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TRACKING BIGHORNS WITH SATELLITES: SYSTEM PERFORMANCE AND ERROR MITIGATION

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Abstract: Performance of satellite telemetry in bighorn sheep (*Ovis canadensis*) habitat was described and error mitigation explored. The lognormal mean error of 304 locations was 2.728 km. Errors ranged from 0.445–12.552 km. The 68 percentile error of 3.276 km was significantly greater than the maximum expected value of 1.510 km. Differences between actual and assumed elevations accounted for about 66% of the error. Terrain apparently limited location quality and, therefore, accuracy by limiting the number of uplinks per satellite pass. Errors were bimodally distributed along the east–west axis and generally occurred toward the satellite, probably because actual elevations were much greater than the assumed elevation of sea level. Locations were obtained for up to 60% of satellite passes ≥5° above the horizon. Terrain reduced location efficiency up to 41%; when deployed on an animal, location efficiency declined an additional 43%. Following error "correction" and subsequent indexing to reject outliers, the 68 percentile error was 0.830 km (range = 0.086–2.263 km, n = 226). A bivariate normal model of the residual error was used to develop a weighted utilization distribution (WUD) that reflected the average probability of an animal occurring in a given space during a given period. The resulting model agreed well with visual observations of an adult ewe. Core ranges and specific travel corridors were identified for the ewe.

Bighorn sheep often occur in relatively small populations and occupy patchily distributed habitats. Many such populations may coexist within a region, suggesting that metapopulation theory may be useful for assessing long-term viability and designing conservation strategies. However, metapopulation analyses require knowledge of the distribution of suitable habitats and dispersal of individuals among habitat patches (Gilpin 1987). Such information has been difficult to obtain. Satellite telemetry, used with a Geographic Information System (GIS) and other remote sensing data, may improve the economic and logistic feasibility of acquiring necessary information (Craighead and Craighead 1987, Fancy et al. 1988), but the likely resolution of resulting models remains uncertain. Although satellite telemetry is well suited to tracking gross animal movements (Fedak et al. 1984; Fretay and Bretnacher 1984; Mate 1984; Priede 1988; Craighead and Craighead 1987; Grigg 1987; Marsh and Rathbun 1987; Mate et al. 1986, 1988; Fancy et al. 1988; Stewart et al. 1989), its ability to support studies of local movements and habitat use has not been demonstrated. We describe performance of satellite telemetry in bighorn habitat and explore error mitigation methods.

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STUDY AREA

Tests were conducted in and adjacent to the Many Glacier Valley, Glacier National Park, Montana, between latitudes 48°45' and 48°50' north, and longitudes 113°35' and 113°40' west. The area is characterized by precipitous peaks and glaciated valleys. Elevations range from 1,463–3,052 m. Major valleys are oriented in a generally east-west direction and drain eastward. Orientations of sub-drainages containing test sites ranged from north-south to east-west. Twenty-three test sites encompassed both winter and summer bighorn ranges, and were stratified by aspect and elevation along 7 transects extending from valley bottoms to mountain peaks. Wherever possible, sites were on mountain peaks, at stream intersections, in shallow gullies, or other similarly obvious landmarks that could be located readily using aerial photographs, 7.5 minute USGS topographic maps, an altimeter, and compass. Universal Transverse Mercator (UTM) coordinates were determined for each site using 7.5 minute USGS topographic maps and a digitizer.

METHODS

Accuracy and Sampling Frequency

During April–August 1986, a Telonics ST-2 Platform Transmitter Terminal (PTT) was moved every 3–5 days among the test sites. The PTT was configured for use on bighorn sheep and transmitted 24 hours per day at about 60-second intervals. The collar included a VHF backup beacon. Under the belief that "[e]rrors associated with PTT altitude only take on real significance in the case of balloons" (Service Argos 1984), location calculations assumed the PTT was at sea level. Fancy et al. (1988) give a detailed description of the satellite system.

Errors were calculated as both Cartesian (x_E, y_E) and polar (r_E, Θ_E) coordinates whose origins were the known test 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 the distributions of x_E and y_E, respectively). Expected values for σ_x and σ_y were 150, 350, and 1,000 m for NLOC = 1, 2, and 3, respectively (Service Argos 1988, Clark 1989). Probabilities (P) for the expected distribution are (Batschelet 1981:267):

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

where

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

To determine if performance was within expected limits we tested 3 null hypotheses: (1) 68% of the r_E were within 226, 528, and 1,510 m for NLOC = 1, 2, and 3, respectively, (2) the θ_E were distributed uniformly, and (3) $(\mu_x, \mu_y) = (0,0)$. A uniform distribution of θ_E is a corollary of the expectation that σ_x and σ_y are 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 error distances 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, 350, and 1,000 m for the 3 location qualities, respectively. 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 and location data, respectively, were calculated as:

$$M_S = M/S \tag{3}$$

$$L_S = L/S \tag{4}$$

where S is the number of "available" satellite passes, 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 and ephemeris data from NASA Prediction Bulletins (NASA Goddard Space Flight Center, Code 513, Greenbelt, Md. 20771) to determine S relative to the Mt. Altyn winter range. Satellite passes with a maximum pass height (P_H) ≥ 5° above the horizon were considered "available" to the PTT. We used a 5° threshold because messages may be received when P_H is as low as 5° (K. A. Keating, unpubl. data), and because it is the threshold used by Service Argos to estimate pass frequency and duration (Service Argos 1984). Mate et al. (1986) also used a 5° threshold. Variables L and M were tabulated from Argos dispose files. Due to a Service Argos software problem, multiple locations sometimes were calculated from 1 satellite pass. When this occurred, we acknowledged only 1 location when calculating sampling frequencies. The problem has been corrected since our study was conducted.

Error Mitigation

Correction, indexing, and weighted utilization distributions (WUDs) were explored as error mitigation techniques. They were employed sequentially in the order described.

Error correction.—To "correct" errors, $\hat{r}_E$ and $\hat{\theta}_E$ were estimated from regressions on P_H and θ_S, respectively. The rationale for using P_H and θ_S to estimate errors is presented in the results. We estimated P_H and θ_S using the Telonics Satellite Predictor Software with ephemeris data from NASA Prediction Bulletins. Using $\hat{r}_E$ and $\hat{\theta}_E$ to determine how far and in

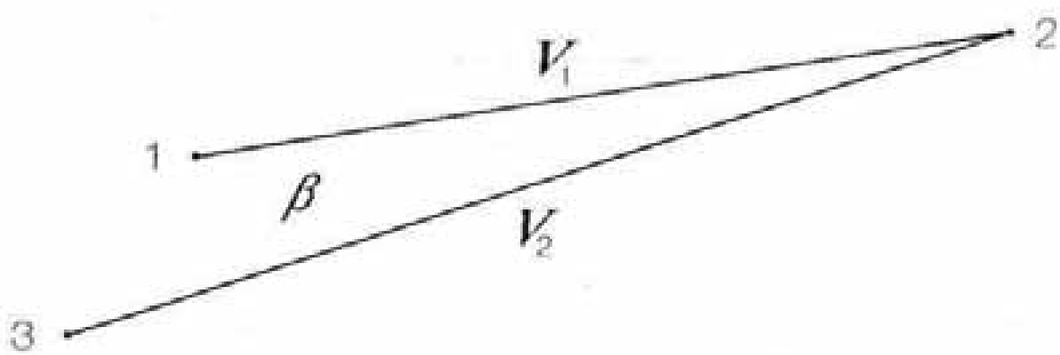


Fig. 1. Schematic representation of 3 consecutive calculated locations (1, 2, 3). The error index for location 2 is calculated from the vectors (V_1 and V_2) and the minimum angle (ß) formed by the 3 locations (see text, eq 5).

what direction to "move" locations, coordinates calculated by Service Argos were modified and compared with uncorrected locations to determine the efficacy of the technique.

Error indexing.—To develop an error index (I), we reasoned that data showing a single, relatively large movement, followed by an immediate return to the point of origin, should tend to be more erroneous than data showing localized movements, movements in unrelated directions, or large movements in the same direction. Such a pattern can be identified by examining 3 consecutive locations, from which 2 vectors (V_1 and V_2) and the minimum angle (ß) formed by the vectors can be calculated (Fig. 1). Larger errors are indicated as ß approaches zero, V_1 approaches V_2, and when V_1 and V_2 are both large. Thus, we calculated I as:

$$I = \left(\frac{V_1 + V_2}{2}\right)\left(\frac{V_{min}}{V_{max}}\right)\left(\frac{\cos\beta + 1}{2}\right) \qquad (5)$$

where V_{min} and V_{max} are the smaller and larger, respectively, of V_1 and V_2. When $V_1 = V_2$ and $\beta = 0°$, I attains a maximum value of $(V_1 + V_2)/2$ and, thus, becomes an estimate of r_E under those conditions. As V_{min}/V_{max} approaches 0 or as ß approaches 180°, I approaches 0. We hypothesized that I is linear on r_E.

By using 3 consecutive locations to index error we implicitly assumed that an extreme movement is not real unless it is confirmed by either the preceding or subsequent location. Clearly, a second, corroborative location will not always be obtained before an animal returns to a location near its point of origin. Error indexing should therefore lead to underestimating the frequency of extreme, short-term movements. The degree to which such movements are underestimated should depend upon sampling frequency and a species' movement patterns. Sampling frequency may vary with terrain, signal strength, or duty cycle (which is programmed into the PTT and defines the daily and seasonal transmission schedules). Short-term movements should be most seriously underestimated when sampling frequency is low and for species making frequent, long-range forays from one, or between 2, activity centers. Little bias is expected for species making large movements infrequently.

WUD.—The distribution of an animal's probability of occurrence has been termed a utilization distribution (UD) (Van Winkle 1975, Ford and Krumme 1979). Ideally, methods for describing UDs should be probabilistic, nonparametric, and insensitive to sample size (Ford and Krumme 1979). Methods based on relocation distance (Ford and Krumme 1979) and Fourier transformations (Anderson 1982) have been proposed. However, the former is computationally cumbersome and limited to small grids (Ford and Krumme [1979] used a 10 x 10 cell grid), while results of the latter may vary greatly with grid size (Anderson 1982). Both methods assume that locations used to compute the UD are precise. This assumption clearly was untenable for satellite telemetry data.

We proposed a method incorporating the error probabilities associated with each location. It is conceptually analogous to that of Ford and Krumme (1979). Noting that samples are seldom large enough to confidently determine UDs for individuals, Ford and Krumme (1979) suggested that UDs from several individuals be averaged to describe the UD of an idealized individual that typifies the population. They termed the result a "population utilization distribution" (PUD). We suggest that each calculated PTT location has a UD that defines the error probabilities associated with the location, and that the UD is the same among locations or classes of locations. We also suggest that UDs for animal locations can be averaged to determine the UD for an animal during a given period (Fig. 2). Because the resulting UD for an animal reflects error-weighted probabilities, we term the distribution a "weighted utilization distribution" (WUD). Our model of error probability is described in the results, as it is contingent upon results of the other analyses.

Animal Tracking and Data Analysis

To assess performance on an animal, an adult bighorn ewe was collared in the Many Glacier Valley and tracked during Nov. 1986–Dec. 1987. During this period, the PTT was programmed to transmit only 6 hours per day to conserve battery life. Actual movements were documented from visual observations during 1985–1988. Sampling frequency was examined relative to deployment status (on versus off the animal) and time since deployment. Error correction and indexing were applied and a WUD was calculated.

Statistical analyses used SYSTAT™ and SYGRAPH™ (Wilkinson 1988*a*,*b*) software. Significance was assumed at the $\alpha = 0.05$ level. Specific tests are identified in the results. Linear and nonparametric tests were applied according to Zar (1984). Circular statistics referenced Batschelet (1981). GRASS software (U.S. Army Corps of Engineers 1989) was used to develop WUDs from the error probability model.

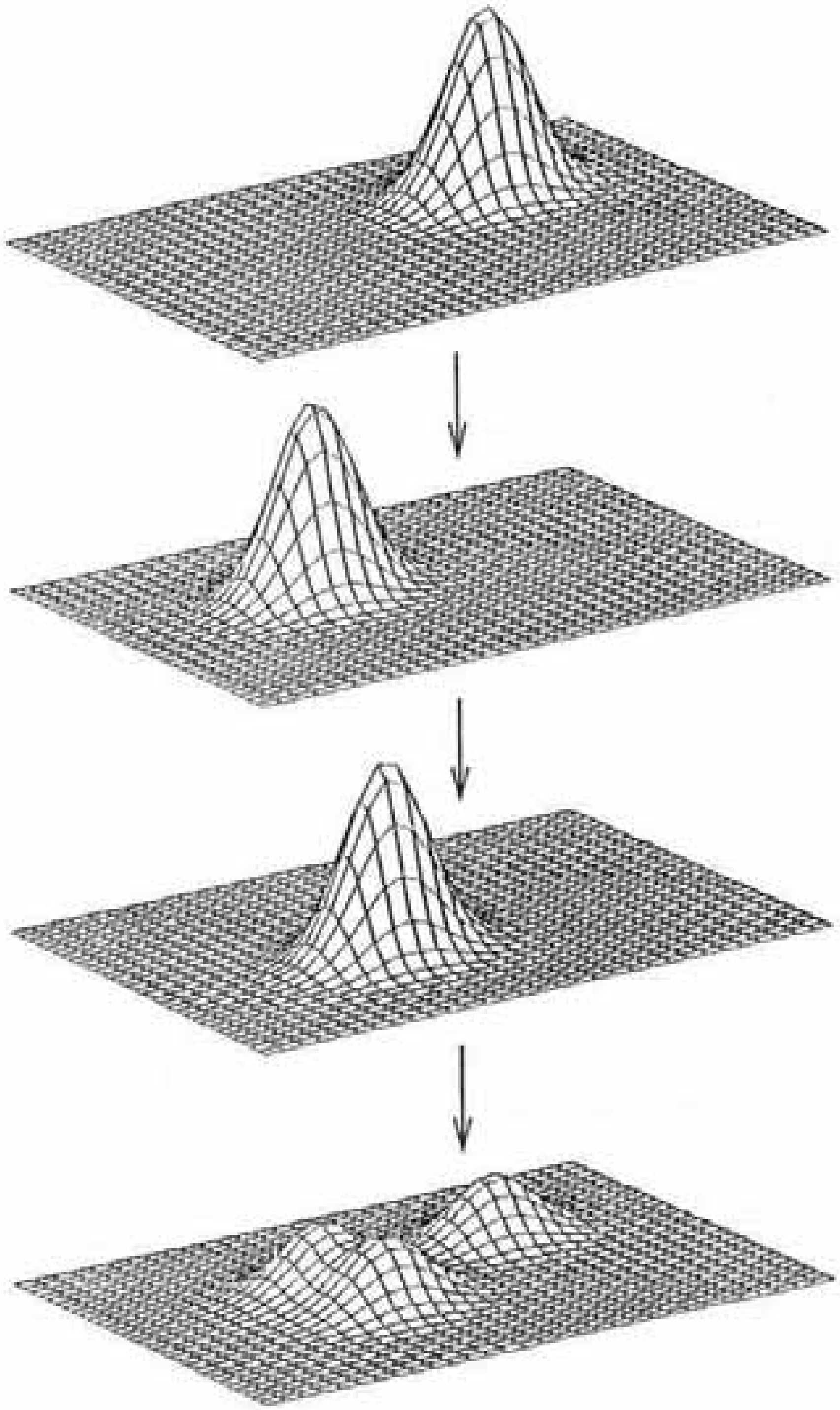


Fig. 2. Construction of a hypothetical weighted utilization distribution (WUD). Shown are 3 hypothetical PTT locations with a binormal model of the error probability superimposed over each location. The binormal model reflects the probability that the PTT was actually located at a point in space other than the calculated location. The WUD is constructed by averaging the probabilities associated with all data points (bottom image).

RESULTS AND DISCUSSION

Accuracy

Accuracy was described from 304 locations (Fig. 3). We rejected the null hypothesis that errors were within expected limits, i.e., 68% within 226 (NLOC = 1), 528 (NLOC = 2), and 1,510 m (NLOC = 3). Normal approximations of the 1-tailed binomial test showed that proportions of locations within expected limits for NLOC = 1 and 3 were less than expected (NLOC = 1: $Z = \infty$, $P = 0.000$; NLOC = 3: $Z = 23.32$, $P = 0.000$). No NLOC = 2 locations were achieved. Errors were considerably greater than have been reported previously. Mate et al. (1986) reported 94% of 46 locations within 0.6 km of the center of an enclosure with a radio-tagged manatee (*Trichechus mantus*), and a maximum error ≤2 km. For 42 locations of 2 PTTs, Craighead and Craighead (1987) reported half-lengths of 1.753 km and 0.516 km for the major axes of the 95% probability ellipses, and 0.405 km and 0.456 km for the minor axes. Fancy et al. (1988), examining 1,265 locations of 12 PTTs, reported a mean error of 0.829 km, with 90% within 1.7 km of the true location and a maximum error of 8.8 km.

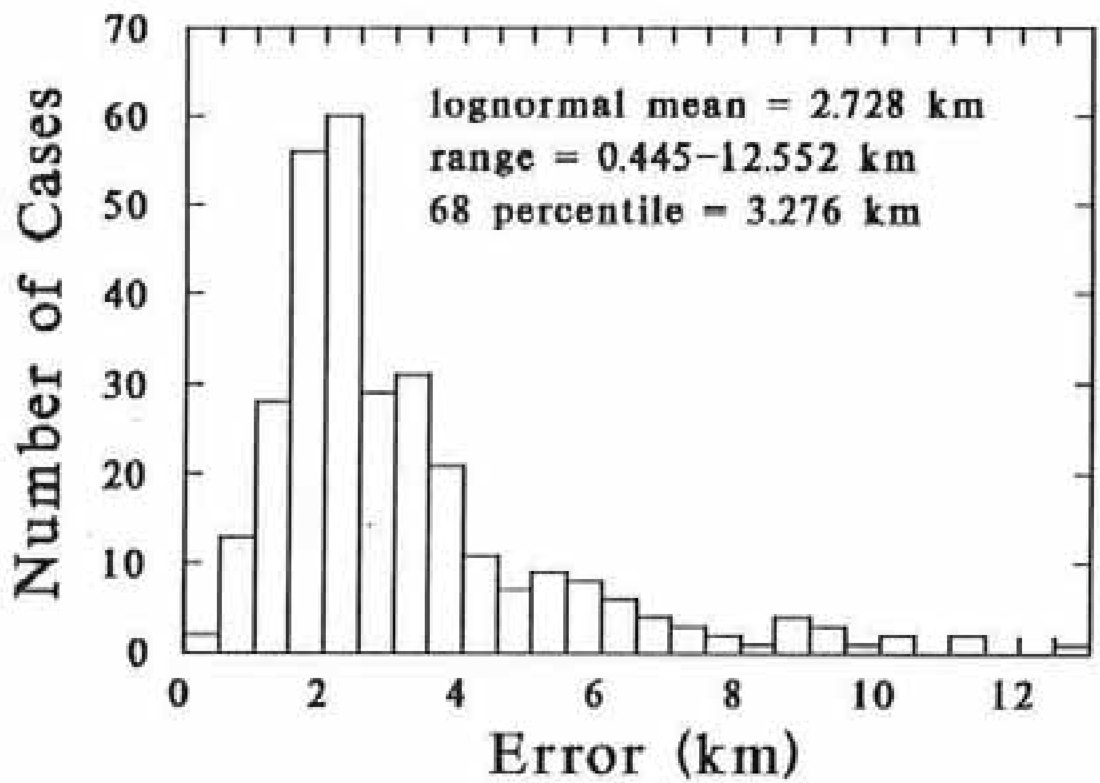


Fig. 3. Distribution of errors for satellite telemetry locations, as determined from 304 locations of a PTT deployed at 23 known sites. Differences between actual and assumed site elevations ranged from 1,462–2,801 m ($\bar{x}$ = 2,154 m, SD = 419 m) and accounted for about 66% of the observed error (see text).

The extreme errors we observed were likely caused by erroneous estimates of PTT elevation. Location calculations assumed that PTTs were at sea level, but actual elevations ranged from 1,462–2,801 m. French (1986) found that differences between actual and assumed PTT elevations may affect location accuracy. We therefore hypothesized that r_E was related to the difference (H_E) between actual and assumed PTT elevations. Linear regression revealed no relationship between r_E and H_E ($r^2 = 0.002$, $P = 0.21$). Fancy et al. (1988), examining 1,265 locations of PTTs at elevations of 20–850 m, also found no such relationship, even though location calculations in their study also assumed that PTTs were at sea level. However, neither analysis considered confounding, nonlinear effects of satellite pass height (P_H). From French (1986, Fig. 5), we estimated theoretical errors ($\hat{r}_E$) due to erroneous elevation estimates for 35 combinations of H_E and P_H. For each elevation, $\hat{r}_E$ was related to P_H by an exponential function:

$$\hat{r}_E = ae^{(bP_H)} \tag{6}$$

where a and b are variables, and e is the base of natural logarithms. Using regression analysis, estimates of a and b were obtained for each elevation. Subsequent regressions of a and b on H_E showed that a increased linearly with H_E ($r^2 = 0.997$, $P = 0.000$), the y-intercept of that relationship was equal to 0 ($P = 0.63$), and b was constant with respect to H_E ($P = 0.24$). Equation (1) was therefore restated as a function of H_E and P_H:

$$\hat{r}_E = a'H_E e^{(bP_H)} \tag{7}$$

where a' was a constant defining the relationship of a to H_E, and b was a constant defining the influence of P_H on the error–elevation relationship. Nonlinear regression was used to estimate a' and b, and yielded the following mathematical estimate of French's (1986) theoretical error–elevation relationship ($r^2 = 0.98$, $P = 0.000$), where $\hat{r}_E$ is in meters:

$$\hat{r}_E = 0.134H_E e^{(0.047P_H)} \tag{8}$$

Comparison of r_E and $\hat{r}_E$ indicated a significant relationship between r_E and H_E when effects of P_H were considered ($r^2 = 0.66$, $P = 0.000$). We concluded that about 66% of the error in this study resulted from specifying incorrect elevations, and that significant variations in accuracy may occur within studies as animals move among different elevations.

We also tested the null hypothesis that directions of errors (Θ_E) were uniformly distributed. Because graphic analyses suggested a bimodal distribution of Θ_E, angles were doubled (Batschelet 1981). The hypothesis was rejected following a Rayleigh test ($z = 134.69$, $P < 0.001$) which indicated that errors were distributed bimodally along an undirected axis of about 174° ± 23° (± mean angular deviation, east = 0°). (We note, however, that the Rayleigh test gives only an approximate indication of the true distribution. A scatter plot [Fig. 4A] clearly showed a quadrimodal distribution.) Other studies (Craighead and Craighead 1987,

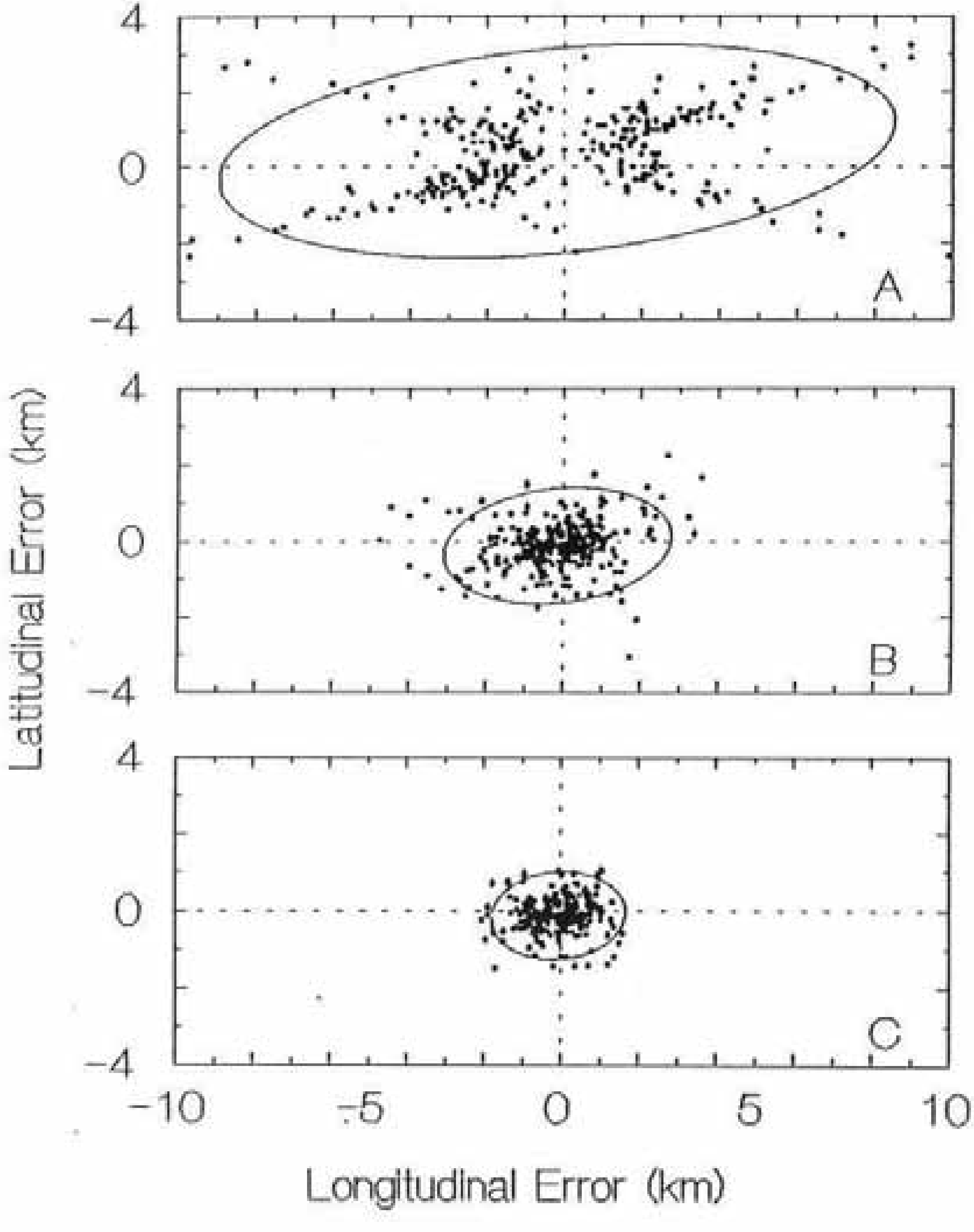


Fig. 4. Scatter plots of location errors for a PTT placed at 23 known sites. Errors were standardized to a true PTT location of (0, 0). Plots are for (A) uncorrected locations (n = 304), (B) locations corrected for effects of elevational error (n = 304), and (C) corrected locations where the error index (I) < 0.906 (n = 226). Ellipses are the 95% probability isoclines and assume a binormal distribution of the errors.

Fancy et al. 1988, Priede 1988, Stewart et al. 1989) also reported greater longitudinal than latitudinal error but offered no explanation. In our study, a Rayleigh test indicated that directions of satellite passes at their maximum pass heights (θ_S) also were distributed bimodally, along an undirected axis of about 176° ± 21° (z = 167.20, $P < 0.001$), suggesting that errors may have occurred either directly toward or away from the satellite. To test this hypothesis we examined distributions of θ_D, where $\theta_D = \theta_E - \theta_S$. A Rayleigh test indicated that θ_D was distributed unimodally (z = 260.49, $P < 0.001$) such that errors tended to occur directly toward the satellite (θ_D = 0° ± 25°).

Finally, we rejected the null hypothesis that locations were unbiased, i.e. (μ_x, μ_y) = (0, 0). Hotelling's 1-sample test indicated that mean location was a biased estimate of true location (T^2 = 55.03, P = 0.000). Relative to the true location, polar coordinates of the mean location were (496 m, 332°). Fancy et al. (1988) observed a similar northwest bias and speculated that it was due to differences among the Clark 1866 ellipsoid that they used and the World Geodetic System 1984 ellipsoid used by Service Argos. We also used the Clark 1866 ellipsoid to reference site coordinates and, therefore, hypothesized that the bias we observed was due to differences between the 2 ellipsoids. Using National Geodetic Survey's NADCON4 program to calculate differences among ellipsoids in our study area, we found that differences averaged 69.8 m (SD = 0.2 m), almost entirely in the easterly direction. We rejected the hypothesis and concluded instead that differences in ellipsoids likely "masked" part of the longitudinal component of the bias. Polar coordinates of the actual bias were estimated to be (532 m, 325°), relative to the true location. Bias may have resulted from the relationship between θ_E and θ_S, and the particular distribution of θ_S in this study. Expected directions of errors ($\hat{\theta}_E$) were estimated as $\hat{\theta}_E = \theta_S$ (Fig. 5) and indicated that more errors were expected toward the northwest simply because more locations were achieved during satellite passes that peaked in the southeast.

Sampling Frequency

Sampling frequencies were calculated for 1,921 satellite passes where $P_H \geq 5°$ (Table 1). Using normal approximations to compare proportions, we tested 2 hypotheses. First, we rejected the null hypothesis that sampling frequencies were unaffected by terrain. For both M_S and L_S, sampling frequencies varied among valley, mid-slope, and mountain peak sites (M_S: X^2 = 27.27, 2 df, P = 0.000; L_S: X^2 = 20.61, 2 df, P = 0.000). A Tukey-type comparison of proportions indicated that M_S was greater at mid-slope than valley bottom sites (q = 5.42, $P < 0.001$), and M_S was greater at mountain peak than mid-slope sites (q = 10.62, $P < 0.001$); L_S was greater at mid-slope than valley bottom sites (q = 10.15, $P < 0.001$), but did not differ significantly among mid-slope and mountain peak sites (q = 1.59, $P > 0.20$). For valley bottom versus mountain peak sites, terrain reduced M_S and L_S by about 17% and 41%, respectively. Craighead and Craighead (1987) similarly reported lower location efficiency for PTTs in mountain valleys.

We also rejected the null hypothesis that sampling frequencies were

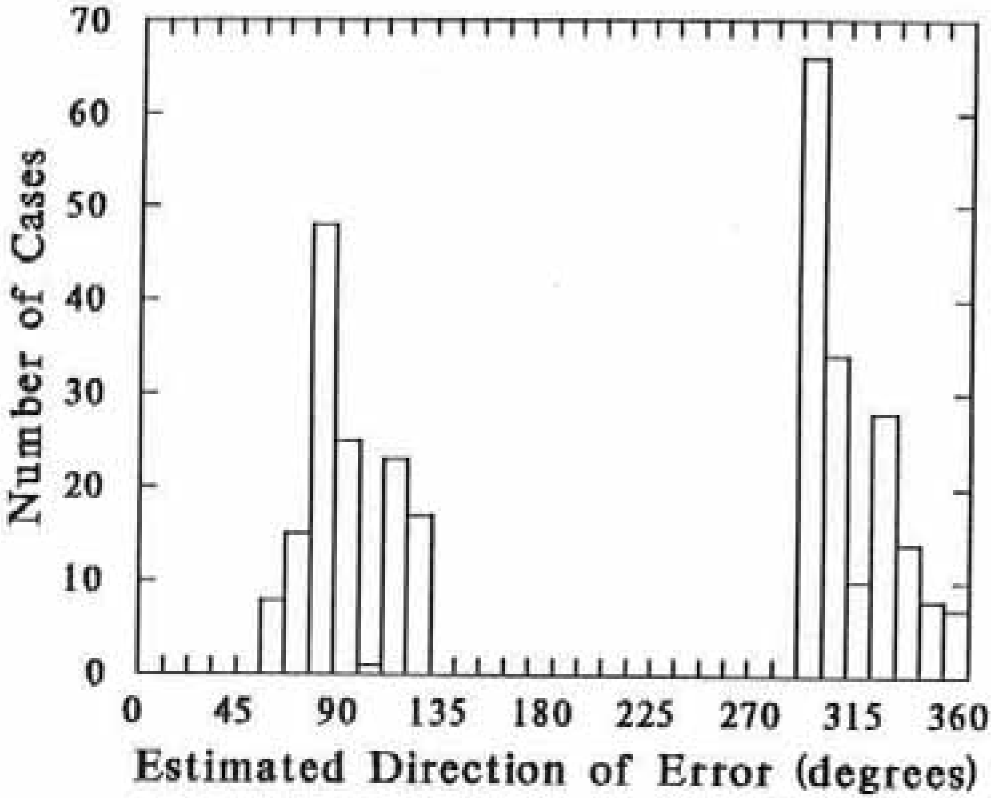


Fig. 5. Distribution of the expected direction (θ_E) of location errors, given the distribution of the directions of satellite passes (θ_S) and the relationship $\theta_E = \theta_S$.

Table 1. Sampling frequencies of sensor and location data for PTT 6160 at valley, mid-slope, and mountain peak sites, and on a bighorn ewe occupying a mid-slope winter range. S is the number of satellite passes "available" ($P_E \geq 5°$) to receive PTT transmissions, M_S is the proportion of passes where ≥1 message was received, and L_S is the proportion of passes in which locations were calculated.

Site	S	M_S	L_S
All Test Sites	454	0.914	0.524
Valley	129	0.822	0.357
Mid-slope	143	0.902	0.573
Peak	182	0.989	0.604
Adult Ewe	1,467	0.768	0.293

the same whether the PTT was deployed on the ground or on an animal. Sampling frequencies for a radio-collared bighorn ewe occupying a mid-slope winter range were compared with mid-slope sampling frequencies from pre-deployment tests (Table 1). When the PTT was deployed on the ewe, M_S declined about 15% and L_S declined about 49%. Differences were significant (M_S: $Z = 3.69$, $P = 0.000$; L_S: $Z = 6.86$, $P = 0.000$).

Sampling frequency is a major determinant of cost-effectiveness. Craighead and Craighead (1987) estimated that satellite telemetry cost about 15 times less than conventional VHF telemetry for tracking caribou (*Rangifer tarandus*), but observed that cost-effectiveness may vary with the number of collars purchased, number of locations made, and study area. Our results indicated that variations within and among study areas may be substantial and that animal use of high elevations may be overestimated due to effects of terrain on sampling frequency.

Error Mitigation

<u>Error correction</u>.—Much of the error in this study was attributed to differences between actual and assumed PTT elevations. We suggest such errors may be partially corrected using estimates of error coordinates ($\hat{r}_E$, $\hat{\Theta}_E$). Because errors tended to occur toward the satellite, Θ_E was estimated as:

$$\hat{\Theta}_E = \Theta_S. \tag{9}$$

As elevational error increases, r_E should increasingly become a quadratic function of P_M (French 1986, Fancy et al. 1988). Using polynomial regression, r_E was estimated as ($r^2 = 0.726$, $P = 0.000$):

$$\hat{r}_E = 2.642 - 0.093P_M + 0.002P_M^2. \tag{10}$$

This relationship should vary among studies depending upon actual elevational error. However, it is probably a good approximation for our study area and illustrates the proposed correction.

Given ($\hat{r}_E$, $\hat{\Theta}_E$), locations were recalculated. Errors for corrected locations were significantly less than for uncorrected locations (Fig. 4B) (Mann-Whitney $U_{304,304} = 81{,}933$, $P = 0.000$) and were unbiased, i.e. $(\mu_x, \mu_y) = (0, 0)$, (Hotelling's $T^2 = 1.99$, $P = 0.75$). The lognormal mean error of the corrected locations was 908 m. There still was no significant difference in accuracies among NLOC = 1 and NLOC = 3 locations (Mann-Whitney $U_{31,273} = 4{,}551$, $P = 0.49$). With 68% of corrected locations within 1,092 m of the true location, accuracy was significantly better than the 1,510 m expected for NLOC = 3 locations ($Z = 3.96$, $P = 0.000$). This suggested that given the correct elevation, performance for NLOC = 3 may be better than advertised by Service Argos. A Rayleigh test indicated corrected locations were distributed bimodally along an undirected axis of about 171° ± 33° ($z = 32.44$, $P < 0.001$), and that Θ_E continued to exhibit a significant, though more variable, relationship to Θ_S ($\Theta_D = 24° \pm 72°$, $z = 13.11$, $P < 0.001$).

We concluded that error correction improved the distribution and

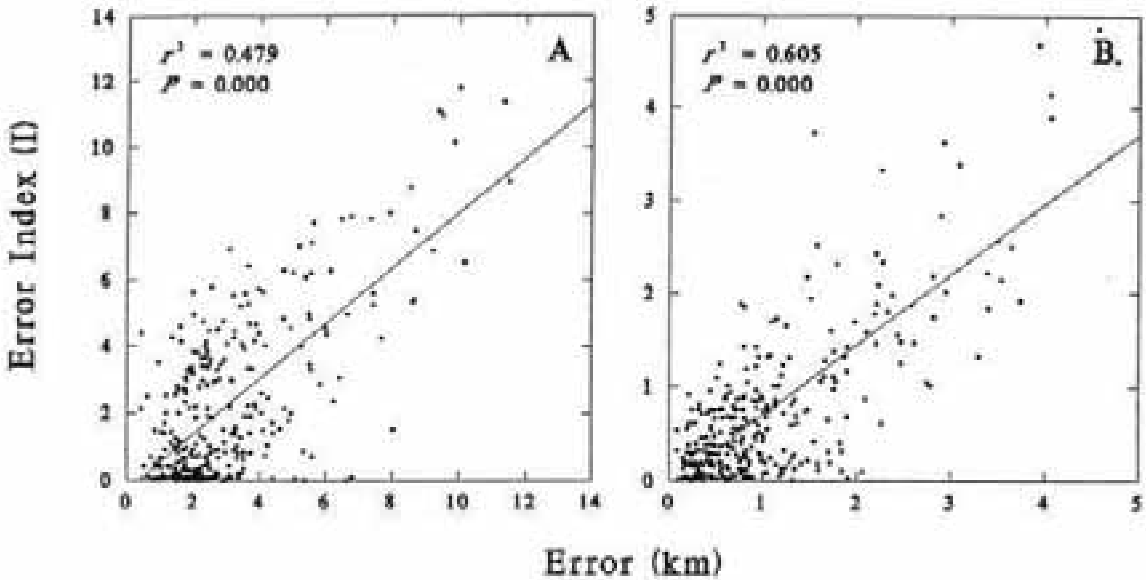


Fig. 6. Relationship of the error index (I) to observed error for (A) uncorrected locations, and (B) for locations corrected for elevational error.

precision of locations. It is potentially valuable for mitigating errors when elevation cannot be reasonably estimated in advance, although more universal models of the relationship between error, elevation, and satellite pass height will be required for the method to be broadly applicable. However, it remains preferable to specify the correct elevation prior to deployment.

Error indexing.—Error indices (I) (Fig. 1, eq 5) were calculated for 302 uncorrected and corrected locations. Regressions of I on error were significant (Fig. 6), suggesting that I was a useful index of both raw and residual error. To determine a threshold value for I, locations with the largest I-values were excluded first and lognormal means of remaining locations were calculated. The resulting relationship of lognormal mean error to sample size suggested that most benefits accrued when about 20–30% of the locations with the largest I-values were rejected (Fig. 7). When more than 80% of locations were rejected results became unpredictable. For this study, we used corrected locations and excluded about 25% of the locations ($I < 0.906$) (Fig. 4C). The lognormal mean error of corrected, indexed locations where $I < 0.906$ was 665 m, and was significantly less than for all corrected locations (Mann–Whitney $U_{304,226} = 41,106$, $P = 0.000$); 68% were within 830 m of the true location. However, the resulting estimate of the true location was slightly biased (Hotelling's $T^2 = 21.07$, $P = 0.000$), with the mean occurring at polar coordinates (147 m, 242°). We concluded that indexing provided an objective basis for rejecting, with a high probability, the most erroneous locations.

Weighted utilization distributions.—A bivariate normal distribution was used to model residual error following error correction and the

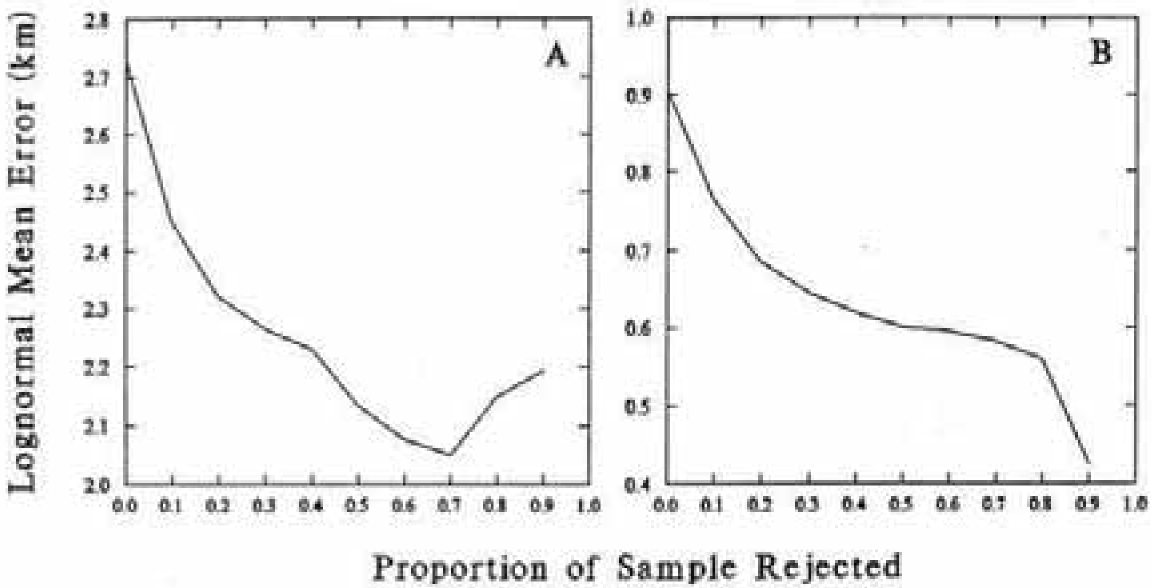


Fig. 7. Relationship among proportion of sample rejected and lognormal mean error, where locations with the largest error indices (I) were rejected first, for (A) uncorrected locations and (B) locations corrected for elevational error.

rejection of locations where $I < 0.906$. The model's probability density is (Batschelet 1981:269):

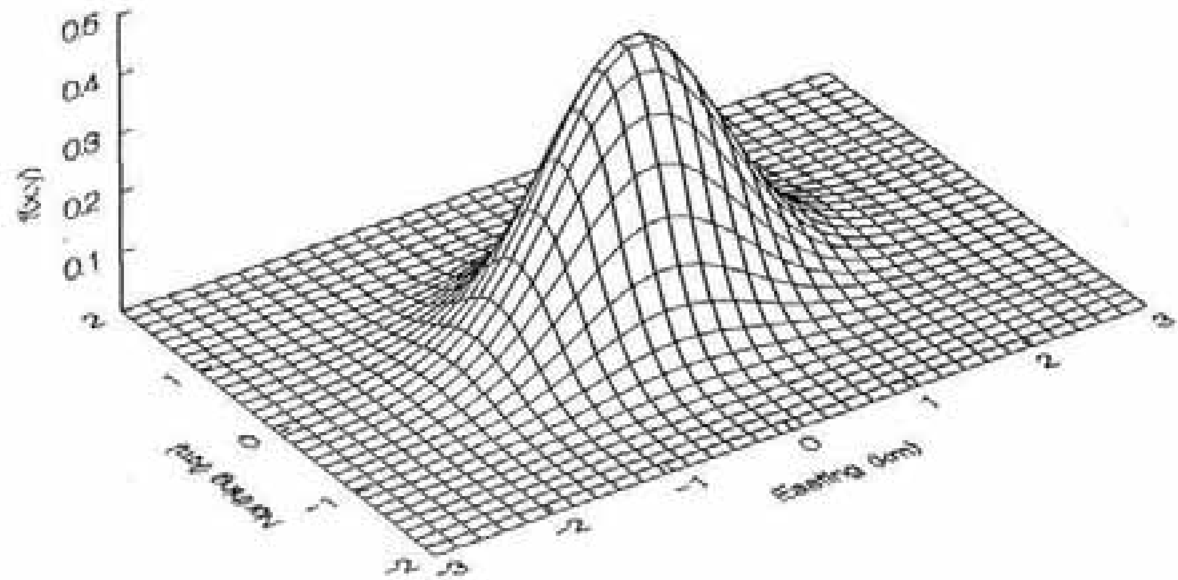
$$f(x, y) = (2\pi\sigma_x\sigma_y)^{-1}[1-(r_{x \cdot y})^2]^{-1/2}\exp[-1/2 g(x,y)] \quad (11)$$

where

$$g(x,y) = \frac{1}{1-(r_{x \cdot y})^2}\left(\frac{(x-\mu_x)^2}{\sigma_x^2} - 2r_{x \cdot y}\frac{(x-\mu_x)(y-\mu_y)}{\sigma_x\sigma_y} + \frac{(y-\mu_y)^2}{\sigma_y^2}\right). \quad (12)$$

Although bias existed following indexing, reasons for the bias were not apparent, nor was it clear that bias was an inherent characteristic of the residual error distribution. Also, the bias was small (147 m). Therefore, we assumed that $(\mu_x, \mu_y) = (0, 0)$ following correction and indexing. Other parameters were estimated as $\sigma_x = 701$ m, $\sigma_y = 457$ m, and $r_{x \cdot y} = 0.076$, where $r_{x \cdot y}$ is the correlation between σ_x and σ_y. The model was compared with the observed distribution of residual errors from the test data (Fig. 8). With data from the bighorn ewe, it was used to construct a WUD.

Animal Tracking.—During Nov. 1986–Dec. 1987, 395 locations were calculated for a PTT-collared ewe. Sampling frequency varied seasonally (Fig. 9), probably due to effects of terrain and loss of battery power over time. About 1 location per day was achieved when tracking began and the ewe occupied a low- to mid-elevation winter range. Sampling frequency



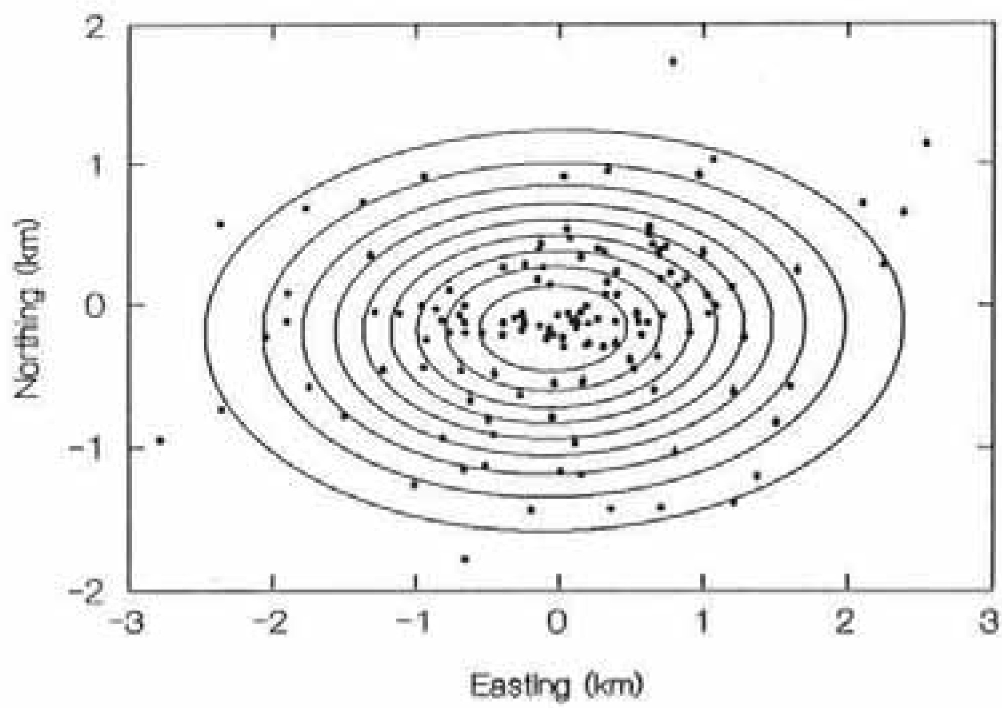


Fig. 8. A bivariate normal model of the distribution of residual error following error correction and rejection of the 25% of locations with the largest error indices (*I*). Both 3-dimensional (top) and 2-dimensional (bottom) views are shown. In the 2-dimensional image, ellipses represent probability isoclines ranging from 0.1 (smallest) to 0.9 (largest) in intervals of 0.1. Observed residual errors (following correction and indexing) from locations of a PTT placed at 23 known sites also are plotted.

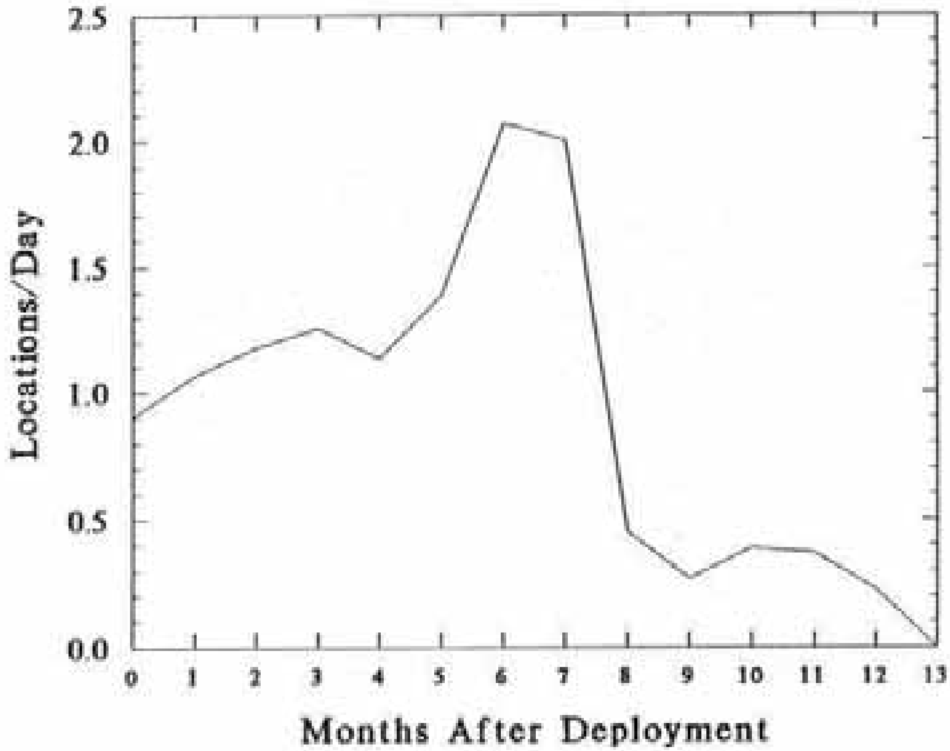


Fig. 9. Variation in sampling frequency as a function of elapsed time since deployment. The PTT was deployed 27 Nov. 1986 and was programmed to transmit 6 hours per day throughout the year.

increased to about 2 locations per day as the ewe moved to lambing and early summer ranges at higher elevations. Although the ewe remained at higher elevations during late summer and early fall, sampling frequency dropped to less than 0.5 locations per day after about 8 months, presumably due to battery failure. Transmissions ended about 13 months after deployment.

Error correction and indexing helped elucidate the ewe's seasonal movements. As expected, uncorrected locations were widely dispersed (Fig. 10A). Elevational error was evident in the clusters of locations east and west of the ewe's winter range, which was centered at UTM coordinates of about 305 km east and 5409 km north (UTM zone 12). After error correction (Fig. 10B), locations were centered approximately around the known winter range on the lower south slopes of Mt. Altyn, and around known spring and summer ranges in the Canyon Creek drainage. Error indexing eliminated a number of apparent outliers (Fig. 10C). It was encouraging that most outliers occurred to the east and west of the major concentrations of locations, as most errors were expected in the longitudinal direction.

The error indexing procedure was modified for analyses of the ewe's movements. As with the test data, a threshold value of *I* was selected so that 25% of the sample was rejected. However, indices were then

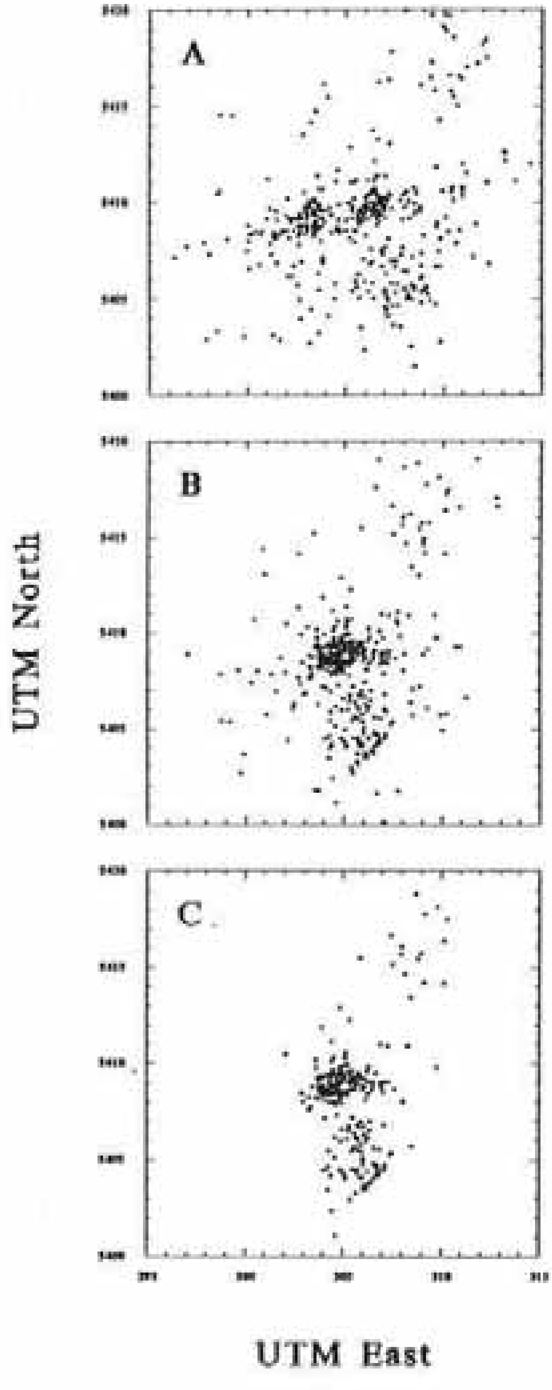


Fig. 10. Distribution of locations for a radio-collared ewe during Nov. 1986–Dec. 1987, showing (A) uncorrected locations, (B) locations corrected for elevational error, and (C) corrected locations with about 38% of the sample rejected based on iterative error indexing (see text).

recalculated for remaining data and additional locations were excluded using the same threshold value of *I*. This was repeated until indices for all locations were less than the threshold value. Three iterations were required and about 38% of the locations were rejected. An iterative approach was used because extreme errors and duplicate locations led to situations not encountered in the test data. Extreme errors (>50 km) occurred when the wrong solution for the location algorithm was selected (each location calculation has 2 possible solutions). Although such errors were correctly identified and excluded as outliers, in several instances smaller outliers (<13 km) occurred immediately before or after an extreme outlier, and in the same direction. The resulting sequence was interpreted by the indexing algorithm as a directed movement where β approached 180°. Consequently, some obvious outliers were not rejected with only 1 iteration. In other instances, 2 locations were calculated from a single satellite pass. The 2 locations were never identical but often were similar, giving the false impression that a second, independent location had been achieved to corroborate the first.

Iterative indexing resolved these problems but altered the assumptions of the procedure. By using 3 iterations we implicitly assumed that >2 locations may be required to corroborate an apparent movement. This change had a substantive effect in only one instance. A movement of about 10 km occurred in late summer after the battery began to fail and sampling frequency was low. Following indexing and rejection of 25% of the sample, the movement was documented by only 2 relatively distant points which were both rejected after subsequent iterations. Evidence of the movement was lost from the final data set. We chose to accept this limitation for the purpose of describing core use areas within the ewe's home range, as rejection of the additional locations did not alter the outcome appreciably. In the future, the problem may be precluded by altering duty cycles to achieve more even sampling throughout the year, thereby reducing the likelihood that significant movements will be documented by only 1 or 2 locations. Alternatively, extreme outliers (>50 km) probably can be identified and rejected prior to indexing, hence only 1 iteration would be needed. Due to changes in the location algorithms in 1987, multiple locations are no longer calculated from a single satellite pass and should not affect error indexing of post-1987 data.

Finally, we calculated a WUD from the 243 locations that remained after iterative indexing. Core use areas occurred on Mt. Altyn, Mt. Allen, and Yellow Mtn. A WUD was then constructed using only those locations within the core areas (Fig. 11). Sequential locations not within a core area were identified as movements. A separate WUD was constructed for each movement and the "ridge line" of the WUD's statistical terrain was digitized to estimate the likely travel corridor. Approximately 4 corridors were identified. A composite of the core areas and travel corridors among areas was constructed (Fig. 12).

The resulting picture of bighorn movement patterns agreed well with visual observations: the ewe occupied the Mt. Altyn range most of the year, lambing took place toward the south end of the Mt. Allen range in the cliffs above Canyon Creek, and some use was observed on Yellow Mtn. in summer. Visual observations indicated greater use near the head of Canyon Creek (Mt. Allen range) than was evident in the WUD (Fig. 12).

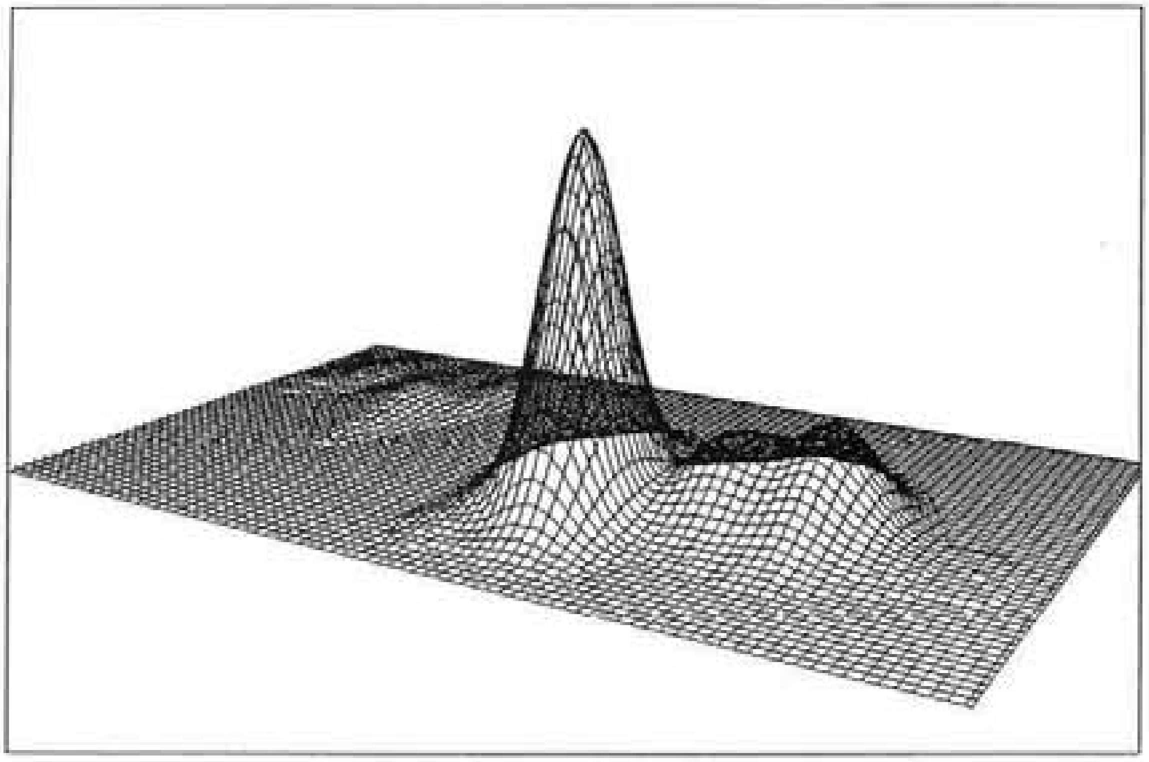


Fig. 11. Weighted utilization distribution (WUD) for core ranges used by a radio-collared ewe during Nov. 1986-Dec. 1987 (250 m UTM grid). The Mt. Altyn winter range is the highest peak, the Mt. Allen lambing and summer ranges are to the right, and summer ranges on Yellow Mtn. are to the left.

However, use of upper Canyon Creek was observed primarily in late summer when sampling frequency was low, presumably due to battery failure. Modification of the PTT's duty cycle to achieve more even sampling throughout the year would likely have resulted in a better picture of late-summer use. Movement corridors between Mt. Allen and Mt. Altyn were confirmed by visual obsetvations and tracks, as was ≈3 km of the corridor leading onto the Yellow Mtn. range. Travel routes identified between Mt. Altyn and Yellow Mtn. were suspected due to the terrain and game trails in those areas, but were not confirmed by sightings. The Windy Creek corridor between Mt. Allen and Yellow Mtn. was unexpected: escape cover is generally poor, the animal had to swim Sherburne Reservoir, and the route is not substantially shorter than alternate routes with good escape cover. Most movements occurred within 1-2 day periods and it is unlikely that travel corridors would have been documented using VHF telemetry.

CONCLUSIONS

Earlier studies (Craighead and Craighead 1987, Fancy et al. 1988) found that satellite telemetry offers important economic and logistic advantages for wildlife research. We concur, particularly if sources of error are recognized and mitigation measures are used. In Montana's East

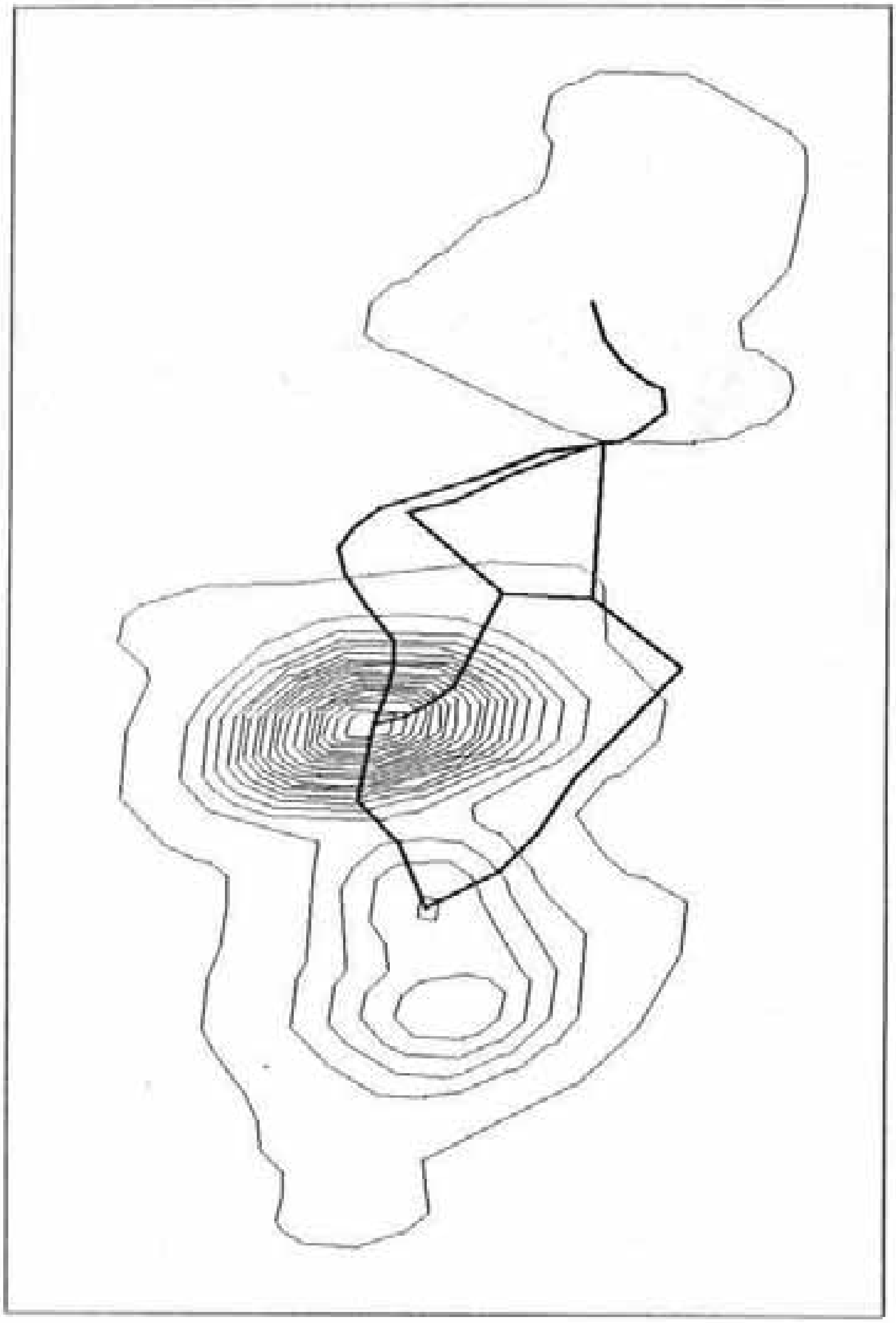


Fig. 12. Core bighorn ranges (thin lines) and their associated travel corridors (dark-lines) in the Many Glacier area, as identified from weighted utilization distributions (WUDs) calculated from 243 locations of a radio-collared ewe (see text). The Mt. Allen range is at the bottom, the Mt. Altyn range is represented by the high concentration in the center, and the Yellow Mtn. range is in the upper right.

Front region, inclement weather and rugged terrain have traditionally confounded telemetry. The 395 locations achieved during a 1-year period for a PTT-collared ewe demonstrated an unprecedented capability to document seasonal movements. Terrain remains a confounding factor, as effects of elevation and topography may greatly impact accuracy and sampling frequency. However, sampling frequency was still >1 location per day and effects on accuracy can be either precluded or mitigated by specifying mean elevation in advance or via corrections. By using WUDs to weight habitat component layers within a GIS environment, we suggest that satellite telemetry data can be used to develop habitat use models and to model the probability of movement among habitat patches and local populations. Coupled with a GIS, such models may be applied over broad landscapes and offer a powerful tool to test and optimize conservation strategies.

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