Fix Success and Accuracy of Global Positioning System Collars in Old-Growth Temperate Coniferous Forests

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ABSTRACT Global Positioning System (GPS) telemetry is used extensively to study animal distribution and resource selection patterns but is susceptible to biases resulting from data omission and spatial inaccuracies. These data errors may cause misinterpretation of wildlife habitat selection or spatial use patterns. We used both stationary test collars and collared free-ranging American black bears (*Ursus americanus*) to quantify systemic data loss and location error of GPS telemetry in mountainous, old-growth temperate forests of Olympic National Park, Washington, USA. We developed predictive models of environmental factors that influence the probability of obtaining GPS locations and evaluated the ability of weighting factors derived from these models to mitigate data omission biases from collared bears. We also examined the effects of microhabitat on collar fix success rate and examined collar accuracy as related to elevation changes between successive fixes. The probability of collars successfully obtaining location fixes was positively associated with elevation and unobstructed satellite view and was negatively affected by the interaction of overstory canopy and satellite view. Test collars were 33% more successful at acquiring fixes than those on bears. Fix success rates of collared bears varied seasonally and diurnally. Application of weighting factors to individual collared bear fixes recouped only 6% of lost data and failed to reduce seasonal or diurnal variation in fix success, suggesting that variables not included in our model contributed to data loss. Test collars placed to mimic bear bedding sites received 16% fewer fixes than randomly placed collars, indicating that microhabitat selection may contribute to data loss for wildlife equipped with GPS collars. Horizontal collar errors of >800 m occurred when elevation changes between successive fixes were >400 m. We conclude that significant limitations remain in accounting for data loss and error inherent in using GPS telemetry in coniferous forest ecosystems and that, at present, resource selection patterns of large mammals derived from GPS telemetry should be interpreted cautiously. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1298–1308; 2007)

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Telemetry using Global Positioning System (GPS) technology has enhanced the ability of researchers to acquire large quantities of animal location data across a wide range of species and environments (e.g., Biggs et al. 2001, Blake et al. 2001, Johnson et al. 2002, Sprague et al. 2004). Data from GPS telemetry studies, however, contains biases and errors associated with data omission and spatial inaccuracy (Moen et al. 1997, D'Eon et al. 2002, Frair et al. 2004). Data losses resulting from obstructed satellite communications are particularly problematic in studies of animal distribution and resource selection because differential rates of data loss among habitats could bias the interpretation of which habitats are most important in fulfilling life-history requirements (D'Eon 2003, Frair et al. 2004).

Data omission occurs when the GPS receiver in a telemetry collar is unable to obtain line-of-sight communication with $\geq$3 satellites to establish the geographic position of the collar through triangulation. A number of factors may hinder communication between the GPS receiver and satellites, but physical characteristics of habitat such as canopy closure and topographic obstruction (Rempel et al. 1995, D'Eon et al. 2002, Frair et al. 2004), animal movement and activity (Bowman et al. 2000, Moen et al. 2001), animal body mass (Graves and Waller 2006), and collar position and orientation (Moen et al. 1996, D'Eon and Delparte 2005) may all reduce the likelihood of a GPS receiver acquiring and storing a location (hereafter a fix). Fine-scale choices in habitat selection may also compound problems with satellite communication. For example, selection of resting sites at the base of large trees would obscure satellite communication to a greater extent than random use of the surrounding habitat, despite the overall habitat characteristics being similar.

Spatial inaccuracy, the discrepancy between the location recorded by the GPS receiver and the true coordinates on the ground, also contributes to GPS telemetry error. Spatial accuracy is a function of satellite configuration (Edenius 1997, D'Eon et al. 2002), satellite availability (2-dimensional [2D] vs. 3-dimensional [3D] locations; Bowman et al. 2000, D'Eon et al. 2002, Di Orio et al. 2003), and habitat attributes (Rempel et al. 1995, D'Eon et al. 2002, Di Orio et al. 2003). Three satellites are used to triangulate a 2D fix while 4 satellites are required for a 3D fix. Two-dimensional fixes are less accurate than 3D fixes because in establishing successive 2D locations the elevation of the most recent 3D fix is used, introducing error in the horizontal position

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estimate (Rempel et al. 1995, Moen et al. 1997, Di Orio et al. 2003).

Previous researchers determined fix success rates and spatial accuracy of GPS collars in a variety of coniferous forests in the northern United States and Canada (Rempel et al. 1995, Moen et al. 1997, D'Eon et al. 2002). More recently, researchers have focused attention on reducing data omission biases by adjusting for data losses using predictive models of fix success rates developed from stationary test collars placed in a variety of environments (D'Eon et al. 2002, D'Eon 2003, Frair et al. 2004). We know of only one published study, however, that determined what proportion of lost data opportunity from GPS collars on free-ranging animals is restored using fix success models to weight raw telemetry data, and what proportion of data loss remains unaccountable due to unmeasured attributes of animals, habitats, or satellite configuration (D'Eon 2003). Additional studies are needed to determine the potential magnitude of bias in GPS telemetry studies and to develop methods to mitigate biases resulting from data omission (D'Eon 2003).

Our primary objectives were to determine fix success rates and spatial accuracy of GPS locations derived from stationary collars and to evaluate the efficacy of models developed to mitigate data omission biases in GPS telemetry studies of black bears in Olympic National Park, Washington, USA. Mountainous forest ecosystems in the coastal Pacific northwestern United States comprise some of the most challenging environments for using GPS telemetry and provide useful benchmarks for comparison to other environments. Specifically, we modeled the effects of physical habitat variables on fix success rates of stationary GPS collars and developed weighting factors that we applied to individual GPS locations obtained from collars on free-ranging bears. We compared telemetry fix rates from stationary GPS collars to those from free-ranging bears and hypothesized that weighting factors derived from models of fix success rate would reduce annual and daily patterns in data losses on free-ranging bears by accounting for habitat-based differences in data omission. Other objectives were to determine the influence of microsite placement of collars on fix success rates, determine location error and bias of 2D and 3D GPS coordinates in old-growth coniferous forests, and determine the influence of elevation change on accuracy of 2D fixes.

STUDY AREA

We investigated performance of GPS collars on black bears and examined biases and errors of GPS telemetry in the Elwha River watershed in Olympic National Park in northwestern Washington. Olympic National Park preserves the largest contiguous block of pristine old-growth coniferous forests remaining in the Pacific northwestern United States and represents one of the most challenging environments anywhere for using GPS receivers. The Elwha Valley encompassed approximately 832 km^2 in north-central Olympic National Park. Elevations ranged from approximately 150 m in the riverine lowlands to >2,000 m on adjacent subalpine peaks and ridges. Precipitation ranged from approximately 152 cm in the riverine lowlands, where it fell primarily as rain, to >300 cm in the high elevations, where much of it fell as snow.

Vegetation in the Elwha Valley formed a gradient ranging from forests of the western hemlock (*Tsuga heterophylla*) zone at low elevations (<800 m), the Pacific silver fir (*Abies amabilis*) zone at mid elevations (800–1,200 m), to the subalpine fir zone (*A. lasiocarpa*) at high elevations (Henderson et al. 1989). Many western hemlock stands within the study area were initiated with stand-replacing wildfire in 1701 (i.e., >300 yr old) and were characterized both by the occasional massive Douglas fir (*Pseudotsuga menziesii*; >205 cm dbh), and multilayered canopies of mature Douglas fir and western hemlock that often reached 60 m in height. Low elevation forests along the river floodplain contained old-growth forest stands of Douglas fir, grand fir (*Abies grandis*), and a mosaic of red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). Pacific silver fir forests at mid elevations were dominated by western hemlock, Douglas fir, and Pacific silver fir. Subalpine fir forests, found mainly on cool dry sites on shallow soils above 1,200 m, were characterized by mixed parkland of subalpine meadows and stands of subalpine fir (Henderson et al. 1989). In general, stature, canopy cover, and productivity of forests decreased with increasing elevation from the western hemlock zone to the subalpine fir zone (Henderson et al. 1989).

METHODS

Field Methods

Fix success rates of GPS collars.—We defined fix success rate as the proportion of scheduled telemetry fix attempts that resulted in successful acquisition of a 2D or 3D fix. We examined fix success rates of 12-channel GPS Simplex™ (Televilt TVP Positioning AB, Lindesberg, Sweden) collars by placing collars at randomly chosen locations within approximately 1 km of trail systems in the Elwha Valley during summers 2002–2003. Using the Geographic Information System (GIS) at Olympic National Park, we identified and developed 2 categorical variables to stratify sampling locations across a wide range of habitat conditions: canopy cover and satellite view. Canopy cover classes associated with each 25 × 25-m pixel included 0–10%, 11–40%, 41–70%, and 71–100%. We defined satellite view associated with each pixel as the proportion of sky that is traversed by GPS satellites and also unobstructed by topography. To determine satellite view from the center point of each pixel, we used Quick Plan software (GPS Pathfinder Office) to create 1 to 5 points in each cardinal and semi-cardinal direction (i.e. southeast aspect at 15°, 30°, 45°, 60°, and 75° above the horizon, etc.), for a total of 48 points in the sky (Fig. 1). Because few GPS satellites were present in the northern sky of the Pacific Northwest (from approx. 315° [northwest] to 45° [northeast]), fewer sample points were distributed in that part of the sky (Fig. 1). We classified satellite view of each pixel into 1 of 4 categories

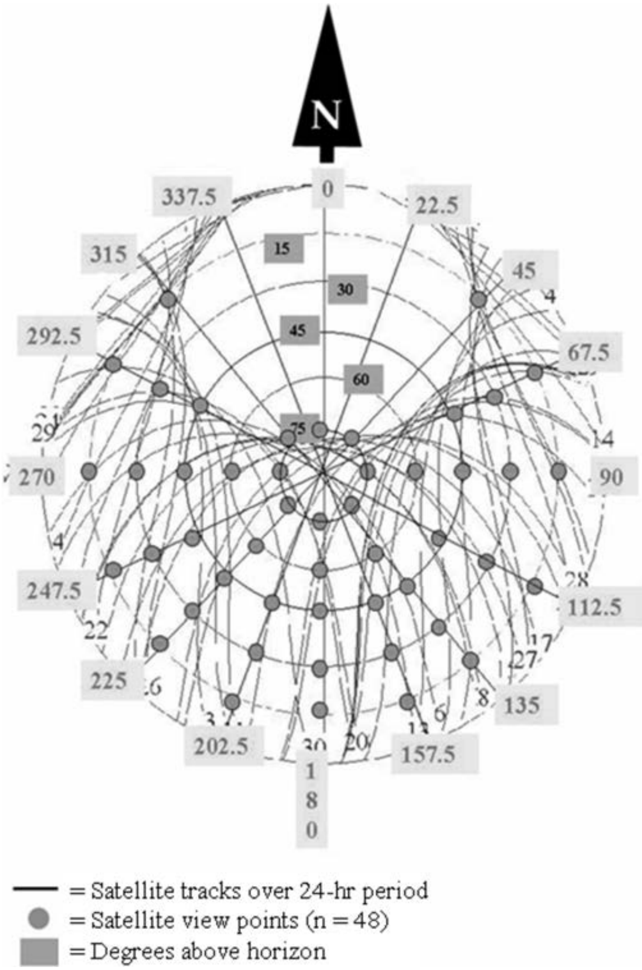

Figure 1. Typical daily satellite availability in the Elwha River watershed, Olympic National Park, Washington, USA, 2002–2003. The variable "satellite view" represents the proportion of 48 potential satellite views that are unobstructed by terrain from any point within the watershed.

based on the percentage of sky (as represented by the 48 points described above) obscured by topographic relief: lowest satellite view (40–100% of the 48 points obstructed by topography), moderate-low satellite view (25–40% obstructed), moderate-high (10–25% obstructed), and highest (0–10% obstructed).

We randomly sampled 3 to 4 locations from the 4 satellite view and 4 canopy cover categories (i.e., 16 categories in the matrix) from trail accessible areas of the watershed resulting in a total of 63 sampling locations. We distributed sampling effort approximately equally between low ($<$1,000 m) and high ($>$1,000 m) elevations in the Elwha River watershed. At each sampling location, we positioned a test collar 0.5–1 m above the ground with the GPS antenna pointed towards the sky. We programmed each test collar to attempt a GPS fix once each hour and left each collar in place for $\geq$24 hours.

For each sampled pixel, we recorded canopy cover class, tree size class (dbh in cm), satellite view, and elevation based on remotely sensed GIS data (Pacific Meridian Resources Vegetation and Landform Database Development, 30 Sep 1996, unpublished data). We also measured and recorded the following vegetation and physical variables within a 30-m radius plot centered on the test collar: percentage of overhead cover contributed by deciduous trees, slope, basal area, height of modal trees, and tree density. We measured slope, basal area, and tree height from the center of each plot. We determined slope with a Silva Ranger® (Silva Sweden AB, Sollentuna, Sweden) compass and basal area with a 5- to 20-factor Cruz-All® (JIM-GEM Forestry Suppliers, Jackson, MS). We measured heights of 4 trees that best represented modal trees in the overstory using a laser range finder from plot center. We calculated tree density using the point–center–quarter method from plot center and from 8 points 30 m from the plot center in each of the cardinal and subcardinal directions (Mueller-Dumbois and Ellenberg 1974). We defined a tree as any live tree greater than 10-cm diameter at breast height. We took all measurements in the summer during the leaf-on season to avoid problems associated with variable deciduous cover and to represent the primary season that bears are active.

Location error and bias of GPS collars.—We measured location error and bias of GPS collars during summer 2004 at 16 sampling sites representing the range of habitat conditions and fix success rates in the Elwha River watershed. Of the 63 sampling sites selected for studies of fix success rates, we measured location accuracy at 4 sites with the lowest fix success rates (0.18 to 0.42), 4 sites with the highest fix success rates (1.00), and 8 intermediate sites that we selected systematically according to increasing fix success rate (0.48–0.94). At each sampling site, we placed a GPS collar programmed to attempt fixes at 30-minute intervals at the same location and orientation as during the previous testing of fix success and left it to collect location data for $\geq$48 hours. We obtained reference coordinates at each sampling site for determining location errors using a Trimble GPS Pathfinder® Pro XR set to average 200–3,289 real-time differentially processed points and record a differentially corrected Universal Transverse Mercator coordinate at the center of each site. At all sites, the 95% confidence limit on the mean reference coordinate was $<$0.85 m, indicating submeter accuracy of the reference coordinates.

Effects of microhabitat selection on fix success rate.—At 8 of the sampling sites used to measure location errors, we examined potential effects of microhabitat selection by positioning a second collar vertically on the ground at the base of a tree (dbh $>$50 cm) within the 30-m plot used to define habitat variables. We paired collars at the center of accuracy testing sites with collars placed at the bases of trees to simulate fine-grained habitat selection such as might occur if black bears selected day beds at the bases of trees.

Fix success rates of GPS collars on free-ranging bears.—For comparison with stationary test collars, we determined fix success rates of Televilt Simplex™ GPS collars placed on 5 male and 2 female bears for $\geq$8 weeks during 2002 to 2004 (Sager 2005; Oregon State University Animal Care and Use Permit no. 3167). We programmed each collar placed on a bear to attempt a fix 4 times daily from 1 April to 31

October. Each collar was equipped with a drop-off mechanism that allowed us to retrieve the collar and download data for each successful fix including: date, time, latitude, longitude, dilution of position, and whether the fix was 2D or 3D.

Statistical Methods

Modeling fix success of GPS collars.—We used logistic regression to model fix success as

$$P_{\text{success}} = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i) \div [1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i)]$$

where P_{success} is the probability of successfully acquiring a GPS fix, β_0 is the regression constant, and β_1 through β_i are coefficients estimated for 1 to i independent variables x_1 to x_i (Hosmer and Lemeshow 2000). Fix success was a binary variable recorded as successful or unsuccessful each time a GPS test collar attempted to acquire a fix. Habitat attributes measured at the site or obtained from remotely sensed data formed the pool of predictor variables in the model. We performed statistical analyses using SAS 8.0 software (SAS Institute, Cary, NC). We treated individual fixes as independent sample units in the analysis. We acknowledge that fixed terrain and vegetation attributes within each sampling site reduced independence of observations obtained within sites; however, the range of satellite availability changed throughout each day and produced highly variable location success among hours within sites. Additionally, logistic regression model parameters are robust generally to violations of the independence assumption despite overestimated precision (Burnham and Anderson 2002). We calculated the variance inflation factor, $\hat{c}$ (Pearson's χ^2/df) to evaluate model fit and determine whether to apply a quasi-likelihood variance expansion term for overdispersed data (if $\hat{c}$ was substantially >1; Burnham and Anderson 2002). Once we had established model adequacy, we used Akaike's Information Criterion adjusted for small sample size (AIC_c), Akaike differences (Δ_i), and Akaike weights (w_i) to identify the most parsimonious model.

We developed an a priori set of candidate models for estimating probability of fix success (P_{success}), which consisted of a global model and its reduced forms. We chose the parameters contained in the global model based on landscape variables known from previous studies to affect GPS fix success (Moen et al. 1996, D'Eon et al. 2002, Di Orio et al. 2003, Frair et al. 2004). We excluded variables that were not significant in univariate tests ($P > 0.10$) and eliminated one variable from each pair of correlated variables (Pearson $r > 0.5$), giving preference to remotely sensed variables. We favored remotely sensed variables because they could also be applied to locations acquired from collared bears. Potential covariates for the logistic regression model were canopy cover class (0–40%, 41–70%, >70%), tree size class (dbh: 0–22.6 cm, 22.7–53.1 cm, 53.2–81.1 cm, 81.2–121.7 cm), satellite view, elevation, percent deciduous cover, slope, basal area, tree height, tree density, and the interaction between canopy cover class and satellite view. Although we used 4 classes of overstory canopy cover to select collar testing sites, we pooled the 0–10% and 11–40% canopy cover classes for the analysis. We treated satellite view as a continuous variable ranging from 0 to 48. For the 2 categorical variables (canopy cover class and tree size class), we coded the most open classes as the reference category.

We used ArcView 3.3 GIS to develop a data layer containing the estimated P_{success} for each pixel in the Elwha Valley. We computed P_{success} from the most parsimonious model based on terrain and forest attributes of each pixel as determined from Olympic National Park's GIS.

Location error and bias of GPS collars.—We calculated location error as the Euclidean distance (m) between the GPS Pathfinder Pro XR reference coordinate at each site and the coordinates obtained by the GPS collar at the same site. We examined location error separately for 2D and 3D fixes and computed 50% and 95% circular error probables (CEP) for each type of fix. The CEP for each distribution is the radius around the presumed true location that encompasses 50% and 95% of all individual location fixes recorded by the stationary test collars. At times, we moved collars over a wide elevational gradient in a short period between successive collar tests, and because 2D locations used the elevation of the most recent 3D fix, we further divided 2D fixes into 2 classes: 1) 2D-quality2 referred to 2D fixes acquired at a new site before a new 3D fix was obtained and 2) 2D-quality1 were 2D fixes obtained at a new site after attaining a 3D fix at that same site.

Fix success rates of GPS collars on free-ranging bears.—We computed hourly and monthly fix success rates of GPS collars on free-ranging bears during the nondenning months as the percentage of fix attempts that resulted in a 2D or 3D location. To mitigate lost fixes, we adjusted these raw location data by weighting each fix by the inverse of its detection probability (i.e., $\text{wt} = 1/P_{\text{success}}$). For example, a fix acquired from a collared bear in a location determined from the model to have $P_{\text{success}} = 0.5$ would be weighted by a factor of 2. Weighting factors accounted for fixes that were missed at different times but under similar environmental conditions and may be used to reduce biases in the data prior to analysis of resource selection (Frair et al. 2004) or home range (Horne et al. 2007). This type of weighting to account for missing data has been applied widely to account for missed observations of large mammals in aerial surveys (Samuel et al. 1987, Bodie et al. 1995, Anderson et al. 1998). We also quantified the percentages of missed data that were accounted for through application of these weights by comparing the average fix success rates of unadjusted and adjusted bear location data. We adjusted bear location data by summing all weighted data points for each bear (i.e., 2 fixes each weighted by a factor of 2 summed to 4 fixes). We graphically examined seasonal and diurnal patterns in data omission biases of collars on black bears and the relative proportion of data loss that was recouped through the weighting process.

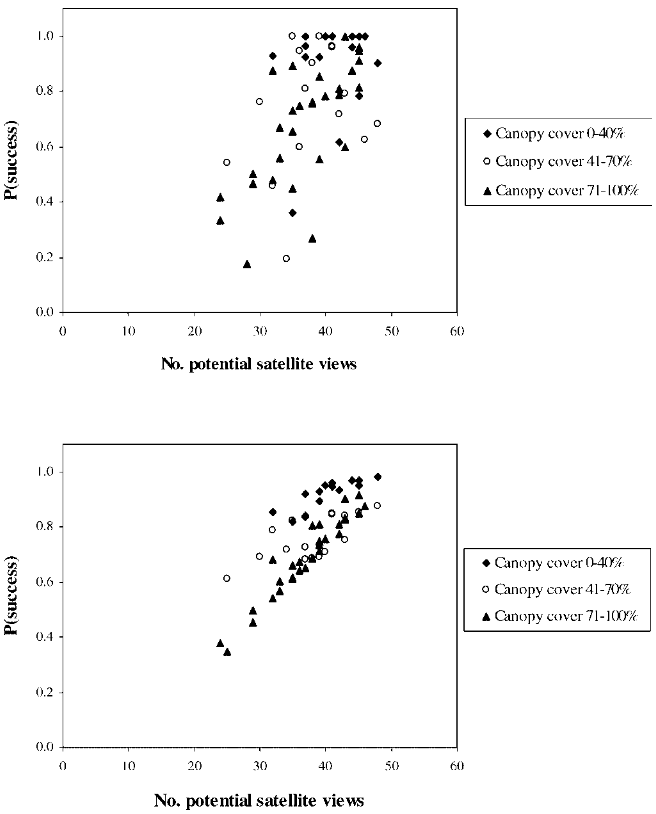

Figure 2. Probability of successfully obtaining a Global Positioning System fix ($P_{success}$) in relation to number of potential satellite views and 3 levels of canopy cover in Olympic National Park, Washington, USA, 2002–2003. We present $P_{success}$ as (top) actual measurements from stationary test collars at 63 sites in the Elwha Valley and (bottom) success rate predicted from the highest ranked logistic regression model.

RESULTS

Fix Success Rates of GPS Test Collars

Stationary test collars successfully acquired locations at each of 63 testing sites (Fig. 2). Fix success rate of test collars averaged 0.76 (SE = 0.03) across all test sites, ranging from 0.18 to 1.0 at individual sites (Fig. 2). Fix success rates of test collars averaged 0.9 (SE = 0.04), 0.75 (SE = 0.06) and 0.68 (SE = 0.04) in forests with ≤40%, 41–70%, and >70% forest overstory cover, respectively. Of 1,727 total fixes acquired at 63 test sites, 21.7% were 3D and 78.3% were 2D. Collars took an average of 64.30 (SE = 1.33) seconds and 45.22 (SE = 1.79) seconds to acquire 2D and 3D locations, respectively.

Fix Success Models

Preliminary univariate logistic regression models indicated that satellite view, canopy cover class, elevation, tree size class, percent cover of deciduous trees, basal area, and tree height all influenced the probability of a GPS collar successfully acquiring locations (Table 1). $P_{success}$ estimated from univariate models ranged from 0.39 to 0.92 across the range of available satellite views and 0.72 to 0.93 across the gradient of canopy cover classes (Table 1). Although percent cover of deciduous trees, basal area, and tree height influenced probability of success, we did not consider them for inclusion in multivariate models because they were correlated (Pearson $r > 0.5$) with other preferred variables or because they were not remotely sensed and could not be applied to free-ranging bears.

We examined the global multivariate model, including the variables canopy cover class, tree size class, satellite view, elevation, and the interaction between canopy cover and satellite view, to evaluate overall model fit and to test for overdispersion in the data. The global model explained significant variation in success rate (Wald $\chi^2 = 196.63$, df = 9, $P < 0.001$), demonstrating overall model suitability. Further, the variance inflation factor was near 1 ($\hat{c} = 1.044$), indicating acceptable model structure and a lack of overdispersion (Burnham and Anderson 2002). Hence, we opted not to apply an overdispersion adjustment to improve model fit (Burnham and Anderson 2002).

The most parsimonious multivariate model for predicting fix success rates of GPS test collars included the covariates canopy cover, satellite view, elevation, and the interaction term canopy cover × satellite view (Wald $\chi^2 = 194.52$, df = 6, $P < 0.001$; Table 2). Model predictions for $P_{success}$ averaged 0.77 (SE = 0.02) and ranged from 0.35 to 0.98 (Fig. 2). $P_{success}$ increased with elevation and increasing satellite views (Table 3). Significant interactions between the effects of satellite view and canopy cover confounded the interpretation of canopy cover independently, but $P_{success}$ was greatest in open canopied forests with the greatest satellite views and was least in dense forests with low satellite views (Fig. 2). Patterns of variation in $P_{success}$ from modeled predictions were consistent with patterns in raw

Table 1. Univariate logistic regression models to predict Global Positioning System collar fix success ($P_{success}$) based on collar tests at 63 test sites in Olympic National Park, Washington, USA, 2002–2003.

Variable	Variable range	Range in predicted $P_{success}$	Wald χ^2	df	P
Satellite view[a]	24–48	0.39–0.92	143.40	1	<0.001
Canopy cover class[b]	1–3	0.72–0.93	79.04	2	<0.001
Elevation (m)	79–1,749	0.65–0.91	92.59	1	<0.001
Tree size class[c]	1–4	0.55–0.93	81.53	3	<0.001
Deciduous cover (%)	0–95	0.63–0.81	23.85	1	<0.001
Basal area (m^2/ha)	0–76	0.72–0.82	8.65	1	0.003
Tree ht (m)	7–66	0.61–0.86	52.94	1	<0.001

[a] Satellite view (continuous variable from 1 to 48, depending upon no. of discrete views obtainable from sample site).
[b] Canopy cover classes (0–40%, 41–70%, 71–100%).
[c] Tree size class (dbh: 0–22.6 cm, 22.7–53.1 cm, 53.2–81.1 cm, 81.2–121.7 cm).

Table 2. Ranks of logistic regression models used to predict Global Positioning System collar fix success based on collar tests at 63 sites, Olympic National Park, Washington, USA, 2002–2003.[a]

Rank	Parameters included in the model	K	-2 LL	AIC$_c$	Δ_i	w_i
1	Canopy cover,[b] satellite view,[c] elevation, canopy × satellite[d]	7	2,037.855	2,053.891	0.000	0.939
2	Canopy cover, satellite view, elevation	5	2,049.689	2,060.742	6.850	0.031
3	Canopy cover, satellite view, size class,[e] elevation, canopy × satellite	10	2,036.557	2,060.788	6.896	0.030
4	Canopy cover, satellite view, size class, elevation	8	2,048.933	2,067.600	13.708	0.001
5	Canopy cover, satellite view, canopy × satellite	6	2,062.643	2,076.143	22.252	0.000
6	Canopy cover, satellite view, size class, canopy × satellite	9	2,059.325	2,080.721	26.830	0.000
7	Canopy cover, satellite view	4	2,072.094	2,080.784	26.892	0.000
8	Canopy cover, satellite view, size class	7	2,070.619	2,086.655	32.764	0.000
9	Satellite view, elevation	3	2,094.945	2,101.352	47.460	0.000
10	Canopy cover, elevation	4	2,113.393	2,122.083	68.191	0.000

[a] K = no. of parameters in model, including intercept; -2 LL = -2 log likelihood; AIC$_c$ = Akaike's Information Criterion adjusted for small sample size; Δ_i = AIC$_c$ difference; w_i = AIC$_c$ wt.
[b] Canopy cover classes (0–40%, 41–70%, 71–100%).
[c] Satellite view (continuous variable from 1 to 48, depending upon no. of discrete views obtainable from sample site).
[d] Canopy cover × satellite view interaction term.
[e] Tree size class (dbh: 0–22.6 cm, 22.7–53.1 cm, 53.2–81.1 cm, 81.2–121.7 cm).

data from the test collars (Fig. 2); $P_{success}$ increased linearly with increasing numbers of satellite views, and was greatest for open forest vegetation.

$P_{success}$ of individual pixels throughout the Elwha Valley, predicted from the best model, ranged from approximately 0.15 to 1.0 (Fig. 3). Areas of low $P_{success}$ (<0.60), characterized by narrow, low-elevation, densely timbered ravines and canyons, were scarce relative to areas of moderate and higher $P_{success}$ (>0.60) in more open terrain and forests (Fig. 3).

Location Error and Bias of GPS Collars

Both GPS collars and the Pathfinder Pro XR successfully acquired locations at 15 of 16 accuracy testing sites. Of 1,705 GPS locations acquired, 32.9% were 3D and 67.1% were 2D. Ninety-five percent of 3D fixes were within 17.7 m of the reference coordinates whereas 95% of 2D fixes were within 264.6 m (Fig. 4). The maximum 3D and 2D errors were 73 m and 2,230 m, respectively. Of 1,144 2D fixes, 86% were preceded by a 3D location at the same site (2D-quality1 fixes) and 14% were computed based on the last 3D location from another site (2D-quality2). When we moved collars from one location to another with an accompanying large change in elevation, 2D fixes had greater location errors than when the collars remained at a relatively constant elevation (Fig. 5). Two-dimensional locations had an average location error of 62.6 m (SE = 7.3) when elevation changes were ≤306 m, whereas accuracy of 2D-quality2 locations averaged 376 m (SE = 60.1) when elevation changes were >400 m (Satterwaite's t test with unequal variances; $t = -5.19$, df = 9.27, $P < 0.01$).

Location errors of GPS fixes were minimally biased (Fig. 4). The mean of 3D locations from test collars was 6.3 m to the southwest of the reference coordinates, whereas 2D locations from test collars were displaced an average 11.1 m to the northwest (Fig. 4).

Effects of Microhabitat Selection on Fix Success Rates

Collars placed at the bases of trees in conditions simulating bear bed sites had lower fix success rates ($\bar{x} = 0.60$, SE = 0.12, $n = 8$; range: 0.05–0.89) than collars placed at site

Table 3. Variables included in the highest-ranked logistic regression model for predicting the probability of a Global Positioning System collar acquiring a fix as a function of environmental characteristics in Olympic National Park, Washington, USA, 2002–2003.

Variable	β	SE	P
Intercept	−3.497	1.614	0.030
Canopy cover 41–70%[a]	3.013	1.785	0.091
Canopy cover 71–100%	0.029	1.694	0.986
Satellite view	0.137	0.041	0.001
Elevation (m)	0.001	≤0.001	≤0.001
Satellite view × canopy cover 41–70%	−0.105	0.046	0.022
Satellite view × canopy cover 71–100%	−0.028	0.043	0.518

[a] Canopy cover 0–40% = reference.

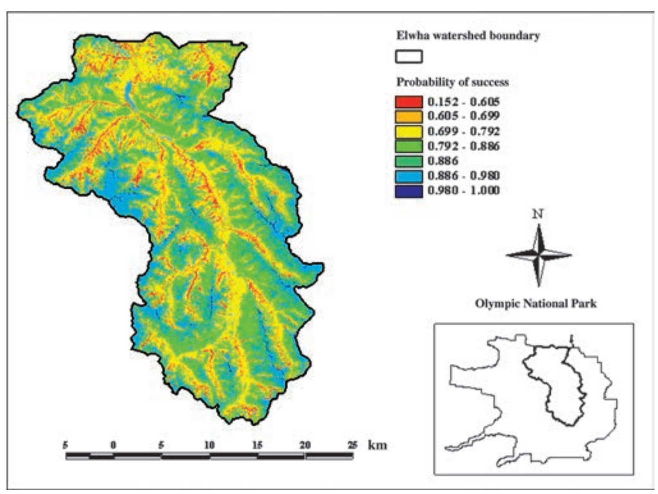

Figure 3. Probability of successfully obtaining a Global Positioning System (GPS) fix ($P_{success}$) for each 25 × 25-m pixel in the Elwha River watershed, Olympic National Park, Washington, USA. We calculated $P_{success}$ based on GPS collar testing at 63 sites in the Elwha River watershed and at Hurricane Ridge, 2002–2003. Predominately blue regions on the periphery of the watershed depict the rim of subalpine peaks, whereas predominately red-orange regions represent river drainages.

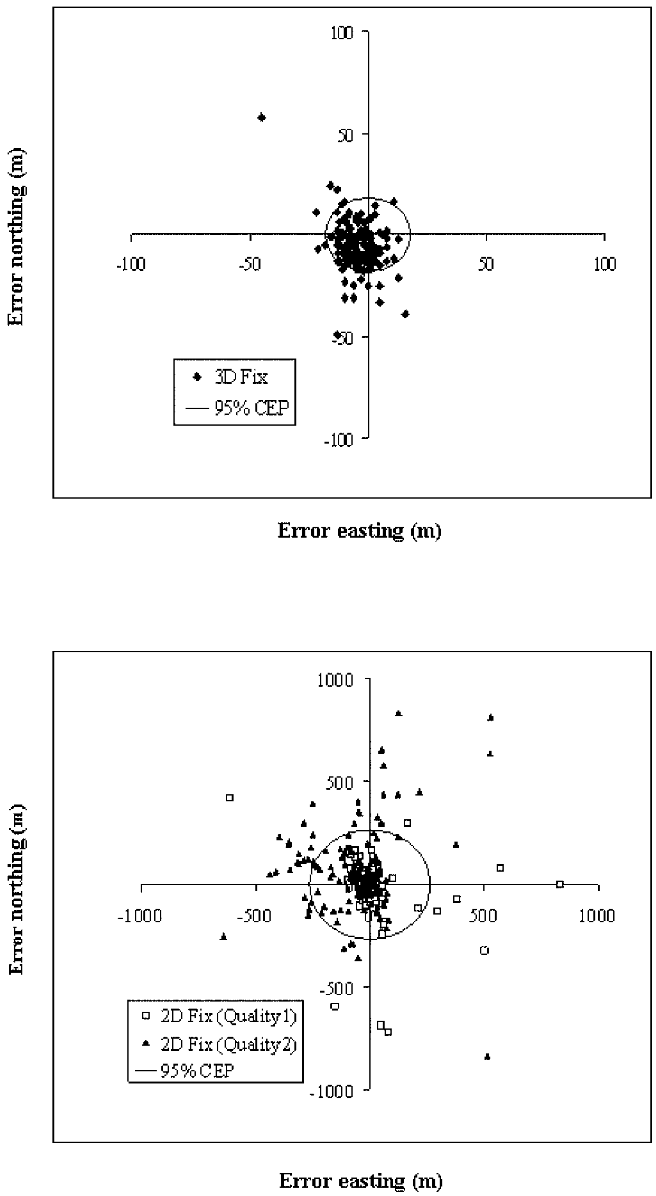

Figure 4. Error (m) of (top) individual 3-dimensional (3D) and (bottom) 2-dimensional (2D) locations from stationary Global Positioning System (GPS) collars compared to differentially corrected GPS reference locations (<1-m accuracy). We tested GPS collars for accuracy in Olympic National Park, Washington, USA, during 2004. The circular error probable (CEP) for each distribution is the radius around the presumed true location that encompasses 95% of all individual location fixes recorded by the stationary test collars. For scaling purposes, 5 2D fixes having errors 1,097–2,230 m are not shown in bottom panel.

centers ($\bar{x}$ = 0.76, SE = 0.10, n = 8; range: 0.17–1.00), equating to a difference in fix success of 0.16 (SE = 0.05; t_7 = 2.97, P = 0.01).

Fix Success Rates of GPS Collars on Free-Ranging Bears

Seven GPS collars retrieved from free-ranging black bears attempted 4,678 fixes; 2,038 fixes were successful, resulting in an average fix success rate of 0.43 (SE = 0.03; Table 4), 0.33 less than the average fix success rate of stationary test collars. Three-dimensional fixes were acquired on 513 occasions, for a mean 3D fix success rate of 0.25 (SE =

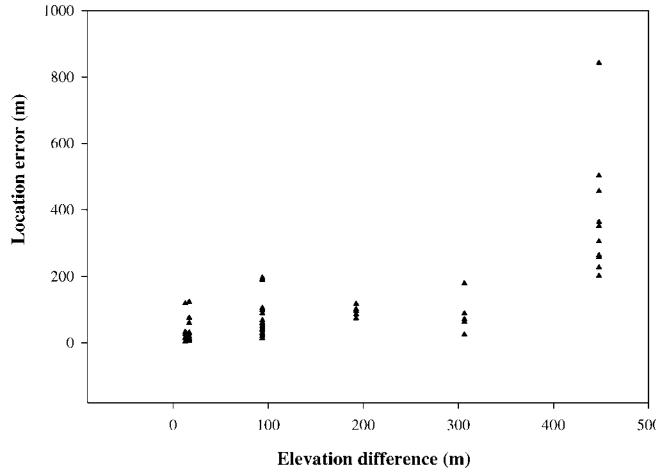

Figure 5. Elevation differences between consecutive test sites (n = 6) and associated location errors of the first 2-dimensional (2D) fixes at a new site. The 2D fixes shown here represent fixes obtained prior to obtaining a 3-dimensional fix during accuracy testing of Global Positioning System collars in Olympic National Park, Washington, USA, 2004.

0.04). Mean fix success rates were lowest during early spring, highest during summer and intermediate during fall (Fig. 6A). Weighting each raw location stored on the GPS collars by the inverse of P_{success} resulted in an adjusted total of 2,336 estimated fixes and an estimated adjusted fix success rate of 0.50 (SE = 0.03; Table 4). This is a total adjustment of 0.06 (SE = 0.004; Table 4). Weighting factors had a greater relative affect on fix success rates during spring than they did during late summer and early fall (Fig. 6B). Adjustments to the raw data based on weighting factors, however, had minimal effect on the observed seasonal patterns of data omission (Fig. 6A).

Mean fix success rates of GPS collars on black bears also varied diurnally, with particularly low fix success observed between 0000 hours and 0300 hours and relatively high fix success at 0600 hours and 1800 hours (Fig. 7). As in the seasonal analysis, weighting successful fixes by the inverse of P_{success} helped to recoup a small measure of lost data but it had negligible effect on diurnal variation in fix success. Diurnal variation in fix success rates of collars on black bears was not positively correlated with success rates of stationary test collars (n = 8, r = −0.69, P = 0.06), indicating that diurnal variation in fix success was not related to temporal variation in satellite availability (Fig. 7).

DISCUSSION

Mountainous, temperate forest ecosystems of Olympic National Park provided a challenging environment for GPS telemetry. Such challenges were manifested in highly variable and occasionally very low rates of fix success of stationary GPS test collars (range = 0.18–1.00), low prevalence of 3D fixes (21.7%), and variable location error rates of 2D locations (1–2,230 m). We speculate that fix success rates and proportion of 3D fixes were lower and location errors of 2D fixes were higher in Olympic National Park than in many other similar studies (i.e., Rempel et al. 1995, Edenius 1997, Moen et al. 1997, D'Eon 2002) due to

Table 4. Fix success rates for unadjusted and adjusted bear data downloaded directly from Global Positioning System collars of 7 black bears in Olympic National Park, Washington, USA, 2002–2004.

Bear no.	No. fix attempts[a]	No. fixes	Fix success rate	Adjusted no. fixes[b]	Adjusted fix success rate	Increase in success rates with adjustment
2002-03	240	79	0.33	99	0.41	0.083
2002-05	831	399	0.48	451	0.54	0.063
2002-06	1,216	507	0.42	592	0.49	0.070
2002-08	795	323	0.41	375	0.47	0.065
2002-10	754	304	0.40	344	0.46	0.054
2003-02	390	161	0.41	183	0.47	0.056
2003-03	452	265	0.59	292	0.65	0.060

[a] Excludes fixes attempted while bears in winter dens.
[b] Sum of successful fixes each weighted by inverse of $P_{success}$.

the steep terrain and dense, tall forest overstories found in old-growth coniferous forests of the Pacific Northwest. We demonstrated a pronounced interaction in the effects of topographic and vegetative obstruction on fix success rates, which we believe also contributed to low success of GPS collars in acquiring fixes and obtaining accurate 3D locations. D'Eon et al. (2002) reported similar interactions between topography and canopy cover and expressed concerns that fix success was particularly affected in topographically obstructed and forested terrain.

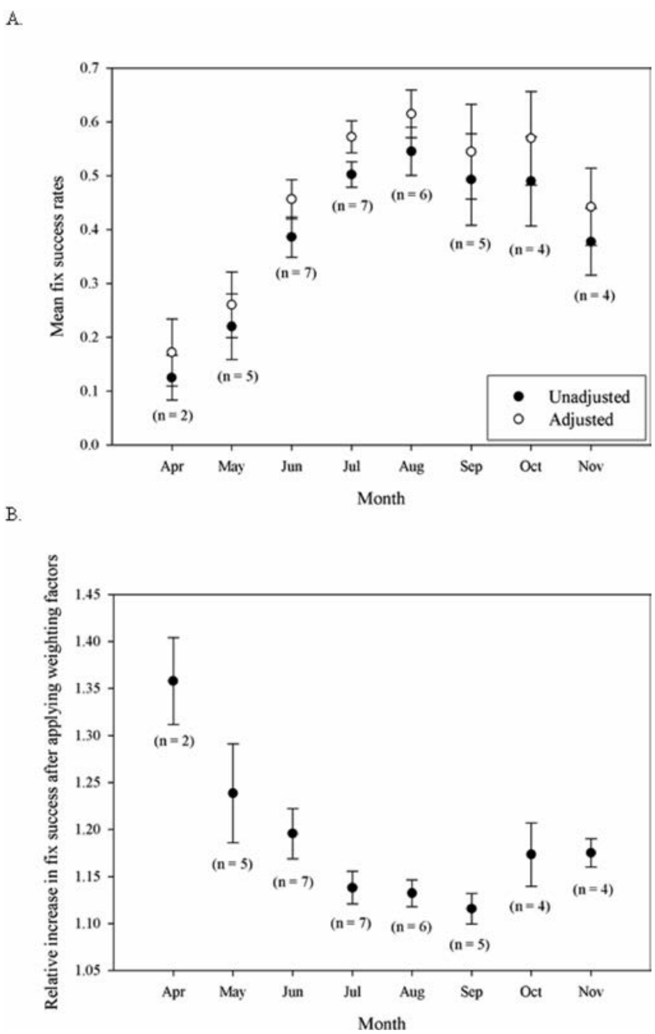

Figure 6. (A) Monthly mean adjusted and unadjusted fix success rates ($\pm$SE) of Global Positioning System collars on free-ranging black bears in Olympic National Park, Washington, USA, 2002–2004, and (B) mean relative increase in monthly fix success after adjustments. We report sample sizes (no. bears) in parentheses.

Inaccurate elevation estimation caused by moving GPS receivers between fixes clearly influenced location error of 2D fixes, with greater elevation shifts resulting in greater errors. Although the effects of elevation errors have been recognized in the literature (Rempel et al. 1995, Di Orio et al. 2003), few studies have examined the magnitude of location errors related to errors in elevation estimation (Moen et al. 1997). Evaluating 2D fix accuracy based upon test collars placed at relatively uniform elevations may underestimate true location error of GPS telemetry on free-ranging animals, particularly in studies of wide-ranging species that are capable of substantial elevational movements between scheduled fixes. Black bears in Olympic National Park frequently moved over wide elevational gradients between successive fixes, with 18% of 2D locations from radio-instrumented bears recorded after bears had moved >400 m from the previous 3D fix location (K. Sager-Fradkin, United States Geological Survey, unpublished data).

Our models of fix success rates indicated that canopy cover, satellite view, and elevation adequately described variations in fix success rates of stationary test collars. Modeled fix rates closely approximated actual fix success rates of test collars; however model fit was poorest under conditions of low fix success rates, similar to results reported by Frair et al. (2004). For example, GPS collars at 4 of 63 test sites had actual success rates (0.18–0.33) that were less than the lowest fix success rate predicted by our best logistic regression model (0.35). Three of those 4 sites were found under the densest canopy cover class, and none were located in areas with high satellite view. These "worst-case" sites were relatively rare within the bear research area (Fig. 3), but we recognize the possibility of overestimating the $P_{success}$ coefficient in areas with dense forests and steep terrain.

We identified substantial disparity in fix success rates between test collars (0.76) and collars placed on free-ranging bears (0.43). Such disparities may result from differences in habitats used by bears as compared to test collar sites and by animal behaviors including movement (Bowman et al. 2000,

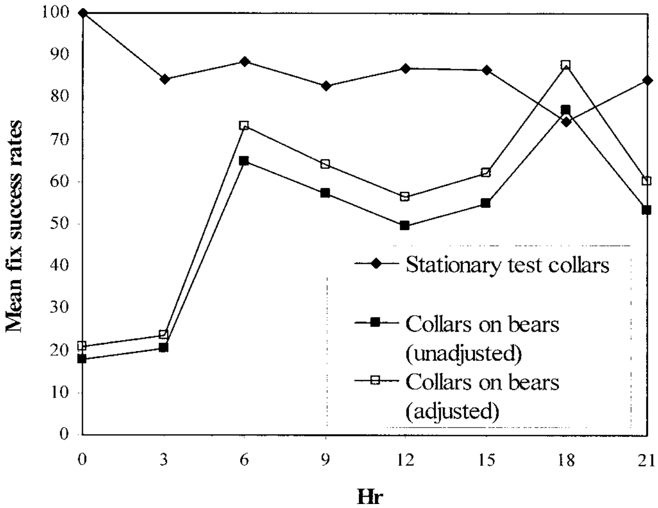

Figure 7. Hourly mean adjusted and unadjusted fix success rates of Global Positioning System (GPS) collars on free-ranging black bears in Olympic National Park, Washington, USA, 2002–2004, and fix success rates of stationary GPS test collars. We limited comparisons between stationary test collars and collars on black bears to hours that collars on free-ranging black bears were programmed to obtain GPS fixes and to the same months that stationary test collars were placed in the field.

Moen et al. 2001), collar position and orientation (Moen et al. 1996, D'Eon and Delparte 2005), head movement (Obbard et al. 1998, D'Eon and Delparte 2005), and microhabitat selection. Differences in fix success rates we observed between test collars placed randomly and those placed at the bases of nearby trees (0.16) suggests that microhabitat selection may be an important factor reducing fix success. Many species of wildlife, particularly bears, use large trees for shelter while resting (Mollohan 1987). Black bear preference for bedding in forests has been documented in Idaho, USA (Unsworth et al. 1989) and in Olympic National Park we frequently found bear beds directly at the bases of trees (K. Sager-Fradkin, personal observation). Because bears and other wildlife select specific microhabitats, the relatively coarse-grained scale at which we tested collars and measured habitat variables may not have been appropriate to account for certain animal behaviors that operate at finer scales.

Another potential cause of disparity in fix success rates between collars used for testing and those placed on wildlife was recently identified by Janeau et al. (2004) and Cain et al. (2005). Each documented a significant relationship between fix success rates and fix intervals, with longer intervals between consecutive fixes resulting in lower fix success rates. Based on a retrospective analysis of published field studies, Cain et al. (2005) reported that fix success varies by approximately 0.08 for collars programmed to obtain fixes at 1-hour to 6-hour fix intervals, which is comparable to the range that we used on test collars and free-ranging bears, respectively. Hence, we acknowledge that our test collars may have overestimated fix success by a factor of 0.08 due to the more frequent fix success schedule used in the test collars than in collars on bears. We conclude, however, that the discrepancy in fix success between test collars and collars on bears (0.33) is too great to be attributed to collar scheduling differences alone.

Our findings revealed that data losses from GPS telemetry on free-ranging bears reflected seasonal changes in bear distribution patterns, with greater data losses occurring during spring when bears were using dense low elevation forests along valley bottoms (Sager 2005). Higher sample weightings applied to fixes acquired during spring helped to compensate for greater data losses when bears were at low elevations than at high elevations but not sufficiently to reduce seasonal variation in fix success appreciably. Success rate of GPS collars on free-ranging bears also varied by hour, with the greatest data losses occurring from 0000 hours to 0300 hours. Black bears in the nearby Cascades Mountain Range are most frequently inactive from 0200 hours to 0400 hours and most active during crepuscular periods (Gaines and Lyons 2003), which corresponds with periods of low and peak fix success rates of GPS collars on black bears in our study, respectively. We speculate that fix success rates of collars on black bears are adversely affected by behavioral aspects of black bears during inactive periods, with microhabitat selection, poor GPS antenna orientation (D'Eon and Delparte 2005), and body mass of bears (Graves and Waller 2006) interfering with collar–satellite communication. Whatever the causes, we conclude that structural attributes of habitats are not sufficient to account for the majority of data loss associated with GPS telemetry on black bears.

We have several concerns over the ability of fix rate modeling to mitigate data loss and associated biases in studies of black bear distribution and resource selection in old-growth coniferous forests of western Washington. First, weighting factors derived from test collars and remotely sensed variables increased average fix success rate by only 0.06, leaving nearly 50% of data opportunity unrealized and unexplained. Second, increased weighting factors during spring were not sufficient to mitigate the obvious seasonal differences in bear distribution and associated data losses. Lastly, diurnal cycles of data loss that cannot be attributed to structural habitat variables suggest a prominent influence of animal activity, behavior, or microhabitat use on data losses. Our results corroborate the finding by D'Eon (2003) that fix success models derived from stationary test collars resulted in data adjustments of only 4.8–7.7%, failing to account for the majority of lost data in a study of resource selection by mule deer.

Significant limitations remain in accounting for data loss and error inherent in the use of GPS telemetry, with additional studies needed to determine the influences of animal activity and microhabitat selection on data omission biases. Recognizing that we examined GPS collars under some of the most challenging environmental conditions for the use of GPS telemetry in the world, we encourage replication of our studies to better document the ranges of data losses and location errors present across the full spectrum of forest and terrain conditions in which GPS telemetry is currently used.

MANAGEMENT IMPLICATIONS

Two primary problems remain in accounting for bias and error of GPS telemetry locations of large mammals in mountainous forest terrain. First, although fix success models derived from remotely sensed environmental variables and used to weight telemetry locations function to reduce data omission biases, only a small fraction of lost data may be restored on the basis of environmental variables alone. Because fix success models are expensive to develop, future researchers should consider the likely costs and benefits of such an expenditure before investing in costly field studies using stationary collars. Regardless of whether or not sample weighting methods are developed and used to reduce biases, future researchers must also consider the magnitude of potential data losses as well as the effects of data omission biases on Type-II errors in their interpretation of resource selection studies (Frair et al. 2004).

Second, large and variable location errors of 2D fixes are potentially problematic in resource selection studies based on GPS telemetry in mountainous terrain. Scheduling GPS collars to attempt frequent fix locations, although demanding of battery power, would minimize the likelihood of animals moving across broad elevations between consecutive fixes and reduce location errors of 2D fixes that are greatly separated in time from a previous 3D fix. Future researchers should consider the influence of elevation changes in determining spatial accuracy of GPS telemetry locations on free-ranging animals.

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LITERATURE CITED

Anderson, C. R., D. S. Moody, B. L. Smith, F. G. Lindsey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. Journal of Wildlife Management 62:1055–1066.

Biggs, J. R., K. D. Bennett, and P. R. Fresquez. 2001. Relationship between home range characteristics and the probability of obtaining successful global positioning system (GPS) collar positions for elk in New Mexico. Western North American Naturalist 61:213–222.

Blake, S., I. Douglas-Hamilton, and W. B. Karesh. 2001. GPS telemetry of forest elephants in Central Africa: results of a preliminary study. African Journal of Ecology 39:178–186.

Bodie, W. L., E. O. Garton, E. R. Taylor, and M. McCoy. 1995. A sightability model for bighorn sheep in canyon habitats. Journal of Wildlife Management 59:832–840.

Bowman, J. L., C. O. Kochanny, S. Demarais, and B. D. Leopold. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141–145.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cain, J. W., III, P. R. Krausman, B. D. Jansen, and J. R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926–934.

D'Eon, R. G. 2003. Effects of a stationary GPS fix-rate bias on habitat-selection analyses. Journal of Wildlife Management 67:858–863.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430–439.

Di Orio, A. P., R. Callas, and R. J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. Wildlife Society Bulletin 31:372–379.

Edenius, L. 1997. Field test of a GPS location system for moose, *Alces alces*, under Scandinavian boreal conditions. Wildlife Biology 3:39–43.

Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

Gaines, W. L., and A. L. Lyons. 2003. Crepuscular and nocturnal activity patterns of black bears in the North Cascades of Washington. Northwest Science 77:140–146.

Graves, T. A., and J. S. Waller. 2006. Understanding the causes of missed global positioning system telemetry fixes. Journal of Wildlife Management 70:844–851.

Henderson, J. A., D. H. Peter, R. D. Lesher, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. United States Forest Service Ecological Technical Paper 001-88, Portland, Oregon, USA.

Horne, J. S., E. O. Garton, and K. A. Sager. 2007. Correcting home range models for observation bias. Journal of Wildlife Management. 71:996–1001.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Janeau, G., C. Adrados, J. Joachim, J. P. Gendner, and D. Pepin. 2004. Performance of differential GPS collars in temperate mountain forest. Comptes Rendus Biologies 327:1143–1149.

Johnson, C. J., D. C. Heard, and K. L. Parker. 2002. Expectations and realities of GPS animal location collars: results of three years in the field. Wildlife Biology 8:153–159.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530–539.

Moen, R., J. Pastor, and Y. Cohen. 2001. Effects of animal activity on GPS telemetry location attempts. Alces 37:207–216.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659–668.

Mollohan, C. M. 1987. Black bear habitat use in northern Arizona. Arizona Game and Fish Department, Phoenix, Arizona, USA.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York, USA.

Obbard, M. E., B. A. Pond, and A. Perera. 1998. Preliminary evaluation of GPS collars for analysis of habitat use and activity patterns of black bears. Ursus 10:209–217.

Rempel, R. S., A. R. Rodgers, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59:543–551.

Sager, K. A. 2005. Black bear distribution patterns in a temperate forest environment, Olympic National Park. Thesis, University of Idaho, Moscow, USA.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.

Sprague, D. S., H. Kabaya, and K. Hagihara. 2004. Field testing a global positioning system (GPS) collar on a Japanese monkey: reliability of automatic GPS positioning in a Japanese forest. Primates 45:151–154.
Unsworth, J. W., J. J. Beecham, and L. R. Irby. 1989. Female black bear habitat use in west-central Idaho. Journal of Wildlife Management 53: 668–673.

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