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Are All Global Positioning System Collars Created Equal? Correcting Habitat-Induced Bias Using Three Brands in the Central Canadian Rockies

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ABSTRACT Global positioning system (GPS) collars are changing the face of wildlife research, yet they still possess biases such as habitat-induced fix-rate bias, which is a serious concern for habitat selection studies. We studied GPS bias in the Central Canadian Rockies, a critical area for wildlife conservation, to provide a statistical approach to correct GPS habitat bias for habitat selection studies using GPS collars. To model GPS habitat bias we deployed 11 different collars from 3 brands of GPS collars (Advanced Telemetry Systems [ATS], Asanti, MN; LOTEK Engineering Ltd., Newmarket, ON, Canada; and Televilt, Lindesberg, Sweden) in a random-stratified design at 86 sites across habitat and topographic conditions. We modeled the probability of obtaining a successful location, P_{FIX}, as a function of habitat, topography, and collar brand using mixed-effects logistic regression in an information theoretic approach. For LOTEK collars, we also investigated the effect of 8 and 12 GPS channels on fix rate. The ATS collars had the highest overall fix rates (97.4%), followed by LOTEK 12 channel (94.5%), LOTEK 8 channel (85.6%), and Televilt (82.3%). Sufficient model selection uncertainty existed to warrant model averaging for logistic regression P_{FIX} models. Collar brand influenced fix rate in all P_{FIX} models: fix rates for ATS and LOTEK 12 channel were not statistically different, whereas LOTEK 8 channel receivers had intermediate fix rates, and Televilt had the lowest. Fix rate was reduced in aspen stands, closed coniferous stands, and sites in narrow mountainous valleys but was higher on upper mountain slopes. Slight discrepancies between fix rates from field trials and observed species fix rates (wolf [*Canis lupus*] and elk [*Cervus elaphus*]) suggest uncorrected behavioral or movement-induced bias similar to other recent studies. Regardless, the strong habitat-induced bias in GPS fix rates confirms that in our study area habitat effects are critical, especially for poorer performance brands. Based on previous studies of effects of the amount of bias on inferences, our results suggest correction for GPS bias should be mandatory for Televilt collars in the Canadian Rockies, optional for LOTEK (dependent on the no. of channels), and unnecessary for ATS. Thus, our GPS bias model will be useful to researchers using GPS collars on a variety of species throughout the Rocky Mountain cordillera. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):2026–2033; 2007)

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Global Positioning System (GPS) collars are revolutionizing wildlife research through their ability to collect an abundance of fine-scale spatial and temporal animal location data (Rempel et al. 1995, Rogers et al. 1999, D'Eon 2003). Compared to conventional very high frequency (VHF) radiotelemetry (Nams 1989, Rettie and McLoughlin 1999), GPS collars provide more data with fewer biases because they can acquire locations at any time (Rogers et al. 1999). Global Postioning System collars also provide researchers with the ability to easily quantify location error and bias resulting from missed or failed location attempts (D'Eon 2003, Frair et al. 2004). Location error has typically been the main error acknowledged in VHF studies (Rettie and McLoughlin 1999), but it is less a concern with GPS collars (but see Jerde and Visscher 2005) because locations are often at least as accurate as habitat mapping products (e.g., <31 m 95% of the time; Rempel et al. 1995, D'Eon et al. 2002). However, several remaining sources of error and bias remain, the most important of which are missed or unsuccessful location attempts.

Missed locations reduce the probability of obtaining a fix (fix rate) to <100%, and researchers have identified several primary factors explaining missed location attempts. Failed attempts can arise because of habitat (or topographic) factors such as dense canopy cover that impose a systematic bias (D'Eon et al. 2002, D'Eon 2003, Frair et al. 2004), animal behavior such as sleeping that influences collar positioning and fix success or movement rates (Moen et al. 1996, D'Eon and Delparte 2005), time between fix-attempts by a collar (Graves and Waller 2006), or even satellite configuration and time of day (Frair et al. 2004, Graves and Waller 2006). For studies of habitat selection, habitat induced fix-rate bias is perhaps the largest source of bias and hence most critical to overcome (Rettie and McLouglin 1999, D'Eon 2003, Frair et al. 2004). Thus, we consider only habitat induced GPS bias (GPS habitat bias). Though many studies have quantified GPS habitat bias (Rempel et al. 1995), only 2 describe methods for its correction (D'Eon 2003, Frair et al. 2004). Both D'Eon (2003) and Frair et al. (2004) developed models for predicting and correcting GPS habitat bias based on landscape covariates. Frair et al. (2004) found fix rate declined on steeper slopes, and D'Eon et al. (2002) found that the percentage of available sky, related to topographic complexity, increased fix rate. Both studies demonstrated significant (10%–40%) data loss due to topography and forest cover, yet both cautioned against naïve extrapolation of

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their models to new landscapes. In the Central Rockies Ecosystem (CRE) of Alberta and British Columbia, Canada (White et al. 1995), numerous GPS-collar studies are underway on cougars (*Felis concolor*), woodland caribou (*Rangifer tarandus*), wolves (*Canis lupus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), and grizzly bears (*Ursus arctos*). Despite the habitat modeling objectives of all studies, no efforts to evaluate GPS habitat bias have been conducted. Given the topography of the CRE, we expected even greater GPS habitat bias compared to the topographically gentler areas of Frair et al. (2004) and D'Eon (2003).

Thus, the main objective of this paper was to develop a GPS habitat bias model for 3 common brands of GPS collars used in the CRE that could be used for correcting habitat induced fix-rate bias in habitat selection studies of wildlife using GPS collars. We deployed GPS collars of 3 different brands at locations stratified across the CRE to estimate bias. We then modeled fix rates following methods of Frair et al. (2004) and developed brand-specific models for correcting coefficients of resource selection models based on Geographic Information System (GIS) coverages in the CRE using sample weighting. For the first time in the literature, we also report field performance of 2 new LOTEK (LOTEK Engineering Ltd., Newmarket, ON, Canada) collar types and a remote release mechanism deployed on wolves and elk from 2002 to 2004. Finally, we compared field performance of LOTEK collars within our study area to Televilt (Lindesberg, Sweden) and Advanced Telemetry Systems (ATS; Asanti, MN) collars from other studies (Gau et al. 2004) to provide guidance for wildlife biologists.

STUDY AREA

The study took place in an approximately 10,000-km^2 section of the CRE (White et al. 1995) along the continental divide of the Rocky Mountains in the provinces of Alberta and British Columbia, Canada (51°15′N, 116°00′W). Our study area included Banff, Kootenay, and Yoho National Parks; Peter Lougheed Provincial Park; and Kananaskis Country Provincial recreation area. Elevation ranged from 1,600 m in valley bottoms to 3,500 m. The study area was dominated by west to east gradients in elevation, precipitation, and topographic complexity, all of which were higher in the western study area (Holland and Coen 1983). Vegetation was classified into 3 ecoregions: montane, subalpine, and alpine. The montane ecoregion was dominated by thick lodgepole pine (*Pinus contorta*) interspersed with white spruce (*Picea glauca*)–willow (*Salix* spp.) areas, aspen (*Populus tremuloides*)–parkland, and grassland systems. Subalpine and alpine ecoregions were comprised of dense Engelmann spruce (*Picea englemannii*)–subalpine fir (*Abies lasiocarpa*)–lodgepole forest interspersed with willow–shrublands, grasslands, and avalanche terrain, grading to open shrub–forb meadows in the alpine (Holland and Coen 1983).

METHODS

We evaluated 3 different brands of GPS collars: LOTEK, Televilt, and ATS. We tested 11 total individual collars comprising 5 different collar models. We tested 3 LOTEK 2200 collars (2 from 2002 and one from 2001 production) and 3 LOTEK 3300sw collars (2004 production). We tested 3 Televilt GPS-Simplex collars (Predator model, 2000 and 2001 production). Finally, we tested the ATS G2000 large animal collar (2001 production). The LOTEK 2200 collar contained an 8-channel GPS receiver, the LOTEK 3300 collar a 12-channel receiver, and both ATS and Televilt contained a 12-channel receiver. Because the number of channels is known to influence fix rate (Moen et al. 1996), we considered LOTEK 8- and 12-channel collars as 2 different brands when evaluating GPS habitat bias. Because GPS acquisition specifications differed between collar brands, we standardized maximum GPS location acquisition time to be <2 minutes, typically at the maximum end of successful GPS location times (M. Hebblewhite, University of Montana, unpublished data). We programmed collars to a consistent 2-hour relocation schedule, and we deployed them for >22 hours (range 22–96 hr, $\bar{x} = 34.1$ hr). Whereas other studies have shown the frequency of locations influences fix rates (e.g., Edenius et al. 1997), we used 2 hours because most ongoing GPS collar studies in our system used this schedule (e.g., Hebblewhite 2006).

Our approach was to develop a statistical model that could correct for GPS habitat bias in habitat selection studies that were based on GIS covariates (e.g., D'Eon 2003, Frair et al. 2004). Although many previous studies used field measurements of canopy coverage, tree height, etc., to model GPS collar fix rate (Rempel et al. 1995), this approach is limited for correcting large numbers of telemetry locations from GPS collars deployed on wildlife because of the absence of similar field measurements from GPS collar locations (Frair et al. 2004). Thus, we took the approach of using GIS-derived covariates to estimate a model for the probability of obtaining a location at each field site.

Field Site Sampling Design

We sampled 86 sites selected using a random-stratified sampling design within 4 main ecological strata in the study area (Krebs 1989). We deployed all GPS collars at sites simultaneously, although a few collars failed to initialize correctly at certain sites (total of 3 collars at 11 sites), causing some unbalance in the design. To facilitate economic sampling, we randomly selected sites representative of the entire study area within a 2-km buffer of a main road to facilitate ease of access using ArcGIS 8.0. We considered ecological strata derived from GIS covariates that influenced GPS fix rates in other studies: canopy cover (open, mixed, closed, deciduous, open cover), elevation (high, low), slope (flat, steep), and aspect (north, south, and flat, which overlapped with flat slopes). For stratification purposes, we discriminated low and high elevations by a cutoff of 1,600 m, and steep slopes by >5° slope (see below for full description). We replicated sampling for treatment combinations at least twice at different locations. We conducted field sampling during 2 periods: 2 February to 31 May 2004 and 9 September to 28 November 2004. We deployed GPS collars 75 cm above ground (snow) in homogenous strata-type areas by suspending collars secured to rope between trees or stakes.

GPS Bias Covariates

We modeled fix rates as a function of collar type and landscape covariates measured with a GIS. We determined the true location for each site using the average location from all GPS locations at a site following Hebblewhite (2006), and intersected this true location with GIS coverages to obtain covariate values. We modeled the effect of collar type using categorical variables for ATS, Televilt, LOTEK 8-channel, and LOTEK 12-channel receivers. We also considered models that grouped all LOTEK to test for the effect of 8 channels versus 12 channels on fix rate in LOTEK collars. We derived landcover types from a LANDSAT-TM landcover model (Franklin et al. 2001). Based on previous research (D'Eon et al. 2002, Frair et al. 2004) we collapsed the 15 landcover types to 5 classes with similar expected GPS habitat bias: 1) open conifer (<40% cover), 2) closed conifer (>40% cover), 3) mixed forest (mixed forest and treed wetlands), 4) deciduous, and 5) open (grasslands, shrubs, rock, ice, water, wetland, regenerating forests, shadow). We modeled the effect of deciduous cover on fix rate using a leaf on (1 Jun to 30 Sep) and off (1 Oct to 31 May) dummy variable. We considered the effects of elevation, slope, aspect class (flat, north, south, east, west), and a slope position index (narrow valley, gentle or flat slope, steep slope, ridgetop; e.g., Graves and Waller 2006) derived from a digital elevation model using a 1000-m window size (Jenness 2005). All GIS variables were at a 30-m^2 pixel resolution. Finally, because previous authors have indicated an effect of time of day on fix rate, often due to satellite configuration (Frair et al. 2004, Graves and Waller 2006), we considered time of day as a categorical variable in 8 time-classes each 3 hours in length.

Statistical Modeling

We modeled the probability of a location attempt being successful (1) or unsuccessful (0); that is, the probability of obtaining a successful fix (P_{FIX}) as a function of brand, topographic, and cover type variables using mixed-effects logistic regression (Hosmer and Lemeshow 2000, Skrondal and Rabe-Hesketh 2004) with a random intercept for each site. We used random effects because of nonindependence of location attempts and collars within a particular field site (Skrondal and Rabe-Hesketh 2004). By including a random effect, we ensured the scope of inference was the entire population of study sites (Skrondal and Rabe-Hesketh 2004). However, it could also be argued that we should have included a random effect for each individual collar used in the study. We felt this was not a valid model structure for 2 reasons. First, there were only a limited number of collars for each brand, limiting the ability to actually model the population of individual collars. As a result, 2-level random effect models with random effects for site and collar frequently failed to converge, or had extremely high condition scores indicating problems with model identifiably (Skrondal and Rabe-Hesketh 2004). Second, the intended objective was to develop a broad approach to correct for GPS habitat bias as a property of the landscape for many different collars. Including a random effect for each individual collar would unnecessarily complicate GPS bias corrections because we were not interested in conditional inferences for a specific collar but rather marginal or population inferences for all sites (Skrondal and Rabe-Hesketh 2004). Thus, accounting for each site as a random effect provided the appropriate scope of inference for our objectives. We fit random effects models using the GLLAMM command (available at http://www.gllamm.org; Rabe-Hesketh et al. 2001) in STATA 8.0 (StataCorp 2003).

We selected the top P_{FIX} GPS habitat bias model(s) using Akaike's Information Criterion adjusted for small sample size (based on $n =$ the no. of sites and no. of parameters (K) that included a parameter for the random intercept; Burnham and Anderson 1998, Rabe-Hesketh and Skrondal 2004) from an a priori list of candidate models composed of plausible combinations of variables and relevant interaction terms (i.e., topographic by closed conifer interaction). We included categorical variables (landcover, season, brand, etc.) using dummy coding, and we considered LOTEK 12-channel collars as the reference or intercept category in models with all 4 brands, and LOTEK as the reference when we ignored effects of number of channels. We screened covariates for collinearity using $r < 0.5$ and variance inflation scores <1 (Menard 2002). We assessed model fit of the top model(s) using goodness of fit measures for both the fixed and mixed-effects model components (Skrondal and Rabe-Hesketh 2004). For the fixed part of the top model, we assessed fit using Hosmer and Lemeshow goodness of fit statistic ($\hat{C}$) and classification diagnostics (Hosmer and Lemeshow 2000). For the mixed-effects model, we assessed goodness of fit using nonparametric receiver operating characteristic (ROC) curves (StataCorp 2003) based on predicted P_{FIX} from the best random effect model, for the overall model, and individual collar brands. We conducted all statistical modeling in STATA 8.0 (StataCorp 2003).

Field Performance of LOTEK GPS Collars

Because their performance has not yet been reported in the literature, we evaluated performance of LOTEK GPS collars and remote timer-release mechanisms deployed on wolves and elk (see Hebblewhite 2006 for capture details for wolves and elk). We compared collar failure in 3 categories: 1) collar functioned within specified parameters normally (i.e., in theory), 2) collar partially functioned, 3) collar failed completely. We did not include animals who died <2 months postcapture. We also compared 1) the maximum number of locations expected if all collars and programmed schedules functioned normally and 2) the average proportions of 2-dimensional, 3-dimensional, and overall percentage of successful locations for collars that functioned at least partially. We used the latter measure because the expected maximum number of locations does not accurately reflect fix rate of collars that worked at least partially. Performance of

Table 1. Mean percentage (SE) of successful location attempts and fix status (2-dimensional [2D], 3-dimensional [3D]) for 3 brands of Global Positioning System (GPS) collars (and 8- and 12-channel LOTEK[a] collars) at randomly selected sites stratified across 5 landcover types in the Central Rockies Ecosystem, Canada, 2004.

	Conifer		Deciduous		Mixed forest		Open		Open conifer		$\bar{x}$	
GPS collar	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**	**%**	**SE**
ATS[b]												
Successful	96	2.3	96.9	1.5	98.9	3.9	99.4	0.7	97	3.0	97.5	1.1
2D	10.3	3.7	1.5	2.6	3.9	3.9	1.2	1.0	3.5	6.1	5.2	1.8
3D	85.7	1.7	95.4	1.8	95.0	1.1	98.2	0.4	93.5	3.0	92.2	0.8
LOTEK 8-channel												
Successful	82.6	2.7	91.4	4.9	97.8	10.0	85.6	4.0	89.3	5.0	85.6	2.1
2D	65.4	2.6	52.1	6.2	43.4	10.8	49.7	4.3	61.4	5.0	57.3	2.4
3D	21.7	3.6	43.2	3.2	55.5	1.1	45	3.6	35.5	3.1	35.1	1.8
LOTEK 12-channel												
Successful	90.6	3.3	95.7	3.8	98.4	3.2	95.7	3.8	92.2	3.9	93.1	1.8
2D	34.8	4	23.1	4.3	21.2	3.5	24.9	4.4	23.6	5.7	27.6	2.2
3D	60.9	2	73.4	1.6	78.2	0.6	73.5	1.1	71.9	2.6	69.3	0.9
Televilt[c]												
Successful	71.9	3.1	83	2.9	86.9	7.8	94	2.9	83.9	4.9	82	1.9
2D	46.4	4.3	42.9	4.7	34.4	12.1	24.9	5.5	38.1	8.9	38.6	3.3
3D	25.6	4.8	40.1	4	52.5	6.3	69.3	3.7	45.8	6.0	43.4	2.4

[a] LOTEK Engineering Ltd., Newmarket, ON, Canada.
[b] Advanced Telemetry Systems (ATS), Asanti, MN.
[c] Televilt, Lindesberg, Sweden.

the remote and timer release mechanisms used to recover both elk and wolf collars was also compared for the first time in the literature. We used chi-square tests to compare performance of collars and remote release devices between species.

RESULTS

Average GPS collar fix rates for stationary test sites ranged from 71.9% to 99.4% across collar brands and cover types, and were lowest in closed coniferous habitats (Table 1). Averaged for collar brands, fix rate was 97.1% for ATS collars, 85.6% for LOTEK 8-channel GPS, 93.1% for LOTEK 12-channel GPS, and 82.6% for Televilt (Table 1). We obtained 6,678 location attempts from the 86 test sites for development of the P_{FIX} model. There was reasonable uncertainty as to what the top P_{FIX} model was (Table 2), so we used model averaging to obtain unconditional parameter estimates and standard errors for coefficients. Regardless, the top supported model held over half the weight of all 5 top models, so we focused evaluating model fit for this top model. For model 1, goodness of fit measures for both the fixed (LR $\chi^2 = 835.1$, $P < 0.001$, Hosmer and Lemeshow $\hat{C}$, $\chi^2_{(8)} = 7.7$, $P = 0.24$) and random-components (nonparametric ROC score = 0.81) indicated good model fit. Evaluated for individual collar brands using this model, nonparametric ROC scores were 0.72 for LOTEK 8-channel, 0.75 for LOTEK 12-channel, 0.71 for Televilt, and 0.74 for ATS. These ROC scores suggest adequate model fit (Hosmer and Lemeshow 2000).

The reference category represented LOTEK collars on flat or gentle slopes on all nonsouth aspects and in open habitats, which functionally included open conifer and mixed forest (Table 3). The top ranked model fit P_{FIX} as a function of 4 collar brands, landcover types of aspen, closed conifer, and topographic position in narrow valleys and steep slopes (Table 2). The second and third ranked models also

Table 2. Model selection results for 3 Global Positioning System (GPS) collar brands deployed at random field test sites stratified across 5 habitat types using Akaike Information Criterion (AIC) for random effects habitat bias models of P_{FIX} from the Central Rockies Ecosystem, Canada, 2004.

Rank and model description[a]	K	log(L)	AIC$_c$	ΔAIC$_c$	w_i	Evidence ratio
1. γ_{0j}, BRAND4, Asp, Conf, TOPO	8	–1,918.1	3,854	0.00	0.516	1.00
2. γ_{0j}, BRAND4, Asp, Conf, Slope	7	–1,920.2	3,855.8	1.79	0.211	2.44
3. γ_{0j}, BRAND4, Asp, Conf, Oconif, TOPO	9	–1,917.9	3,856.1	2.10	0.181	2.86
4. γ_{0j}, BRAND3, Asp Conf, TOPO	7	–1,921.5	3,858.5	4.55	0.053	9.71
5. γ_{0j}, BRAND3, Asp, Conf, Oconif, Mixfor, S, TOPO	11	–1,917.5	3,860.6	6.63	0.019	27.57

[a] Models are shown in decreasing rank with covariate structure and information theoretic model selection diagnostics AIC adjusted for small sample size (AIC$_c$), ΔAIC$_c$, Akaike wt (w_i), and the evidence ratio of each model against the top ranked model. Note for all models the no. of trial sites = 86. γ_{0j} random intercept for site $j = 1 \ldots 86$. BRAND4 refers to LOTEK 12-channel (reference; LOTEK Engineering Ltd., Newmarket, ON, Canada), LOTEK 8-channel, Advanced Telemetry Systems (ATS; Asanti, MN), and Televilt (Lindesberg, Sweden). Landcover type abbreviations are Asp = aspen (both seasons); Conf = closed conifer; Mixfor = mixed forest; Oconif = open conifer. Open habitats were the reference category. TOPO refers to only narrow valley and steep slopes, Ridge and Flat or gentle are combined as the reference category. BRAND3 refers only to LOTEK (reference), ATS, and Televilt—no distinction between 8- or 12-channel LOTEK receivers. S = South-facing aspects (135°–225°); all other aspects are the reference category. K indicates no. of parameters; log(L), log likelihood.

Table 3. Model averaged coefficient and structure for the top 5 models of the probability of obtaining a successful Global Positioning System location (P_{FIX}) in the Central Rockies Ecosystem of Alberta and British Columbia, Canada, 2004.

Covariate	Coeff.	SE	*P* value
Intercept[a]	2.453	0.1346	<0.001
Collar brand (LOTEK[b] 12-channel receiver is the reference)			
Televilt[c]	−2.236	0.1744	<0.001
ATS[d]	0.170	0.2259	0.49
LOTEK 8-channel	−0.725	0.1760	<0.001
Vegetation type (open habitats the reference)			
Aspen	−1.092	0.3098	0.03
Closed conifer	−1.708	0.1988	<0.001
Open conifer	−0.168	0.0590	0.04
Mixed forest	−0.012	0.0063	0.08
Topographic position (ridge and flat the reference)			
Steep slopes	0.356	0.1550	0.039
Narrow valleys	−1.061	0.1374	<0.001
Terrain variables			
South aspects	−0.004	0.0027	0.18
Degrees slope (continuous)	−0.00002	0.00001	0.25
Random effect intercept[e]	Variance	SE(Var)	
γ_{0j}	2.062	0.281	

[a] Intercept represents LOTEK 12-channel receivers in open, ridge, or flat sites.

[b] LOTEK Engineering Ltd., Newmarket, ON, Canada.

[c] Televilt, Lindesberg, Sweden.

[d] Advanced Telemetry Systems (ATS), Asanti, MN.

[e] This is the variance in the intercept (β_0) attributable to the random effect of site.

contained all 4 brands, but the fourth and fifth ranked models contained only 3 brands, indicating some uncertainty regarding the magnitude of the difference between 8- and 12-channel LOTEK GPS collars (Table 2). Because these 2 models had low weight, however, it is likely the reduced performance of 8-channel receivers was real (Table 3). Televilt had the lowest probability of obtaining a fix among all collar brands, followed by LOTEK 8-channel collars; which were the second worst, but still quite better than Televilt (Table 3). Although ATS collars had slightly higher fix rates than the reference category, which were LOTEK 12-channel collars, the difference was not statistically significant amongst final model averaged estimates (Table 3), nor was it in the top model. Aspen habitats and closed coniferous stands had a consistent negative effect across all top 5 models (Tables 2, 3), whereas effects of other cover types including open conifer and mixed forests were weaker and not statistically significant (Table 3). Curiously, effects of leaf-on and leaf-off were not retained in the final models. Topographic position in narrow valleys had a strong negative effect on P_{FIX}, but being located on steep slopes (often near the tops of ridges in the Rockies) increased P_{FIX} significantly. While other covariates of slope and south facing aspects were retained in some of the top models, their influences on P_{FIX} were not statistically significant (Table 3). Finally, time of day did not influence fix rates in the CRE.

Using the top model, P_{FIX} predictions ranged from 0.91 to 0.99 for ATS collars, 0.83 to 0.99 for LOTEK in general, 0.81 to 0.97 for LOTEK 8-channel, 0.89 to 0.99 for LOTEK 12-channel, and 0.52 to 0.94 for Televilt. The close correspondence between predicted and observed probabilities (Table 1) supports the adequate fit of the top model in addition to the non-significant Hosmer and Lemeshow goodness of fit statistic ($\hat{C}$). When extrapolated to the study area using ARCGis 9.0 raster calculator and GIS covariates, the predicted probability of acquiring a fix ranged from 0.94 to 0.99 for ATS, 0.84 to 0.98 for LOTEK 8-channel, 0.90 to 0.99 for LOTEK 12-channel, and 0.64 to 0.97 for Televilt. The GIS raster maps of P_{FIX} for the 4 different collar brands are available via an FTP site from the senior author.

Field Performance of LOTEK GPS Collars

We evaluated performance of LOTEK GPS collars through deployment of 19 collars of 2 models on 22 wolves from December 2002 to June 2004. During 2002–2003, we deployed 6 LOTEK GPS3300s collars, and we experienced a 66% total failure rate ($n = 4$). We never recovered half of all failures, but the 2 recovered failures had chewing damage to the GPS antenna and battery housing, with associated water damage. No data were recovered from either failed collar. The remaining 2 collars only functioned partially, failing early due to a design flaw in the GPS antenna housing. Following these failures, we worked with LOTEK engineers to develop a wolf-resistant GPS collar, the GPS 3300sw. Improvements included a wider collar belting from stronger materials and encasing the GPS battery housing seal with an aluminum gasket to prevent chewing. During 2003–2004, we deployed 13 of the new GPS3300sw collars on wolves. Collar failures declined to one total (8%) and 2 partial failures (16%). We detected no failures from chewing in GPS3300sw collars. To summarize wolf deployments, we deployed 19 collars, 59% of which functioned normally (10), 26% of which failed completely (5), and 21% of which functioned partially (4). We programmed wolf GPS collars to collect approximately 97,100 locations, but they only collected 48,601 location attempts (theoretical fix rate of 50%) given failures. On the 15 collar deployments that were at least partially successful, overall fix rate for the 15 GPS collared wolves was 81.4% (ranging from 49.1% to 95.9%; see Hebblewhite 2006 for details). Note that fix rate on wolves was approximately 12% lower than LOTEK 12-channel (i.e., 3300sw) fix rates from stationary field sites above (Table 1).

For elk, we deployed 26 different GPS collars on 38 adult female elk from 2002 to 2004. We used 3 types of LOTEK GPS collars: 2 GPS 2000 collars, 16 GPS 2200 collars, and 8 GPS 3300 collars. We experienced only 22% ($n = 7$) total collar failures. Some collars (16%, $n = 5$) partially worked with problems due to GPS antennas or battery failures, but most (61%, $n = 19$) functioned normally during deployment. The 31 successful elk deployments had the potential to collect approximately 218,000 GPS locations, but only collected 138,498 locations (theoretical fix rate of 65%). Considering only the 31 partially successful deployments, fix rates were 85.1% (range 28.9–99.9%; Hebblewhite 2006), about 5% lower than stationary trials averaged across LOTEK collars. Split by 8-channel and 12-channel GPS collars, elk had 80.2% and 90.1% fix rates, respectively (Hebblewhite 2006), approximately 5% lower than fixed trials (Table 1). Comparing overall collar performance for wolf and elk collars, there were no significant differences in the frequency of successful, partial, or total failures ($\chi^2 = 0.37$, df $= 2$, $P = 0.82$).

In contrast, we found species-specific differences in the success of remote release devices ($\chi^2 = 0.37$, df $= 1$, $P = 0.82$) with ground and aerial attempts to recover collars with the remote releases more successful on elk than wolves. For wolves, we recovered only 31% ($n = 5$) of all collars successfully, requiring an average of 2.8 attempts per collar. But for elk, we recovered approximately 65% ($n = 20$) of collars following 2.7 ground or 1.9 aerial attempts via the remote release mechanism. The remaining approximately 35% ($n = 11$) of remote release mechanisms completely failed with >3 attempts. We recaptured unsuccessfully released wolf and elk collars via helicopter net gunning.

DISCUSSION

Although GPS collars are changing the face of wildlife research, our study confirms habitat-induced GPS bias will continue to affect their probability of obtaining a successful location, and these will differ substantially between brands. Our logistic regression P_{FIX} model corrected for this GPS habitat bias and was consistent with previous studies that showed fix rates declined in landcover types with denser canopy cover and in topographically more complex habitat (Rempel et al. 1995, Moen et al. 1996, Dussault et al. 1999, D'Eon et al. 2002, Frair et al. 2004). We found few effects of leaf-cover on fix rate, and suspect that leaf-cover is less important in the CRE because deciduous stands are rare (<1% of the landcover) and often classified as mixed conifer (White 2001). Like Frair et al. (2004), but not D'Eon et al. (2002) and Graves and Waller (2006), we found no support for time-induced effects on GPS bias. At the same time, we did find some support that aspects influenced fix-rate bias, similar to D'Eon et al. (2002) but not Frair et al. (2004). D'Eon et al. (2002) and our study found slightly reduced GPS fix rates on north aspects, or higher on south aspects. In exploratory analyses, fix rates were 92% on south aspects, and 86% on all other nonflat aspects, but effects were variable and weak (Table 2). At higher latitudes aspect-induced bias may increase in importance given GPS satellite geometry (D'Eon et al. 2002), but in the CRE its effect was minimal. Previous studies also related a variety of topographic measures to fix-rate bias including slope, which decreased fix rates (Frair et al. 2004) and the percentage of available sky, indexing topographic complexity (D'Eon et al. 2002). By comparison, we used a simple topographic position index (Jenness 2005) and found fix rates declined in narrow valley bottoms (generally <500 m wide), were the same on flat or gentle lower slopes and ridge tops, and were slightly higher on steeper upper slopes. The combination of habitat and topographic features resulted in GPS habitat bias and caused average data loss of between 3% and 19% among GPS collar brands.

D'Eon (2003) and Frair et al. (2004) suggest that habitat-induced data loss <10% did not dramatically influence inferences for habitat selection studies. Thus, fix rates were high enough for ATS collars (>90%) to suggest corrections would be unnecessary, and perhaps even so for LOTEK 12-channel collars. Researchers using Televilt or 8-channel LOTEK collars in the CRE, however, will likely have to correct for GPS bias given their low fix rates. We recommend the simple methods of Frair et al. (2004) that we used to correct GPS bias based on the statistical theory of sample weighting (Pfefferman 1993). To correct using sample weighting, the predicted P_{FIX} is estimated for each GPS telemetry location, and each location's contribution to a habitat selection model is then weighted by the inverse of P_{FIX}. Sample weighting is easily achieved in several statistical software packages, including STATA (StataCorp 2003) and R (R Development Core Team 2006). It may be wise for researchers using any brands of GPS collars to first test for habitat biases using our P_{FIX} models.

This conservative approach may be warranted because fix rates at stationary sites were higher (e.g., 94.5% for LOTEK 12-channel) than observed fix rates from collars deployed on wolves and elk (e.g., 81.4% and 85.1%). Lower animal fix rates could arise from preferential selection of habitats with lower fix rates, whereas our trial sites were stratified randomly. For example, wolves showed stronger selection for closed conifer habitats relative to elk in our study area (Hebblewhite et al. 2005). Alternatively, animal behavioral differences such as bedding with the GPS antenna pointed towards the ground (D'Eon and Delparte 2005) or rapid movements (Moen et al. 1996, Edenius et al. 1997) could explain the lower observed fix rates. Considering that all bias is either only habitat- or behavior-induced GPS bias, our study suggests that GPS habitat bias causes at least approximately 50% or more of the missing fixes for elk, but less for wolves in the CRE. And behavioral bias could be more important in poorer performing collars because of the greater magnitude of missing locations in general. Unfortunately, approaches to correct for behavioral bias are unavailable at present. But if behavior and habitat biases interact (i.e., bedding under dense forest cover), then correcting for GPS habitat bias will account for some component of inherent behavior differences. Empirical or simulation-based approaches to test and correct for potential behavioral biases are sorely needed in GPS studies.

Fix rates and factors influencing them were similar or slightly lower in the CRE compared to results of an earlier study in the adjacent upper foothills region of Alberta (Frair et al. 2004). The coefficient for closed cover ($\beta_{\mathrm{CRE}} = -1.71$ [Table 1], $\beta_{\mathrm{FOOTHILLS}} = -1.83$ [Frair et al. 2004]) was similar between studies. But effects of open conifer were weaker in the CRE than foothills ($\beta_{\mathrm{CRE}} = -0.16$, $\beta_{\mathrm{FOOTHILLS}} = -0.85$). And deciduous forests reduced fix rate more in the foothills study area compared to the CRE ($\beta_{\mathrm{CRE}} = -0.99$, $\beta_{\mathrm{FOOTHILLS}} = -1.71$). Similarly, mixed forest types had mildly negative, but statistically insignificant, effects on fix rates ($\beta_{\mathrm{CRE}} = -0.15$, $\beta_{\mathrm{FOOTHILLS}} = -0.27$). Curiously, ATS collars preformed better than LOTEK 8-channel but similar to LOTEK 12-channel collars in the CRE, whereas they performed worse in the foothills ($\beta_{\mathrm{CRE}} = 0.65$, $\beta_{\mathrm{FOOTHILLS}} = -0.45$). Televilt collars had the lowest fix rates in both areas, but relatively worse in the CRE ($\beta_{\mathrm{CRE}} = -2.24$, $\beta_{\mathrm{FOOTHILLS}} = -1.10$). Mean fix rates were similar or lower to results from Frair et al. (2004); fix rates for LOTEK (12-channel), ATS, and Televilt in the CRE and Foothills ecosystems were, respectively, 94.5% versus 93.5%, 97.4% versus 91.8%, and 82.3% versus 80.8%.

Given the similarities between these 2 studies, a valid question is whether fix-rate models could be used interchangeably or extrapolated to new areas. The main ecological difference between these adjacent mountain and foothills study areas was topographic complexity. In mountainous topography, steep slopes are associated with open and barren terrain at upper elevations, where fix rates were high. The topographic position index we used described relative slope position, which determines the percent of available sky (and hence satellite coverage) in mountains (Jenness 2005). Topographic differences between foothills and mountain regions make it difficult to model fix-rate bias consistently across regions, but within foothills and the Rocky Mountain cordillera researchers should be able to correct habitat bias using Frair et al. (2004) and this study, respectively.

Collar performance of LOTEK GPS collars was similar to previous reviews of ATS (Merrill et al. 1998), Televilt (Gau et al. 2004), and earlier LOTEK collars (Johnson et al. 2002). As discussed above, overall fix rates for partially or fully successful deployments were 81% and 85% for wolves and elk. For wolf and elk deployments, we experienced an 18% ($n = 9$) total failure rate, a 24% ($n = 12$) partial failure rate, and normal collar function for 58% ($n = 29$) of GPS collar deployments. Collar deployments on wolves had higher failure rates than elk due to chewing damage, but wolf collar performance improved following upgrades to the LOTEK GPS3300sw. By comparison, Merrill et al. (1998) reported ATS wolf collars had an 18% failure rate ($n = 2$), 9% ($n = 1$) partial failure, and 73% partial success rate. For Televilt collars, Gau et al. (2004) reported of 71 deployments, 54% ($n = 38$) functioned normally, 28% ($n = 20$) experienced partial failure, and 18% ($n = 13$) completely failed. Johnson et al. (2002) deployed 23 LOTEK 1000 GPS collars on caribou and experienced only 17% ($n = 4$) normal functioning deployments, 78% partial failures ($n = 18$), and 5% ($n = 1$) total failure. Comparing all 4 studies using chi-square tests revealed similar overall performance measures between collars of 51% normal function, 16% failure, and 33% partial failure rates ($\chi^2 = 1.75$, df $= 3$, $P = 0.26$).

We were twice as successful at recovering elk (65%) than wolf GPS collars (31%) using the LOTEK radio and timer release mechanisms. Only Merrill et al. (1998) reported a higher 73% success rate ($n = 8$) of timer only release collars on wolves. We feel that the reasons for the lower release success on wolves were due to wariness of human activity, faster movement rates, and preference to avoid open areas. Consequences of remote release mechanism failure were approximately $36,000 (CDN) in additional animal capture costs, a substantial unexpected budgetary burden. This illustrates a risk of GPS failure that previous studies have not often explicitly highlighted (but see Johnson et al. 2001). Costs of failure, repair, and recovery are difficult to anticipate, yet can be a huge financial burden to research.

MANAGEMENT IMPLICATIONS

Researchers in the CRE and the Canadian Rockies will be able to use our probability of fix models to correct for habitat induced GPS bias in habitat selection models estimated with GPS collar data. Users of Televilt and 8-channel GPS collars will definitely need to make use of GPS bias corrections described herein in the CRE. To be conservative, ATS and LOTEK users could test for bias using our models. This will allow more valid inferences for wildlife management throughout the Rocky Mountain cordillera where GPS bias conditions are expected to be similar. Managers should assume that uncorrected habitat selection models in GPS collar studies overestimate the strength of selected habitats and underestimate the strength of avoided habitats (Gu and Swihart 2004), by underestimating selection for closed conifer or steep valleys. The importance of habitat-induced bias was indicated by the close correspondence of observed fix-rates and those predicted by statistical models. Despite this support for habitat bias, there were additional missed locations on wolves and elk in the CRE that are likely explained by behavioral biases. Correcting for behavioral biases may prove difficult, but at the very least, simulation studies may help reveal the magnitude of the potential problem. Hopefully the growing evidence that wildlife researchers must plan to correct GPS habitat bias and for GPS collar failure will increase the utility of GPS technology in the future.

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