SATELLITE TELEMETRY: PERFORMANCE OF ANIMAL-TRACKING SYSTEMS

KIMBERLY A. KEATING, Science Center, Glacier National Park, West Glacier, MT 59936
WAYNE G. BREWSTER, Science Center, Glacier National Park, West Glacier, MT 59936
CARL H. KEY, Science Center, Glacier National Park, West Glacier, MT 59936

Abstract: We used 10 Telonics ST-3 platform transmitter terminals (PTT's) configured for wolves and ungulates to examine the performance of the Argos satellite telemetry system. Under near-optimal conditions, 68 percentile errors for location qualities (NQ) 1, 2, and 3 were 1,188, 903, and 361 m, respectively. Errors (r_E) exceeded expected values for $NQ = 2$ and 3, varied greatly among PTT's, increased as the difference (H_E) between the estimated and actual PTT elevations increased, and were correlated nonlinearly with maximum satellite pass height (P_H). We present a model of the relationships among r_E, H_E, and P_H. Errors were bimodally distributed along the east-west axis and tended to occur away from the satellite when H_E was positive. A southeasterly bias increased with H_E, probably due to the particular distribution of satellite passes and effects of H_E on r_E. Under near-optimal conditions, ≥ 1 sensor message was received for up to 64% of available ($P_H \geq 5°$) satellite passes, and a location ($NQ \geq 1$) was calculated for up to 63% of such passes. Sampling frequencies of sensor and location data declined 13 and 70%, respectively, for PTT's in a valley bottom and 65 and 86%, respectively, for PTT's on animals that were in valley bottoms. Sampling frequencies were greater for ungulate than for wolf collars.

J. WILDL. MANAGE. 55(1):160–171

Satellite telemetry's advantages are contingent upon location accuracy and sampling frequency. Informed decisions regarding study design, therefore, require estimates of accuracy and sampling frequency and an understanding of how performance may vary. Previous estimates of animal-tracking performance (Mate et al. 1986, Craighead and Craighead 1987, Fancy et al. 1988, Stewart et al. 1989) were limited by small sample sizes, imprecise measures of accuracy, incomparable reporting, inappropriate measures of underlying statistical distributions, and/or pooling locations of varying qualities (*NQ* or, before April 1987, *NLOC* values). Except for Stewart et al. (1989), all were conducted before improvements in 1987 in Service Argos' algorithms for calculating locations and assigning quality indices and, therefore, may not reflect current performance. None emphasized the need to estimate variations in performance over a range of conditions.

We describe accuracy and sampling frequency of satellite telemetry with animal platform transmitter terminals (PTT's), test the hypothesis that accuracy is within expected limits, and describe and model effects of selected determinants of performance.

This study was funded by the National Park Service. Service Argos, Inc., graciously undertook the special data processing required. Telonics, Inc., provided material and technical support. The U.S. Forest Service Missoula Technology Development Center provided the Geographic Positioning System. Our special thanks to D. W. Beaty, W. P. Burger, D. D. Clark, R. Liaubet, D. D. Mitchum, H. M. Sparks, and S. M. Tomkiewicz; their support was invaluable. A. E. Jasumback and F. L. Gerlach provided expertise in Geographic Positioning Systems. D. R. Doyle provided coordinate conversion software and insights on geodetic ellipsoids. M. W. Anstead, J. S. Jacobson, C. K. and T. K. Kingery, S. M. Menke, C. J. Potter, and M. M. Sloan generously volunteered the study animals. We thank W. P. Burger, D. D. Clark, K. M. Dimont, S. G. Fancy, R. Liaubet, and S. M. Tomkiewicz for constructive reviews of the manuscript.

STUDY AREA

Our study was conducted in the Flathead River Basin of northwest Montana between 3 September and 10 October 1989. Eight test sites were within latitudes 48°1′ and 48°31′ north, and longitudes 113°33′ and 114°15′ west. Site elevations ranged from 2,109 m at Scalplock Lookout to 934 m at Columbia Falls. Horizontal and vertical controls were surveyed for 7 sites. The first site, at Scalplock Lookout, was a second-order National Geodetic Survey marker. Given National Geodetic Survey standards (D. R. Doyle, Natl. Geodetic Surv., pers. commun.), horizontal and vertical controls were considered accurate to ±0.1 m. During Phase 1, all PTT's were deployed at the Scalplock Lookout site. Six additional sites were surveyed with a Pathfinder II® Global Positioning System in autonomous mode. With position dilution of precision values <6, estimated errors for sites surveyed with this system were <10 m for horizontal controls and <15 m for vertical controls (A. E. Jasumback, U.S. For. Serv. Missoula Tech. Dev. Cent., pers. commun.). Elevation for one of these sites was estimated from a nearby site and was believed to be within 20 m of the actual elevation. During Phase 2, PTT's were deployed among the 6 sites surveyed with the Global Positioning System. At the eighth site, near Avalanche Lake, horizontal and vertical controls were estimated with a digitizer, 7.5 minute topographic map, and aerial photos. During Phase 3, all PTT's were deployed at the Avalanche Lake site.

Topography varied greatly among sites. The Scalplock Lookout site was relatively unobstructed. Its elevation exceeded that of adjacent landforms within 2.5 km, and no peak within 9 km exceeded the site elevation by ≥500 m. Phase 2 sites were located in fourth- or fifth-order drainages or in the Flathead Valley. At the most constricted of these sites, peaks within 2 km exceeded the site elevation by about 1,000 m. Average relief among the sites was much less. The Avalanche Lake site was chosen to maximize topographic interference with transmissions. Located in a narrow glacial valley with precipitous peaks rising in all directions, peaks within 1 km rose ≥1,500 m above the site.

METHODS

We used 10 Telonics ST-3 PTT's and the Argos satellite telemetry system to gather data on 15 variables (Appendix A). Five PTT's were configured for wolves and 5 for ungulates. Duty cycles for wolf PTT's were 6 hours on, 4 hours off, 10 hours on, and 4 hours off; ungulate PTT's transmitted 24 hours per day. Although VHF backup beacons were not used, wolf collars contained VHF antennas because of the suggestion that the proximity of the VHF and PTT antennas might undermine PTT performance (W. P. Burger, Telonics, Inc., pers. commun.). Platform transmitter terminals were turned on at about 1900 hours Rocky Mountain daylight savings time and transmitted at about 60-second intervals at 401.650 MHz. Because uplink success rate declines as the number of messages received by the satellite per second increases (Fancy et al. 1988), 1 PTT was switched on every 6 seconds to minimize simultaneous transmissions. Two satellites (Natl. Oceanic and Atmos. Adm. satellites G and H) were operational throughout the study. Fancy et al. (1988) described the satellite system.

Platform transmitter terminals were deployed in 3 phases. In Phase 1, they were placed upright at 36° intervals in a circle (radius = 2 m) around the Scalplock Lookout site with antennas facing north. When calculating errors, we assumed the PTT's were directly on the site marker, as the 2 m difference was considered trivial. In Phase 2, we deployed wolf collars on dogs, and ungulate collars on horses and mules. Data collected when dogs were indoors or removed from the test sites were excluded. Horses and mules remained in an outdoor corral; when an animal was removed from the corral, its transmitter was transferred immediately to another animal. Animals generally were confined to enclosures with radii <20 m. In Phase 3, PTT's were deployed at the Avalanche Lake site in the same manner described for Phase 1. Records from Phases 1 and 2 were processed 5 times; assumed elevation was altered each time, such that the difference (H_E) between assumed and actual elevations was 0, 500, 1,000, 1,500, and 2,000 m. Locations where $NQ = 0$ were calculated only during Phase 2.

Before calculating errors, we transformed latitudes and longitudes to Universal Transverse Mercator (UTM) coordinates. Coordinates for the Scalplock Lookout site referenced the Clark 1866 ellipsoid and were converted directly to UTM coordinates. Coordinates surveyed with a Global Positioning System referenced the World Geodetic System 1984 ellipsoid and were converted to North American Datum 1927 equivalents (which are based on the Clark 1866 ellipsoid), then to UTM coordinates. Coordinate conversions used National Geodetic Survey software, and assumed that the World Geodetic System 1984 and North American Datum 1983 coordinate systems were identical (differences between them are considered trivial [D. R. Doyle, Natl. Geodetic Surv., pers. commun.]). Zone 11 UTM coordinates were standardized to zone 12 equivalents with the GEOCON program (C. H. Key, Glacier Natl. Park, pers. commun.).

Errors were calculated as both Cartesian (x_E, y_E) and polar (r_E, Θ_E) coordinates whose origins were the known site locations. Advertised performances (Service Argos 1988, Clark 1989, R.

Liaubet, Service Argos, Inc., pers. commun.) implied that expected error distributions were bivariate normal with $(\mu_x, \mu_y) = (0, 0)$, $\sigma_x = \sigma_y$, and no correlation among σ_x and σ_y (where μ_x and μ_y are the means, and σ_x and σ_y are the standard deviations of x_E and y_E, respectively). For *NQ* = 1, 2, and 3, expected values for σ_x and σ_y were 1,000, 350, and 150 m, respectively (Service Argos 1988, Clark 1989). Probabilities (*P*) for the bivariate normal distribution are (Batschelet 1981:267):

$$P = 1 - \exp(-c/2) \quad (1)$$

where

$$c = \frac{(x_E - \mu_x)^2}{\sigma_x^{\,2}} + \frac{(y_E - \mu_y)^2}{\sigma_y^{\,2}}. \quad (2)$$

To determine if performance was within expected limits, we tested 3 null hypotheses: (1) $(\mu_x, \mu_y) = (0, 0)$, (2) the Θ_E were distributed uniformly, and (3) 68% of the r_E were within 1,510 (*NQ* = 1), 528 (*NQ* = 2), and 226 m (*NQ* = 3). A uniform distribution of Θ_E is a corollary of the expectation that σ_x and σ_y were equal and uncorrelated. Expected 68 percentile values of r_E follow from equations (1) and (2). They differed greatly from previous studies, which misinterpreted predicted values for σ_x and σ_y as the 1 standard deviation (SD) error distance of the r_E. For example, Stewart et al. (1989) stated that predicted performance of the system was such that 68% of the locations are accurate to within 150 (*NQ* = 3), 350 (*NQ* = 2), or 1,000 m (*NQ* = 1). Such an interpretation greatly overstates expected accuracy. From equations (1) and (2), it follows that only about 39% of the locations are expected within the distances indicated by Stewart et al. (1989).

Sampling frequencies of sensor data and location data, respectively, were calculated as:

$$M_S = M/S \quad (3)$$

$$L_S = L/S \quad (4)$$

where *S* is the number of "available" satellite overpasses, *M* is the number of passes in which ≥1 message was received by the satellite, and *L* is the number of passes in which a PTT location was calculated. We used Telonics Satellite Predictor software, together with surveyed horizontal and vertical controls, and ephemeris data from NASA Prediction Bulletins (NASA Goddard Space Flight Center, Code 513, Greenbelt, MD 20771) to determine *S*. Satellite passes with a maximum pass height $(P_H) \geq 5°$ above the horizon were considered "available." We used a 5° threshold because messages were received when P_H was as low as 5°, and it was the threshold used by Service Argos (1984) to estimate pass frequency and duration. Mate et al. (1986) also used a 5° threshold. Variables *L* and *M* were calculated from Argos dispose files.

Statistical analyses used SYSTAT® and SYGRAPH® (Wilkinson 1988*a*,*b*) software. Significance was assumed at the $\alpha = 0.05$ level. Logarithmic transformations were calculated, and linear and nonparametric tests were applied, according to Zar (1984). Kruskal-Wallis and Mann-Whitney tests were used to compare distributions of r_E; least-squares regressions were used to model relationships of r_E to H_E and P_H, and x_E and y_E to H_E; regressions were compared using an overall test for coincidental regressions; and sampling frequencies and error quantiles were compared using normal approximations of the binomial test. Mean angles, mean angular deviations, and transformations of circular variables were calculated, and circular and bivariate tests were applied, according to Batschelet (1981). Hotelling's T^2 test was used to test for biases in bivariate error distributions, and Rayleigh tests were used to examine uniformity of the directions of errors and satellite passes.

RESULTS AND DISCUSSION

Accuracy

Near-Optimal Conditions.—Location accuracy is a function of many interacting factors. It is affected by PTT elevation, velocity, and frequency stability (which, in turn, is affected by temp shifts), and by the number and temporal distribution of messages received by the satellite, the distance of the PTT from the satellite ground track, and by satellite position error (which, in turn, is influenced by ionospheric propagation error resulting from sun spot activity) (French 1986, Fancy et al. 1988, R. Liaubet, Service Argos, Inc., pers. commun.). Location quality (*NQ*) is an ordinal index that reflects the influence of some of these factors, including frequency stability, number and temporal distribution of messages received, and distance from the satellite ground track (Table 1). A PTT's environment may inhibit transmissions (Stewart et al. 1989), thereby affecting the *NQ* value assigned to a location.

At the Scalplock Lookout site, PTT's were stationary, topographic interference was mini-

Table 1. Criteria for assigning location quality indices (*NQ*) to calculated locations (Service Argos 1988, Clark 1989).

Location quality (predicted performance)[a]	Criteria
$NQ = 3$ ($\sigma_x = \sigma_y = 150$ m)	>4 messages received by satellite, pass duration >420 seconds, internal consistency <0.15 Hz, 5° < DT[b] < 18°, quality control on oscillator drift, and unambiguous solution
$NQ = 2$ ($\sigma_x = \sigma_y = 350$ m)	>4 messages received by satellite, pass duration >420 seconds, internal consistency <1.5 Hz, 1.5° < DT < 24°, quality control on oscillator drift, and unambiguous solution
$NQ = 1$ ($\sigma_x = \sigma_y = 1{,}000$ m)	≥4 messages received by satellite, pass duration >240 seconds, internal consistency <1.5 Hz, 1.5° < DT < 24°, and 1 test to determine correct solution
$NQ = 0$ (Quality of results to be determined by user, depends on number of messages received)	≥2 messages received by satellite

[a] σ_x and σ_y are the standard deviations of the longitudinal and latitudinal components of the error, respectively.
[b] DT = distance from satellite ground track.

mal, and precise elevation was known. Although PTT's were not insulated, temperature shifts during the study were not exceptional. These conditions were considered to be near-optimal relative to conditions in most animal-tracking studies. We examined 796 calculated locations from the Scalplock Lookout site ($H_E = 0$ m) (Fig. 1) to determine if errors were distributed as expected for PTT's under near-optimal conditions. Tests differentiated among *NQ* values because accuracy varied with *NQ* (Kruskal-Wallis test statistic = 119.594, 2 df, $P = 0.000$), with accuracy of $NQ = 3 > NQ = 2 > NQ = 1$ (Fig. 1).

First, we tested the null hypothesis that errors were centered about the true location, i.e., $(\mu_x, \mu_y) = (0, 0)$. Hotelling's 1-sample test indicated that the sample means $(\bar{x}_E, \bar{y}_E)$ were not significantly different from (0, 0) for any of the location qualities (Table 2). We concluded that calculated locations were unbiased estimates of true location when $H_E = 0$ m.

Second, we tested the null hypothesis that directions of errors (Θ_E) were uniformly distrib-

Table 2. Means of calculated locations relative to the Scalplock Lookout site, by elevational error (H_E) and location quality (*NQ*). Hotelling's T^2 statistic was used to test the hypothesis that $(\bar{x}_E, \bar{y}_E) = (0, 0)$. One-tailed probabilities (*P*) were estimated from the *F* distribution using the relationship described by Batschelet (1981, eq 7.4.5). H_E, $\bar{x}_E$, $\bar{y}_E$, and standard errors (SE) are in meters.

H_E	*NQ*	*n*	$\bar{x}_E$	SE	$\bar{y}_E$	SE	T^2	*P*
0	All	796	91	57	38	40	2.728	0.256
	1	376	133	106	81	76	1.916	0.386
	2	291	89	73	12	47	1.517	0.471
	3	129	−27	41	−27	37	0.964	0.621
500	All	782	166	66	−71	42	13.074	0.001
	1	368	157	116	−29	78	2.764	0.253
	2	285	230	97	−117	51	12.019	0.000
	3	129	50	59	−93	38	6.038	0.054
1,000	All	782	235	80	−175	44	31.339	0.000
	1	367	198	131	−127	81	7.052	0.031
	2	285	350	132	−231	58	24.388	0.000
	3	130	84	91	−188	46	17.565	0.000
1,500	All	779	303	98	−282	47	52.876	0.000
	1	366	239	153	−230	84	13.176	0.000
	2	284	476	173	−348	66	35.932	0.000
	3	129	119	125	−286	54	28.490	0.000
2,000	All	778	377	118	−385	51	73.458	0.000
	1	370	286	174	−330	88	20.685	0.000
	2	279	605	222	−465	77	44.619	0.000
	3	129	147	161	−370	63	36.516	0.000

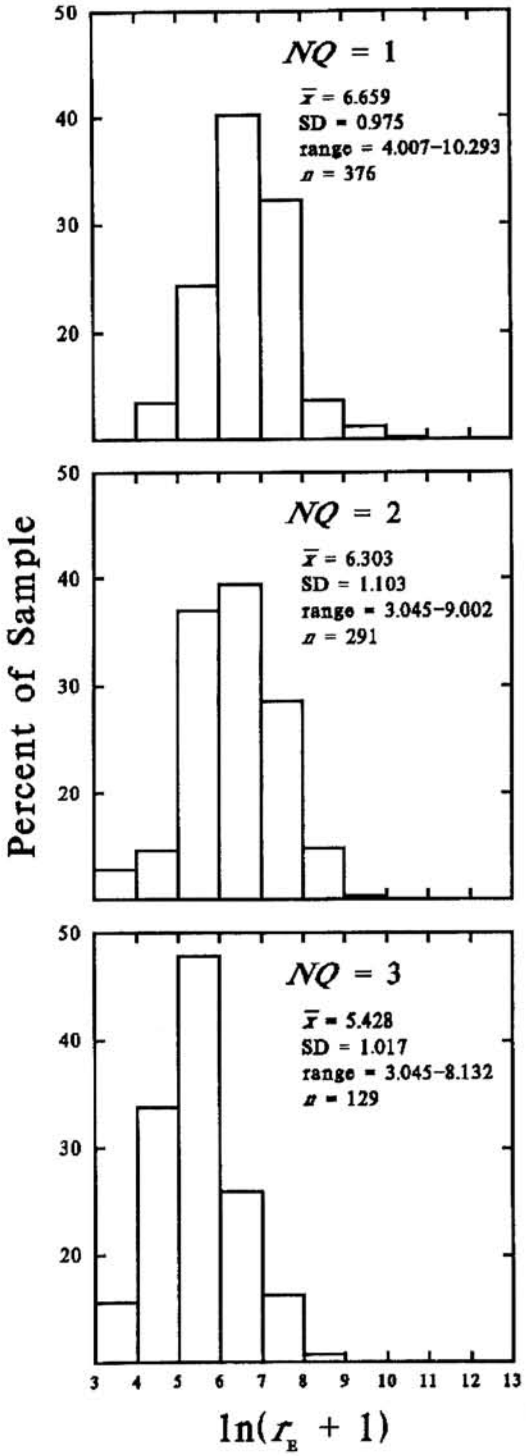

Fig. 1. Distributions of the logarithmic transformations of the error vectors, $\ln(r_E + 1)$, where r_E is in meters, for locations of varying qualities (*NQ*), based on 796 locations from the Scalplock Lookout site. Elevational error (H_E) for all locations was 0 m.

uted. Because graphic analyses suggested bimodal distributions of Θ_E for all *NQ* values, angles were doubled according to Batschelet (1981). Rayleigh tests indicated that for all *NQ* values, the Θ_E were distributed bimodally along undirected axes of 189–197° (Table 3). Other studies (Craighead and Craighead 1987, Fancy et al. 1988, Priede 1988), including one in which PTT elevation was correctly specified (Stewart et al. 1989), also reported greater error along the east-west axis but offered no explanation. In our study, directions of satellite passes at their maximum pass heights (Θ_S) were distributed bimodally along undirected axes of 190–198°, suggesting that errors may have occurred either directly toward or directly away from the satellite. To test this hypothesis we examined distributions of Θ_D, where $\Theta_D = \Theta_E - \Theta_S$. For all *NQ*, the Θ_D were distributed unimodally such that errors tended to be directed 166–213° away from the satellite (Table 3). We concluded that the relationship of Θ_E to Θ_S tended to produce an east-west bias among locations.

Finally, we rejected the null hypothesis that the magnitudes of the errors (r_E) were distributed as expected, i.e., 68% within 1,510 ($NQ = 1$), 528 ($NQ = 2$), and 226 m ($NQ = 3$). For $NQ = 1$, 2, and 3, respectively, 77, 51, and 46% of the locations were within predicted limits. A normal approximation of the binomial test showed accuracy was greater than expected for $NQ = 1$ ($Z = 4.193$, $P = 0.000$), but less than expected for other location qualities ($NQ = 2$: $Z = 12.691$, $P = 0.000$; $NQ = 3$: $Z = 8.568$, $P = 0.000$).

We examined the hypothesis that failure to achieve expected accuracies for $NQ = 2$ and 3 may have been due to the PTT's. Animal PTT's are believed to be less accurate than larger models with more stable frequency oscillators, greater power, and superior antennas (Clark 1989), although differences should lead to fewer high-quality locations for animal PTT's rather than greater error within an *NQ* class (R. Liaubet, Service Argos, pers. commun.). Results were equivocal. A normal approximation of the binomial test showed that proportions of locations within the 1 standard deviation error distances reported by Clark (1989) (who used a theoretically superior CML-86 PTT) were less than expected for $NQ = 1$ and 2, but were not significantly different for $NQ = 3$ ($NQ = 1$: $Z = 5.442$, $P = 0.000$; $NQ = 2$: $Z = 3.283$, $P = 0.001$; $NQ = 3$: $Z = 1.460$, $P = 0.144$). Clark (1989)

Table 3. Analyses of directions (Θ_E) of errors, and differences (Θ_D) between Θ_E and directions of satellite passes (Θ_S) at their maximum pass heights, by elevational error (H_E) and location quality (*NQ*). H_E is in meters; Φ_E is the mean axis of the bimodal distribution of Θ_E and is referenced to a Cartesian plane where 0° is east; Φ_D is the mean angle of the unimodal distribution of Θ_D and is relative to Θ_S; *s* is the mean angular deviation of Φ; and *z* is the Rayleigh statistic (Batschelet 1981). $P < 0.02$ where $H_E = 0$ m and $NQ = 1$ or 3; otherwise $P < 0.001$.

H_E	*NQ*	*n*	Φ_E	*s*	*z*	Φ_D	*s*	*z*
0	All	796	193°	36°	29.538	197°	72°	36.114
	1	376	189°	38°	3.932	213°	73°	12.182
	2	291	193°	33°	29.474	166°	70°	18.042
	3	129	197°	37°	3.920	201°	69°	10.041
500	All	782	193°	31°	134.398	183°	50°	298.665
	1	368	197°	34°	30.976	188°	56°	102.204
	2	285	183°	28°	73.134	179°	49°	116.371
	3	129	207°	26°	46.884	182°	33°	90.806
1,000	All	782	195°	28°	216.434	182°	40°	448.737
	1	367	192°	31°	65.941	184°	46°	168.207
	2	285	190°	26°	95.945	181°	38°	175.624
	3	130	206°	22°	65.981	182°	22°	110.991
1,500	All	779	193°	26°	267.776	181°	34°	531.805
	1	366	189°	29°	90.600	182°	39°	214.192
	2	284	190°	24°	115.736	181°	32°	201.346
	3	129	208°	20°	73.719	181°	15°	120.128
2,000	All	778	193°	25°	290.440	181°	30°	582.344
	1	370	187°	28°	101.040	182°	35°	245.161
	2	279	191°	24°	122.670	181°	28°	217.041
	3	129	209°	19°	80.563	181°	13°	122.128

also failed to achieve expected accuracies for 2 of 3 *NQ* classes, reporting 1 standard deviation error distances of 821, 637, and 385 m for $NQ = 1$, 2, and 3, respectively. We concluded that use of animal PTT's was not, by itself, a sufficient explanation for failing to achieve expected accuracies for $NQ = 2$ and 3, and that such accuracies probably are not achievable under field conditions. Potential accuracy, using ST-3 PTT's under near-optimal conditions, was estimated for selected percentiles (Table 4).

Variation Among PTT's.—Examining 796 locations from the Scalplock Lookout site ($H_E = 0$ m), accuracy varied among PTT's (Kruskal-Wallis test statistic = 39.920, 9 df, $P = 0.000$), with 68 percentile errors ranging from 593 to 1,816 m. Because sample size varied greatly among PTT's (range = 35–107), we hypothesized that differences in accuracy were due to differences in proportions of high-quality locations ($NQ = 2$ or 3) achieved for different PTT's. We rejected the hypothesis when analysis showed different accuracies among PTT's within *NQ* classes ($NQ = 1$: Kruskal-Wallis test statistic = 19.807, 9 df, $P = 0.019$; $NQ = 2$: Kruskal-Wallis test statistic = 36.491, 9 df, $P = 0.000$; $NQ = 3$: Kruskal-Wallis test statistic = 17.412, 9 df, $P = 0.043$). Ungulate collars were more accurate than wolf collars (Mann-Whitney $U_{347,449} = 84{,}098$, $P = 0.054$), but differences were not significant when PTT 6163 (a wolf collar that was an outlier) was excluded (Mann-Whitney $U_{271,449} = 59{,}812$, $P = 0.704$). Thus, variations among PTT's probably were not due to collar

Table 4. Observed and estimated potential accuracies for different location qualities (*NQ*). Estimated values are based on a *t*-distribution and the lognormal means, standard deviations, and sample sizes listed in Figure 1. Values for $NQ = 0$ are based on data from Phase 2 ($H_E = 0$ m); all other values are based on data from Phase 1 ($H_E = 0$ m).

	Percentile error (m)							
	68		90		95		99	
NQ	Obs	Estimated	Obs	Estimated	Obs	Estimated	Obs	Estimated
0	12,090	14,275	61,554	50,111	116,552	88,022	260,240	255,414
1	1,188	1,230	2,452	2,726	3,765	3,891	9,298	7,604
2	903	914	2,271	2,250	3,104	3,370	4,304	7,207
3	361	366	705	843	1,331	1,227	2,526	2,499

design. Fancy et al. (1988) reported variations in accuracy among 12 PTT's transmitting from the same site during the same 12-hour period, and they attributed differences to variations in oscillator stability and temperature-compensation circuitry. Though unproven, their hypothesis is the most plausible yet offered.

Effects of Elevation and Orbitography.—We evaluated elevational and orbitological effects with 3,919 locations from the Scalplock Lookout site, 3,121 of which were calculated by reprocessing the original data so that elevational error (H_E) was >0. m. First, we tested the hypothesis that error (r_E) was a function of H_E and satellite pass height (P_H). The relationship of r_E to P_H should be nonlinear (Fancy et al. 1988) and should change with H_E (French 1986). Therefore, using stepwise polynomial regression, we regressed r_E on P_H for each combination of NQ and H_E. Results (Fig. 2) indicated (1) for a given NQ and H_E, r_E was nonlinearly related to P_H, (2) for a given NQ and P_H, r_E increased with H_E, and (3) as H_E increased, optimum P_H decreased. There were 3 exceptions: the regression for $NQ = 3$ and $H_E = 500$ m was not significant ($P = 0.797$), and regressions for $NQ > 1$ and $H_E = 0$ m were linear ($NQ = 2$: $r^2 = 0.073$, $P = 0.000$; $NQ = 3$: $r^2 = 0.041$, $P = 0.012$). Graphic analyses suggested that the linear regressions were spurious, a result of decreasing variance with increasing P_H. We concluded that elevational error and orbitography were important determinants of accuracy except when location quality was high ($NQ = 2$ or 3) and elevational error was low ($H_E <$ 500–1,000 m).

Results demonstrated that PTT elevation must be accurately specified to maximize location accuracy, but elevation cannot always be known or may vary substantially over short periods. A model was developed to estimate error, given H_E and P_H. Because the magnitude of the error (r_E) is believed not to vary with the direction of elevational error (R. Liaubet, Service Argos, Inc., pers. commun.), the model used the absolute value of H_E. Regressions (Fig. 2) are of the form:

$$\hat{r}_E = c + bP_H + aP_H^2. \tag{5}$$

Using regression analysis, values for c, b, and a varied with H_E. For $NQ = 1$:

$$c = 2{,}342.272 + 0.367|H_E| \quad (r^2 = 0.947,\ P = 0.003), \tag{6}$$

$$b = -80.596 - 0.018|H_E| \quad (r^2 = 0.959,\ P = 0.002), \tag{7}$$

and

$$a = 1.070 + 0.001|H_E| \quad (r^2 = 0.979,\ P = 0.001). \tag{8}$$

For $NQ = 2$:

$$c = 1{,}608.759 + 0.633|H_E| \quad (r^2 = 0.978,\ P = 0.007), \tag{9}$$

$$b = -29.430 - 0.033|H_E| \quad (r^2 = 0.992,\ P = 0.003), \tag{10}$$

and

$$a = 0.174 + 0.001|H_E| \quad (r^2 = 0.999,\ P = 0.000). \tag{11}$$

For $NQ = 3$:

$$c = 766.598 + 0.559|H_E| \quad (r^2 = 0.987,\ P = 0.052), \tag{12}$$

$$b = -30.921 - 0.006|H_E| \quad (r^2 = 0.417,\ P = 0.363), \tag{13}$$

and

$$a = 0.342 + 0.005|H_E| \quad (r^2 = 0.975,\ P = 0.072). \tag{14}$$

Error estimates were calculated by making appropriate substitutions of equations (6)–(14) into equation (5). Comparisons with original regressions (Fig. 2) indicated good fits for all but $NQ = 3$ and $H_E = 1{,}000$ m. French (1986) developed a graphic model for estimating effects of elevational error. Our model extends French's results by (1) providing a mathematical means of calculating $\hat{r}_E$, (2) distinguishing among NQ values, and (3) providing a model empirically based upon post-1987 algorithms for calculating locations and assigning NQ values.

Second, we tested the null hypothesis that directions of errors (Θ_E) were uniformly distributed when H_E was >0 m. Because graphic analyses suggested bimodal distributions of Θ_E, angles were doubled (Batschelet 1981). Using a Rayleigh test, we rejected the hypothesis for all NQ and H_E (Table 3). We also examined the relationship between Θ_E and the direction of the satellite pass (Θ_S) when H_E was >0 m. Rayleigh tests indicated that Θ_D ($= \Theta_E - \Theta_S$) was distributed unimodally, with Θ_D approaching 180° and the mean angular deviation of Θ_D decreasing as H_E increased (Table 3). This supported the conclusion that errors tended to occur directly away from the satellite. We attributed this tendency to the fact that assumed elevations were greater than actual elevations. Earlier findings (Keating and Key 1990) indicated that errors tended to occur toward the satellite ($\Theta_D = 0°$) when as-

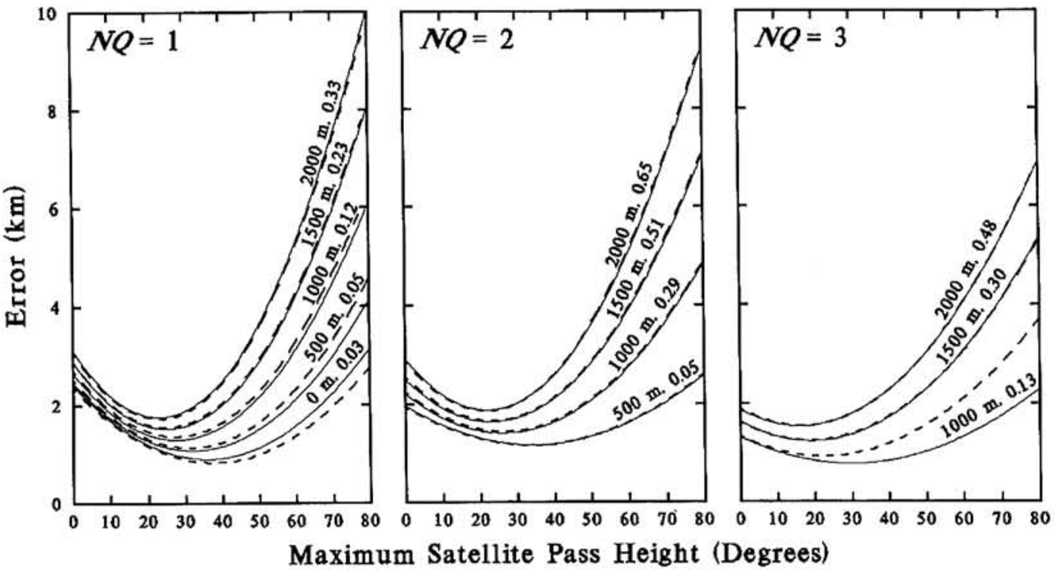

Fig. 2. Regressions of error on maximum satellite pass height, by location quality (*NQ*) and PTT elevational error (H_E). For each regression, H_E is listed in meters, followed by the regression's coefficient of determination (r^2). $P < 0.002$ for all regressions. Dashed lines indicate error estimates from the modeled relationship, given the same elevational errors (see text, eqs 5–14).

sumed elevation was less than the actual elevation. Because errors in our study tended to occur away from the satellite when $H_E = 0$ m, the transition point between these 2 states (i.e., the point where Θ_D is uniformly distributed and Θ_E is uncorrelated with Θ_S) probably occurs when H_E is slightly negative. Our findings conflicted with Fancy et al. (1988), who found no correlation between Θ_E and Θ_S for 9 PTT's at greater than assumed elevations. However, their analysis may have been confounded by the fact that H_E was nearly 0 m at 2 sites. We suggest that errors may have occurred away from the satellite at those 2 sites, whereas errors at remaining sites should have occurred toward the satellite. Thus, the correlation between Θ_E and Θ_S may have been masked by pooling data from all sites.

Finally, we rejected the null hypothesis that locations were unbiased when H_E was >0 m, i.e., $(\mu_x, \mu_y) = (0, 0)$. Hotelling's 1-sample test indicated that mean locations gave biased estimates of actual location when H_E was >0 m (Table 2). Bias increased toward the east and south as H_E increased (Table 5). Regressions of $\bar{x}_E$ and $\bar{y}_E$ on H_E varied with *NQ*, indicating that direction of the bias varied somewhat with location quality (overall test for coincidental regressions; $\bar{x}_E$: $F_{4,9} = 490.996$, $P = 0.000$; $\bar{y}_E$: $F_{4,9} = 184.348$, $P = 0.000$). Fancy et al. (1988) observed a northwesterly bias and speculated that it was due to differences between the Clark 1866 ellipsoid that they used and the World Geodetic System 1984 ellipsoid used by Service Argos, but our study controlled for differences between ellipsoids. Instead, biases were likely due to the negative correlation between Θ_E and Θ_S and the particular distribution of Θ_S in our study. Because errors tended to occur directly away from the satellite, expected directions of errors were estimated as $\Theta_S + 180°$ (Fig. 3) and indicated that more errors were expected in the southeast quadrant because more locations were achieved during satellite passes that peaked in the northwest quadrant. Variations in distributions of Θ_S probably accounted for differences among *NQ* values. Also, the magnitude of the bias probably was influenced by the relationship between r_E, P_H, and H_E (Fig. 2), so that bias was amplified

Table 5. Relationships of mean locations ($\bar{x}_E$, $\bar{y}_E$) to elevational error (H_E) for data of different qualities (*NQ*). H_E, $\bar{x}_E$, and $\bar{y}_E$ are in meters; $n = 5$ for all regressions.

NQ	Regression equation	r^2	*P*
All	$\bar{x}_E = 92.600 + 0.142H_E$	1.000	0.000
	$\bar{y}_E = 36.400 - 0.211H_E$	1.000	0.000
1	$\bar{x}_E = 125.000 + 0.078H_E$	0.985	0.001
	$\bar{y}_E = 77.600 - 0.205H_E$	1.000	0.000
2	$\bar{x}_E = 94.400 + 0.256H_E$	0.999	0.000
	$\bar{y}_E = 7.200 - 0.237H_E$	0.999	0.000
3	$\bar{x}_E = -8.800 + 0.083H_E$	0.939	0.004
	$\bar{y}_E = -17.000 - 0.176H_E$	0.995	0.000

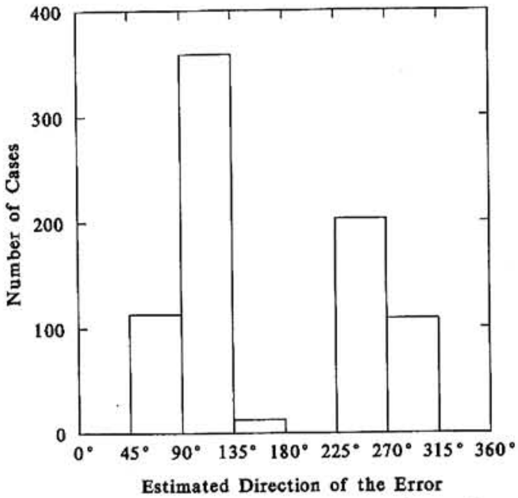

Fig. 3. Expected distribution of the directions of errors from Phase 1, given the directions of satellite passes in which locations ($NQ \geq 1$) were calculated, and the finding that errors occurred directly away from the satellite; 0° = north.

as H_E increased. Biases observed by Fancy et al. (1988) probably resulted from the particular distribution of satellite passes during their study and because they specified incorrect PTT elevations.

Results suggested that some corrections for effects of elevational errors may be possible. Error correction requires estimates of the magnitude (r_E) and direction (Θ_E) of errors. We suggest that, given an estimate of the magnitude and direction of the elevational error, r_E may be estimated from equation (5), and Θ_E may be estimated from the direction of the satellite pass (Θ_S). Error correction would be particularly useful for data collection before about 1988, when location calculations most often assumed sea-level elevations because of the belief that "[e]rrors associated with PTT altitude only take on real significance in the case of balloons" (Service Argos 1984:23). Correction may also be useful when elevation cannot be estimated reliably before the data are examined. We are continuing to explore the potential for corrections and other forms of error mitigation.

Effects of Animals.—We used 125 locations from Phase 2 ($H_E = 0$ m) to analyze effects of animals on performance. First, we tested the null hypothesis that accuracy was not affected by body mass. For PTT's deployed on dogs versus horses or mules, differences in distributions of r_E were not significant for $NQ = 1$ (Mann-Whitney $U_{32,68} = 1{,}188$, $P = 0.460$). Small sample sizes precluded meaningful analyses for $NQ =$ 2 and 3. Analysis did not control for differences in P_H distributions among species because differences were not significant ($NQ = 1$: Mann-Whitney $U_{32,68} = 885$, $P = 0.132$). We concluded that accuracy did not vary with body mass, but we acknowledge the need for more definitive studies.

Locations from study Phases 1 and 2 ($H_E = 0$ m) were compared to test the null hypothesis that accuracy was the same whether PTT's were deployed on the ground or on animals. Results were inconclusive. For Phases 1 and 2, respectively, 68 percentile errors for $NQ = 1$ were 1,188 and 1,312 m, and for $NQ = 2$ were 903 and 1,510 m. For $NQ = 1$, accuracy did not differ significantly among phases (Mann-Whitney $U_{99,376} = 17{,}178$, $P = 0.184$). For $NQ = 2$, accuracy was lower following deployment on animals (Mann-Whitney $U_{24,291} = 2{,}005$, $P = 0.001$). For $NQ = 3$, sample size was too small for meaningful analysis. Results could not be explained by differences in P_H distributions between $NQ = 1$ and 2 locations, as differences were not significant (Phase 2: Mann-Whitney $U_{24,99} = 965$, $P = 0.153$).

"Animal-Tracking" Quality.—At least 4 messages from a single overpass normally are required to calculate a PTT's location, but it is difficult to achieve ≥4 messages in some environments. Service Argos therefore offers an "animal-tracking" service in which locations ($NQ = 0$) are calculated from as few as 2 messages (Courrouyan 1987). Accuracy of these locations is not guaranteed nor has it been well documented. During Phase 2 of our study, 184 locations were obtained in which $NQ = 0$ (Fig. 4). The 68 percentile error was 14,272 m, and errors ranged from 128 to 396,170 m. Stewart et al. (1989) reported an error of 3,733 m for 1 location ($NQ = 0$) during laboratory tests, and a mean error of 15.1 ± 14.9 (±SD) km for 13 such locations of a free-ranging harbor seal (*Phoca vitulina richardsi*). Although many $NQ = 0$ locations were reasonably accurate, our results indicated that errors much greater than those observed by Stewart et al. (1989) are relatively common. Also, distinguishing extreme errors may be more difficult than for higher quality locations. Among Phase 2 $NQ = 1$ locations, a single outlier >365 km was easily identified and excluded because of a hiatus in the error distribution between 30 and 365 km. The outlier presumably resulted from selecting the wrong solution to the location algorithm (each

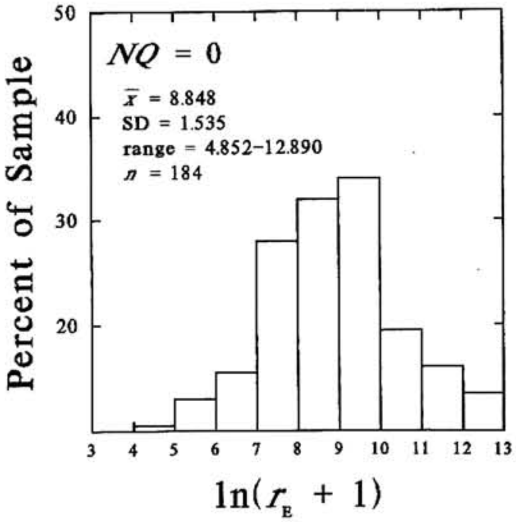

Fig. 4. Distribution of the logarithmic transformations of the error vectors, $\ln(r_E + 1)$, where r_E is in meters, for locations where $NQ = 0$, based on 184 locations of radio-collared dogs, horses, and mules. Elevational error (H_E) for all locations was 0 m.

location calculation has 2 possible solutions). However, there was no comparable hiatus for locations where $NQ = 0$, making objective identification of outliers difficult.

Sampling Frequency

Sampling frequencies of sensor (M_S) and location (L_S) data (Table 6) were similar to those reported in previous studies, although there were some differences under near-optimal conditions. In an environment virtually free of topographic interference and for passes where P_H was ≥5°, Mate et al. (1986) found that $M_S = 0.76$ and $L_S = 0.44$. Craighead and Craighead (1987) reported that locations were calculated for 32% of the passes in which ≥1 message was received (this is equivalent to stating that $L_S/M_S = 0.32$). In our study, $M_S = 0.57$, $L_S = 0.56$, and $L_S/M_S = 0.99$ for PTT's under near-optimal conditions. For PTT's on animals in valley bottoms, $M_S = 0.20$, $L_S = 0.08$, and $L_S/M_S = 0.39$. In the future, performance may be lower. Our PTT's transmitted at about 60-second intervals, whereas Service Argos now requires 90-second intervals. The change should result in fewer uplinks, thereby reducing sampling frequency and the proportion of higher quality ($NQ = 2$ or 3) locations. Waivers are available to users demonstrating a genuine need for a shorter repetition period (D. D. Clark, Service Argos, Inc., pers. commun.).

Table 6. Sampling frequencies of sensor (M_S) and location (L_S) data for 10 PTT's deployed on a mountain peak (Phase 1), on animals in valley bottoms (Phase 2), and in a narrow valley bottom (Phase 3), where S is the number of satellite passes "available" ($P_H \geq 5°$) to receive transmissions, M_S is the proportion of passes where ≥1 message was received, and L_S is the proportion of passes in which locations ($NQ \geq 1$) were calculated.

Study phase	Collar type	S	M_S	L_S
1	All	1,420	0.569	0.561
	Wolf	710	0.494	0.489
	Ungulate	710	0.644	0.632
2	All	1,635	0.197	0.077
	Wolf	765	0.142	0.046
	Ungulate	870	0.245	0.105
3	All	1,080	0.496	0.168

Using a normal approximation to compare proportions, we tested 3 hypotheses regarding sampling frequencies. First, we rejected the null hypothesis that sampling frequencies were the same for PTT's on mountain tops versus valley bottoms. Sampling frequencies were lower at the Avalanche Lake (valley bottom) site than at the Scalplock Lookout (mountain peak) site (M_S: $Z = 3.627$, $P = 0.000$; L_S: $Z = 19.947$, $P = 0.000$). Terrain apparently reduced M_S and L_S by about 13 and 70%, respectively. Craighead and Craighead (1987) similarly reported lower location efficiency in mountain valleys. In our study, terrain also limited location quality. For the Scalplock Lookout site, 47, 37, and 16% of 796 locations were $NQ = 1$, 2, and 3, respectively; for the Avalanche Lake site, all 184 locations were $NQ = 1$. Differences in proportions of various quality locations were significant ($NQ = 1$: $Z = 13.000$, $P = 0.000$; $NQ = 2$: $Z = 9.717$, $P = 0.000$; $NQ = 3$: $Z = 5.812$, $P = 0.000$). Because maximum pass heights (P_H) for most satellite passes tend to be quite low (Fig. 5), we speculate that topographic influence was likely exponential, such that most of the effects of terrain will be manifested in situations with relatively moderate relief.

Second, we rejected the null hypothesis that sampling frequencies for PTT's on animals were greater than or equal to sampling frequencies for PTT's on the ground. Sampling frequencies were lower when PTT's were on animals than when deployed at Avalanche Lake (M_S: $Z = 16.402$, $P = 0.000$; L_S: $Z = 7.330$, $P = 0.000$). Deployment on an animal reduced M_S and L_S by about 60 and 54%, respectively, relative to sampling frequencies at Avalanche Lake. Be-

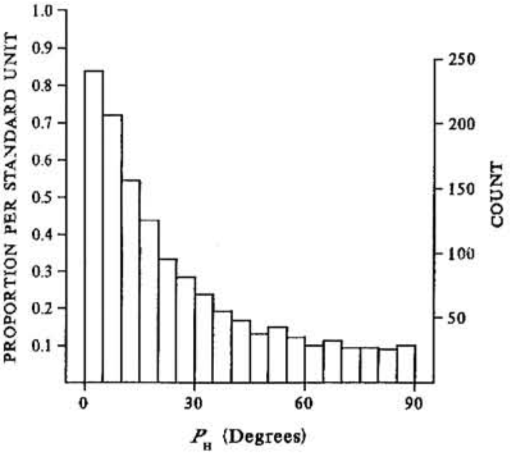

Fig. 5. Distribution of maximum pass heights (P_H) for 1,366 satellite passes observed from the Scalplock Lookout site.

cause test animals were located in valley bottoms, sampling frequencies for Phase 2 were potentially affected by both terrain and animals. However, all animals were in valleys considerably less precipitous than the Avalanche Lake site. Therefore, estimates of animal effects are believed to be conservative. Combined effects of terrain and animals reduced M_S and L_S by about 65 and 86%, respectively, relative to sampling frequencies under near-optimal conditions (Phase 1).

Finally, we rejected the null hypothesis that sampling frequencies were the same for wolf and ungulate collars. In examining data from the Scalplock Lookout site, we found that both M_S and L_S were about 23% lower for wolf collars (M_S: $Z = 5.707$, $P = 0.000$; L_S: $Z = 5.429$, $P = 0.000$). Differences may be greater under field conditions; data from Phase 2 indicated that M_S and L_S were 42 and 56% lower, respectively, for wolf versus ungulate collars. These estimates are likely conservative because 2 of 5 wolf collars were deployed on animals in the Flathead Valley where transmissions were probably less affected by terrain.

CONCLUSIONS

Satellite telemetry offers important economic and logistic advantages for wildlife studies (Craighead and Craighead 1987, Fancy et al. 1988). However, users should consider carefully the caveat implicit in the many determinants of system performance: marked variations in accuracy and sampling frequency may occur within and among studies.

Elevational error was the most important determinant of accuracy we studied. Due to its effects, location accuracy should vary among species and study areas. Best results are expected when PTT elevations change little and can be estimated precisely, e.g., marine species, where uplinks occur only when the PTT is at or near the water's surface. Poorest results are expected when PTT elevations change frequently and substantially, e.g., avian species. For species that move seasonally among different elevations, errors may be mitigated by periodically revising elevation estimates. This approach is likely to produce greater accuracy than specifying a year-long mean elevation. Still, precision of elevation estimates is likely to vary seasonally in relation to seasonal changes in the variance of the mean elevation that an animal occupies. Such variations could induce biases in, for example, estimates of seasonal home ranges.

Accuracy also varied among PTT's. We observed a 3-fold difference in the 68 percentile error among 10 PTT's. Fancy et al. (1988) reported a 5-fold difference in mean error among 12 PTT's. Although overall accuracy was acceptable for documenting gross animal movements, the degree of variation among PTT's suggested that satellite telemetry data should be evaluated cautiously and that some data sets may not be comparable.

Because the satellite orbits are circumpolar, sampling frequency varies with latitude, being greater at the poles than at the equator (Fancy et al. 1988, Service Argos 1988). It also varies with the environment. In our study, topographic interference reduced location efficiency up to 70%, and deployment on an animal reduced it at least an additional 54%. Stewart et al. (1989) reported that location efficiency almost doubled for a harbor seal that was ashore versus at sea, and almost no locations were achieved when the animal was actively diving. Sampling frequency (and cost-effectiveness) should, therefore, be greatest in open, terrestrial habitats at high latitudes. It should be lowest and most variable for species in, for example, marine, mountain, or canyon habitats, and for species exhibiting elevational or long-distance latitudinal migrations.

Finally, sampling frequency varied with collar design. Under field conditions, location efficiency was 56% lower for wolf than for ungulate collars. Differences suggested the extent to which collar design may affect cost. Expected battery life for wolf PTT's is only about half that of ungulate PTT's (S. M. Tomkiewicz, Telonics, Inc., pers. commun.). Together with disparities in sampling frequencies, this implies that the cost of achieving comparable sample sizes may vary by a factor of 4, exclusive of capture and other expenses. Differences in sampling frequencies may have been due to VHF antennas in the wolf, but not the ungulate, collars. If so, the cost of using VHF backup beacons may greatly exceed the price of the beacons themselves.

Depending upon a study's objectives, the range of variation in performance may not be consequential. For example, satellite telemetry's value for tracking gross animal movements is firmly established (Craighead and Craighead 1987, Fancy et al. 1988, Stewart et al. 1989). However, its very potential also has made satellite telemetry an alluring alternative for studying relatively localized movements and habitat use (Craighead and Craighead 1987, Fancy et al. 1988). Our results suggest that unless an animal occupies a very coarse-grained environment, improvements will be needed to realize that potential. The potential itself suggests that those improvements merit the investment they will require.

LITERATURE CITED

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, New York, N.Y. 371pp.

CLARK, D. D. 1989. Use of Argos for animal tracking in the Rocky Mountain Region of North America. Pages 129–176 *in* Proc. North American Argos users conference and exhibit. Service Argos, Inc., Landover, Md.

COURROUYAN, P. 1987. Wildlife. Argos Newsl. 32: 13–15.

CRAIGHEAD, D. J., AND J. J. CRAIGHEAD. 1987. Tracking caribou using satellite telemetry. Natl. Geogr. Res. 3:462–479.

FANCY, S. G., L. F. PANK, D. C. DOUGLAS, C. H. CURBY, G. W. GARNER, S. C. AMSTRUP, AND W. L. REGELIN. 1988. Satellite telemetry, a new tool for wildlife research and management. U.S. Fish Wildl. Serv. Resour. Publ. 172. Fairbanks, Alas. 138pp.

FRENCH, J. 1986. Environmental housings for animal PTT's. Argos Newsl. 26:7–9.

KEATING, K. A., AND C. H. KEY. 1990. Tracking bighorns with satellites: system performance and error mitigation. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 7:In Press.

MATE, B., G. RATHBURN, AND J. REED. 1986. An Argos-monitored radio tag for tracking manatees. Argos Newsl. 26:2–7.

PRIEDE, I. G. 1988. Tracking of birds. Argos Newsl. 34:1–3.

SERVICE ARGOS. 1984. Location and data collection satellite system: user's guide. Service Argos, Landover, Md. 36pp.

———. 1988. Users manual, version 1. CLS/Service Argos, Landover, Md.

STEWART, B. S., S. LEATHERWOOD, P. K. YOCHEM, AND M.-P. HEIDE-JORGENSEN. 1989. Harbor seal tracking and telemetry by satellite. Mar. Mammal Sci. 5:361–375.

WILKINSON, L. 1988*a*. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill. 822pp.

———. 1988*b*. SYGRAPH: the system for graphics. SYSTAT, Inc., Evanston, Ill. 922pp.

ZAR, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Englewood Cliffs, N.J. 718pp.

Received 11 June 1990.
Accepted 2 August 1990.
Associate Editor: Pollock.

Appendix A. List of variables and their definitions.

Variable	Definition
(r_E, Θ_E)	Polar coordinates of the error, where the origin is the true PTT location, and r_E and Θ_E are the magnitude (m) and direction (degrees) of the error, respectively.
(x_E, y_E)	Cartesian coordinates of the error, where the origin is the true PTT location, and x_E and y_E are the east-west and north-south error components (m), respectively.
PTT	Platform transmitter terminal; refers to any Argos-compatible transmitter.
NQ	Location quality; an ordinal index (range = 0–3) assigned by Service Argos.
H_E	Elevational error; the difference (m) between the PTT elevation specified by the user for location calculations and the true PTT elevation.
P_H	Maximum satellite pass height (degrees) above the horizon.
Θ_S	Direction (degrees) of the satellite at its maximum pass height relative to the true PTT location.
Θ_D	The difference (degrees) between Θ_E and Θ_S.
S	Number of satellite passes "available" ($P_H \geq 5°$) to receive transmissions.
M	Number of passes in which ≥1 message was received.
L	Number of passes in which a PTT location was calculated.
M_S	M/S
L_S	L/S