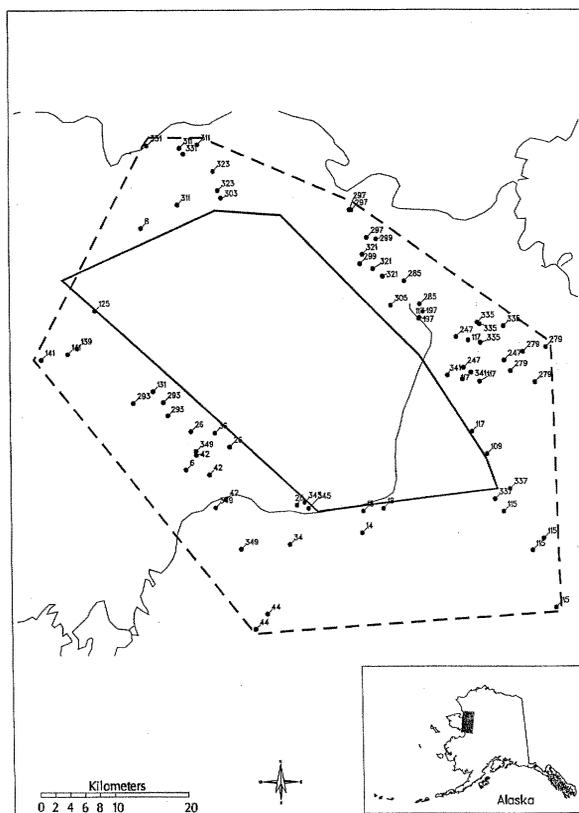


Fig. 4. Comparison of annual minimum convex polygons (MCP) for locations obtained by VHF versus satellite telemetry for the Rabbit Mountain Pack (wolf 00) in northwest Alaska from 17 April 1987 through 17 April 1988. Solid dark line depicts polygon provided by VHF telemetry; dashed line depicts polygon provided by satellite telemetry. Numbers reflect Julian dates of locations not encompassed by VHF MCP (Note: not all locations outside of VHF polygon were depicted because of spatial constraints).

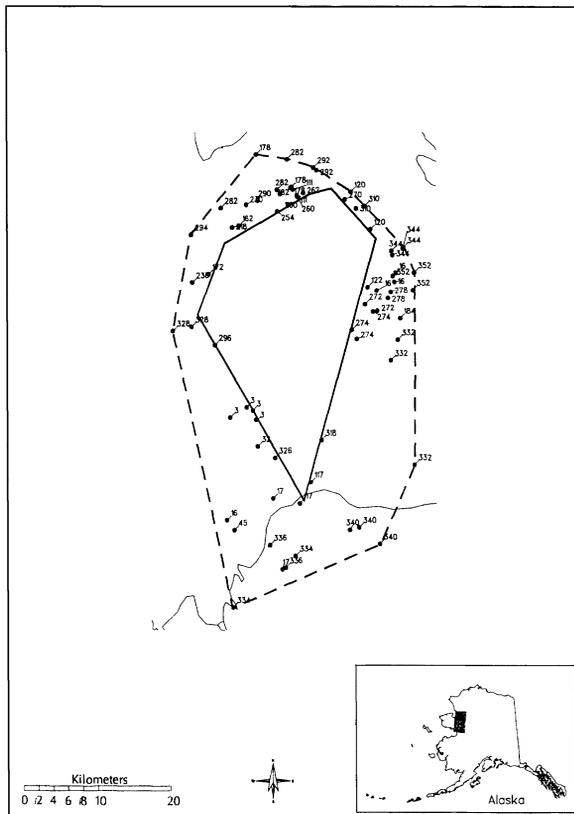


Fig. 5. Comparison of annual minimum convex polygons for locations obtained by VHF versus satellite telemetry for the Dunes Pack (wolf 09) in northwest Alaska from 7 April 1989 through 1 February 1990. Solid dark line depicts polygon provided by VHF telemetry; dashed line depicts polygon provided by satellite telemetry. Numbers reflect Julian dates of locations not encompassed by VHF MCP (Note: not all locations outside of VHF polygon were depicted because of spatial constraints).

Use of PTT data provided larger average estimates of wolf territory sizes than did data derived from VHF telemetry. VHF telemetry was limited by weather, day length, logistics, financial constraints, and other project objectives. Although location estimates derived from PTT data were less accurate than those obtained from VHF data, these errors were not large enough to account for the large differences in estimates of territory size between the 2 data sets. Estimates of territory size were not statistically different between VHF and PTT data when similar numbers of locations were used; however, because of small sample sizes, our power to detect differences was low. Available data suggest that the larger estimates of territory size derived from PTT data resulted from a combination of more frequent locations, greater number of locations, acquisition of PTT locations when it was impractical to obtain VHF locations, and location error associated with PTT locations.

Although PTTs provided larger estimates of territory size than did VHF data sets, only 8 of 22 wolf territories were adequately estimated according to area-observation curves. Failure to reach an asymptote for the remaining 14 transmitters was caused by the relatively short battery life span of the PTTs. PTTs deployed during 1987 through 1990 achieved from 57 to 175% of their expected battery life (Ballard et al. 1995). Variance in life spans of PTTs depend primarily on variability among battery packs, specific current drains, repetition periods, duty cycles, operating temperatures, and standing voltage wave ratios (Ballard et al. 1995). Average life span of PTTs declined each year of the study. In the future, biologists may obtain longer PTT life spans and better estimates of territory sizes by switching to a less frequent duty cycle so that PTTs transmit for longer periods. Also, advances in battery power and retention, in addition to improvements in manufacturing, will undoubtedly lead to longer PTT life spans.

Ballard et al. (1995) reviewed the cost:benefit ratios associated with use of satellite telemetry versus VHF telemetry in a 3-year study and reported that cost per location was \$44 and \$148 for satellite and VHF telemetry, respectively. Ideally, a combination of both satellite telemetry and VHF telemetry would satisfy most project objectives.

Management implications

In arctic, subarctic, and other areas where wolf territories are likely to be $>1,000 \text{ km}^2$, more locations are necessary to describe 90% of territory size than the 30–80 locations previously reported (Fritts and Mech 1981, Messier 1985, Ballard et al. 1987, Fuller and Sampson 1988, Fuller 1989). We recommend an average of 123, 73, and 98 locations to describe annual, summer, and winter territories, respectively.

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