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Decomposing Bias in GPS Relocations of Caribou and Moose in North-central British Columbia

Version 2

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Decomposing Bias in GPS Relocations of Caribou and Moose in North-central British Columbia

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ABSTRACT We applied a combination of previously published techniques to understand the potential bias in relocations of free-ranging, radio-collared animals obtained using global positioning system (GPS) technology. A total of 107 receiver deployments were made on 49 caribou (*Rangifer tarandus caribou*) and 8 moose (*Alces alces*) between March 1996 and June 2001 in three study areas within the Mackenzie Timber Supply Area of north-central British Columbia. We collected 27,551 field days of collar activity representing a possibility of 119,222 relocations. The two types of differentially correctable collars deployed collected relocations at about the same rate (55 %, n = 66,126) implying significant systematic error in operation. Overall success of each deployment was related to individual collar (P = 0.0341, df = 35) and study area (P = 0.0476, df = 2) but independent of other measured factors. To investigate this result further, we used logistic regression to model the probability of unsuccessful relocation attempts based on factors associated with vegetation, geography, and deployment scenario. Ellipses drawn between successive pairs of relocations (n = 19,459) were used as the basis for characterizing potential site conditions for unsuccessful relocation attempts. The highest ranked logistic regression models used percent canopy closure and viewable sky. Based on assessment of model parameters, we concluded that missed relocations within the lower quartile of deployment success (9 % of locations and 30 % of missed relocations) largely resulted from malfunctioning collars and were unlikely biased. We concluded that missed relocations in the top 3 quartiles of deployment success were biased due to poor communication with satellites. We suggest that this bias would likely have led us to underestimate the use of steep alpine and areas of balsam forest with low canopy closure in locations where viewable sky was obscured by adjacent topography. Use of spatial modeling could improve estimates of animal movement patterns and habitat use. Accounting for the bias associated with 91 % of our data was considered important, especially for habitat use studies, because our viewable sky index was known to have disproportionate amounts of forest cover types among other potentially important characteristics.

KEY WORDS *Alces alces*, British Columbia, caribou, global positioning system, GPS, moose, radio-telemetry, *Rangifer tarandus caribou*, relocation bias.

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Global positioning system (GPS) technology has changed the methods for processing and interpreting relocations of radio-collared animals (Rempel et al. 1995, Moen et al. 1996, Rodgers et al. 1996). Initial use of GPS focused on field trials and technical methods for improving performance; largely with the use of differential correction (Rempel and Rodgers 1997, Moen et al. 1997, Dussault et al. 2001). Johnson (2000), Dussault et al. (1999), and Merrill et al. (1998) among others reported their experiences in preliminary field applications and outlined several technical obstacles in collecting animal relocations using GPS technology. With more frequent use of GPS, discussion has turned to understanding error and bias (D'Eon et al. 2002) and to potential ways to identify and correct those errors (Frair et al. 2004). Such error is not unique to GPS technology (White and Garrot 1986) but the abundance of available data and tendency for remote, indirect observation has exacerbated the potential for misinterpretation. Systematic unsuccessful attempts to collect relocations when using GPS has been shown to occur from specific topographic conditions (D'Eon et al. 2002, Cain et al. 2005), forest conditions (Moen et al. 1996, Moen et al. 1997, Rumble and Lindzey 1997, Rempel and Rodgers 1997, Dussault et al. 1999, D'Eon et al. 2002), satellite constellation (Moen et al. 1997), animal activity patterns (Bowman et al. 2000), and animal movement rates (Graves and Waller 2005). Researchers are now more aware of the potential implications of systematic, lost information and have even demonstrated failure to detect significant habitat selection when such bias occurs (Rettie and McLoughlin 1999, Frair et al. 2004).

Our objective was to assess potential bias in GPS observations collected from differentially correctable GPS receivers deployed on free-ranging caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) from March 1996 to June 2001 in north-central British Columbia. We focus on interpreting bias resulting from systematic failed relocation attempts and the potential implications the bias may have on analyses concerning habitat selection. In this study, we do not treat accuracy of the observed relocations.

STUDY AREA

Our study extended from the town of Mackenzie (N 55^{o} 18’ 16’’, W 123^{o} 07’ 56’’) in north-central British Columbia throughout the Omineca Mountains on the west side of Williston Reservoir and north to the Ingenika River (Figure 1). It also included an area north of the Williston Reservoir and east of Fort Ware (N 57^{o} 30’ 00’’, W 125^{o} 24’ 00’’) through the Rocky Mountains to Red Fern Lake. Study areas were based on the relatively distinct ranges of three woodland caribou herds described by Heard and Vagt (1998): the Wolverine area, named after the Wolverine Mountain Range; the Chase area named after Chase Mountain; and the Finlay area named after the primary river drainage with headwaters in the Rocky Mountains. The Wolverine area was 8,443 km^{2} in rolling, high-elevation foothills; the Chase area was 17,330 km^{2} and situated in relatively more steep, mountainous terrain; and the Finlay area was 2, 483 km^{2} with a range of terrain from steep mountainous areas to the broad u-shaped Finlay River valley. Valley bottoms and mid-slopes of the three areas were dominated by relatively cool and dry, or cool and moist, macroclimates of short growing seasons leading to boreal ecosystems of white and black spruce (*Picea glauca* and *P. mariana*) (Meidinger and Pojar 1991). Large-scale and frequent wildfires were characteristic prior to fire control policy (DeLong 2002). Common in these ecosystems were large, relatively flat areas of well-drained fluvial deposits which, in combination with frequent fires, gave rise to large areas of forest stands dominated by even-aged lodgepole pine (*Pinus contorta*). Generally, a cold moist macroclimate with long, cold winters characterized upper slopes where Engelmann spruce (*P. engelmannii*), or it’s hybrid with white spruce, and subalpine fir (*A. lasiocarpa*) dominated. At the northern extent of the Chase and

Finlay areas, deciduous shrubs can dominate the upper slopes. Alpine tundra prevailed above tree line (~1600 m) throughout all three study areas.

METHODS

Collar Deployment and GPS Data Recovery

We collected data using Televilt (GPS-Simplex g01-01010, Televilt International, Lindesberg, Sweden) and Lotek (GPD 1000, Lotek Engineering, Newmarket, Ontario) receivers attached by collars fitted on free-ranging caribou and moose. We activated, programmed, and tested the receivers prior to deployment. We caught the animals using a net propelled by a 0.308 caliber rifle fired while hovering above the animal in a rotary-wing aircraft. Animals were blindfolded, hobbled, and manually restrained while fitting radio collars. We fitted the collars to minimize disturbance to the animal. In most cases, we retrieved the collars by recapturing the animal. We also retrieved collars if the collar was removed from the animal prematurely (e.g., ripped off) or after death. We inspected the animals, during recapture or after death, for any evidence that would indicate collar-related health problems. Deployments of Lotek collars were usually configured to collect 1 location every 3 hours (Johnson 2000). Exceptions to that schedule occurred for receivers having larger battery packs which were configured to collect locations once every 4 hours Saturday to Thursday and additional locations to that schedule every 20 minutes on every fourth hour on Friday. Televilt collars were deployed as part of the Omineca Northern Caribou Project (ONCP) and were usually configured to collect locations every 6 hours. We modified that schedule after the first year of use to collect locations every 12 hours on Monday, Wednesday, and Friday and every 6 hours on other weekdays. Random error to the satellite-based estimates of retrieved locations was intentionally introduced by the United States Department of Defense until May 1st, 2000. We partially corrected that error using independent location data from stationary base stations for both the Lotek (Johnson 2000) and the Televilt data. During the ONCP portion of the work, we established a GPS base station in Mackenzie and used SIMPPOST (Televilt International, Lindesberg, Sweden) to correct random error.

Assessment of Deployment Success

We calculated deployment success as the percent of potential relocations that were actually retrieved from the GPS receiver once it was recovered and data downloaded. The number of potential relocations was calculated from deployment and recovery dates, and the specific relocation collection schedule, for each deployment. We conducted the assessment of success through single- and higher-factor analysis of variance where factors we considered were: collar manufacturer (Lotek or Televilt), individual collar identification (n = 48), frequency of individual collar deployment (first or subsequent), number of weekly relocation attempts (n = 56, 42, 28, or 22), study area (Chase, Wolverine, or Finlay), individual animal identification (n = 57), and animal species (caribou or moose). A balanced 2-factor analysis of variance was used to investigate relocation success for deployments of 12 collars, 6 nested within each collar type, replicated =3 times each on different caribou.

Assessment of GPS Bias

To investigate the relative amount of, and possible explanations for, bias in success of collecting individual relocations, we began by sorting all data from each deployment chronologically. Then, based on interval checks consistent with collar– and deployment-specific data collection schedules, we determined unsuccessful attempts to collect relocations. Although we did not specifically address location accuracy, we did exclude successful relocation attempts from Lotek receivers whenever the horizontal dilution of precision exceeded 16. Televilt receivers were manufactured to only accept locations with =4 viewable satellites so all data from Televilt collars were used. Each pair of location coordinates representing single, double, triple, or more than triple missed relocations were used to construct ellipses where the minor axis was arbitrarily chosen to be half the distance between the pair of location co-ordinates (i.e., major axis). We screened an independent set of relocations collected using Very High Frequency (VHF) technology, retaining samples that fit temporally between any GPS pair representing vertices of missed-relocation ellipses. The VHF relocations were sampled during daylight hours using a Cessna 185, fixed-wing aircraft where locations were assumed to have a positional accuracy of approximately 100 m for visuals and 250 m for fixes. We categorized the retained VHF samples as those occurring within 40-60 % of the time interval between the ellipse vertices (1) or not (0) and as those occurring within the ellipse (1) or not (0). Error rates from a confusion matrix were used to assess the potential for the missed-relocation ellipses to have enclosed the actual location of the radio-collared animal.

We used a frequency plot of ellipse size to arbitrarily distinguish and exclude outliers resulting from stationary collars (minor axis =10 m) and collars that were likely malfunctioning or where we felt it was improbable to reasonably identify unique environmental factors that potentially contributed to relocation bias (minor axis >10,000 m). We chose independent factors largely on the basis of previously reported research. Factors associated with forest conditions were: site index (height of trees at 50 years old), stand height (m), percentage canopy closure (classified as 0, 1-20, 21-40, >40), tree stem density (number per ha), and the most common dominant vegetation type (classified as that having relatively no canopy [deciduous in winter, brush species, alpine tundra, and nonproductive forest areas including rock, sand, mud, road, open range, and water], tall, skinny canopies [spruce and alpine fir], and short, light canopies [pine, deciduous in summer]), where these data were collected from the British Columbia Forest

Inventory and Planning (FIP) database. We characterized geographical setting using slope (degrees) and proportion of viewable sky (classified as <0.50, 0.51-0.70, 0.71-0.90, >0.90) where both factors were modeled using data collected from the British Columbia Terrain and Resource Information Management system. We derived slope from a digital elevation model and viewable sky was defined as the proportion of sky directly visible at each location (i.e., not blocked by topography) using the viewshed function (Fu and Rich 2000) of Solar Analyst (Helios Environmental Modeling Institute, Lawrence, Kansas), an extension to ArcView (Environmental Systems Research Institute, Redlands, California). Deployment scenario was characterized by season (Calving – April through June, Summer – July through September, Post-rut – October through December, and Winter – January through March), quarter of day (classified as 01:00-06:59, 07:00-12:59, 13:00-18:59, 19:00-00:59), and time since deployment (duration in days). We also characterized location attempts by deployment success (%) determined from the previous analysis. We systematically sampled missed relocation ellipses using a 200 m grid (4-ha cells). Together these data resulted in a spatial layer depicting the point locations of all cell centroids. Raster coverage's of the environmental factors were used to attribute each cell centroid. The mode for each environmental variable, weighted by the inverse of sample size, was used to generalize ellipse characteristics in subsequent analyses.

We used logistic regression with maximum likelihood estimation to model the probability of a relocation attempt being unsuccessful. Probability of an unsuccessful relocation attempt (P_{ULA}) took the form:

$$P_{ULA} = \frac{\exp(b_0 + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n)}{1 + \exp(b_0 + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n)}\text{; where}$$

$ß_0$ was the regression intercept and $ß_1 \ldots ß_n$ were coefficients for independent variables $x_1 \ldots x_n$. To construct potential models, we iteratively used forward stepwise logistic regression of all non-correlated (Pearson r < 0.5 when P < 0.05) variables to determine the most promising variable set. We then considered candidate models representing all possible combinations of the resulting variable set. We used the Akaike's Information Criterion with small-sample bias adjustment (AICc), output from Proc Logistic (SAS Institute Inc., Cary, North Carolina), to help identify a suite of parsimonious models that explained our data best among the possible combinations of variables (Burnham and Anderson 2002). Further, we calculated the relative probability of each model being best as (Anderson et al. 2000):

$$W_m = \frac{\exp(-.5\Delta_n)}{\sum_{n=1}^{N} \exp(-.5\Delta_n)} \text{; where}$$

N was the total number of models compared and $\Delta_n = (AICc_n - \min(AICc))$. Finally, we assessed the proportion of relocation attempts correctly classified as unsuccessful (sensitivity) against the proportion of relocation attempts incorrectly classified as unsuccessful (1 – specificity) for all possible thresholds of predicted relocation probability using Receiver Operating Characteristic Curve analyses output from Proc Logistic; specifically, Area Under the Curve (AUC) (Hanley and McNeil 1982).

To understand the potential implications of GPS relocation bias, we compared basic descriptive statistics of two key forest variables that would normally be used for habitat analyses (canopy closure and leading or dominant vegetation type). A Chi-square analysis was used to test equality in distribution of the variables across the following comparisons: (1) pooled missed-relocation ellipses (inside ellipses, outside ellipses, <0.5 viewable sky inside ellipses), (2) relocations (successful relocations, individual unsuccessful relocation ellipses), and (3) relocation technique (VHF relocations, daytime GPS relocations).

RESULTS

Collar Deployment and GPS Data Recovery

Johnson (2000) reported 26 deployments of 11 GPS collars on 23 individual caribou. We were provided with data for 12 collars deployed 31 times on 23 individual caribou. During the ONCP, we made a further 76 deployments of 36 collars on 34 caribou and 8 moose; 60 deployments with caribou and 16 with moose (Table 1). We continued deployment of GPS collars on 8 caribou that were originally used by Johnson (2000). In total, we collected data from 107 GPS receiver deployments. Upon inspection of animals during recapture or after their death, we found no evidence (e.g., skin abrasions or hair loss) that would indicate collar-related health problems. Anecdotal observations taken during VHF telemetry flights revealed that, on occasion, the batteries of the Televilt collars tended to collect ice balls that would have added weight to the collar but we did not detect obvious side effects on either the GPS receiver or the animals. Out of 143 captures through this study, it was necessary for us to dispatch 1 animal that suffered a broken leg during a recapture attempt. Johnson (2000) reported a number of collar malfunctions including those that collected from 0 to <50 % of the anticipated data (n = 10 deployments of 9 collars) and only 3 collars meeting expected battery lives. We experienced similar results with 31 deployments of 22 collars collecting less than 50 % of the target relocations, including collars that, upon deployment, went immediately into “low battery” mode (n = 3) thereby placing extra burden on the battery and reducing the overall function of the collar. Most collar downloads went well and despite apparent malfunction of collars in the field, we were able to obtain and post-process all stored data.

Success of Individual Deployments

In general, the overall relocation success rate across deployments was 55 % (n = 107, se ± 3 %) with quartile successes ranging from 80 % in quartile 4 to 26 % in quartile 1 (Figure 2). Single-factor analysis of variance did not indicate differences in relocation success for individual deployments between collar types ($F_{1,106}$ = 0.64, P = 0.427), first or subsequent deployments of each collar ($F_{1,106}$ = 0.03, P = 0.864), or animal species ($F_{1,106}$ = 0.00, P = 0.948) or among individual animals ($F_{56,106}$ = 0.89, P = 0.667), study areas ($F_{2,104}$ = 1.18, P = 0.311), or the frequency of relocation attempts per week ($F_{3,106}$ = 0.89, P = 0.451). Individual collar identification was the closest single factor related to variance of relocation success for individual deployments ($F_{47,106}$ = 1.59, P = 0.047). In cases where, within each collar type, individual collar deployment was replicated =3 times, pooling across collar type was not important ($F_{1,39}$ = 0.00, P = 0.946). However, pooling deployment success across study areas was found to be inappropriate ($F_{2,75}$ = 3.30, P = 0.048) for individual collars ($F_{35,75}$ = 1.84, P = 0.034) resulting in the best model to explain deployment success (R^2 = 0.65, $F_{37,75}$ = 1.92, P = 0.025) but only for Televilt collars since Lotek were deployed in only one study area.

Ellipses of Failed Relocation Attempts

Based on the location collection schedule for each collar we expected 119,222 relocations but collected only 66,126 (Table 2). We therefore calculated 53,096 failed relocation attempts. These relocation failures were distributed spatially among 19,884 ellipses (Figure 3) with minor axis lengths categorized as: <10 m (n = 165), >100 m or =10,000 m (n = 19,459), or >10,000 m (n = 260). Most ellipses contained 1-3 missed relocations and ranged in size from <1 ha to, in one case, almost 8,000 ha (Figure 4, Table 3). Time between successful relocations for those ellipses that were deleted from further analysis (i.e., 10 m < minor axis >10,000 m) ranged from

6 hours, in cases where animals were traveling relatively quickly, to months where collars were assumed to be malfunctioning. Ellipse areas totaled 12.4 million ha or, for those ellipses used in subsequent analyses, 2.4 million ha. Furthermore, these latter ellipses were spatially correlated (Figure 3) enough to cover only 847,006 ha and resulted in 228,181 samples of landscape conditions.

Although we retrieved 875 VHF samples observed temporally between vertices of missed relocation ellipses, 710 of those were potentially very close to one of the two vertices. Even so, 453 were found to be spatially consistent with the ellipses and the false positive error rate was 19 % (i.e., 80 of the 422 locations observed outside ellipses should have fallen within them).

Decomposing Bias

Significant correlation existed among stand height, canopy closure, and site index as well as between slope and the viewable sky index. In competing models between viewable sky and slope, the former was always selected first and always produced the model with the highest AUC. In competing models among stand height, canopy closure, and site index, these variables were always selected second but models with canopy closure produced highest AUC. In iterative use of forward, stepwise logistic regression, stems per hectare and dominant vegetation form were either rejected as a significant variable or was last to be added to the resultant. We therefore constructed a model set for further analysis using 6 of the available 11 variables for a total of 65 possible models (including the null model): viewable sky, canopy closure, duration since deployment, deployment success, quarter of day, and season.

Based on our model comparison criteria, the highest ranked model of P_{ULA} used 5 of the 6 available non-correlated independent variables with an AUC of 0..819 for the moose relocation model and .762 for the caribou relocation model (Table 4). All of the top-ranked models for caribou and half of the top-ranked models for moose used viewable sky and canopy closure while about half the models in each case used deployment success, duration since deployment, or quarter of day. The top models in each case also included season as a contributing variable. Models based solely on quarter of day, duration since deployment, and deployment success quartile, and the models combining those variables were among the lower ranked models based on AUC. Although the AICc weight indicated that the models with 5 variables were probably the best of those evaluated, AUC only varied from 0.822 to 0.816 and from .771 to .762 across the top 8 models for both moose and caribou, respectively (Table 4). Our choice of models for subsequent discussion favored the relatively simple 3-variable models that were relatively consistent with the lowest AICc yet still had the highest (caribou) and second-highest (moose) AUC scores. For moose that was the model with viewable sky, canopy closure, and season and for caribou that was the model with viewable sky, canopy closure, and deployment success. P_{ULA} was strongly associated with sites having =50 % of viewable sky obscured by surrounding topography (Table 5); this was a much stronger relationship for GPS receivers deployed on moose than for those deployed on caribou.

Canopy closure averaged only 2 % (n = 3,820, SE < 0.001) in areas of missed-relocation ellipses where viewable sky was =0.5, in other areas the average ranged from 27-40 %, and the average indicated by successful relocations was 17 % (n = 63,777, SE < 0.001) (Figure 5). Leading, or dominant vegetation type was distributed markedly different for areas of missed-relocation ellipses where viewable sky was <0.5 than for the average of all ellipses or for the average of areas indicated by successful relocation attempts. Most notably, alpine, deciduous, spruce, and brush forests were represented less, and pine forests more, in individual error ellipses and in the actual GPS relocations than in the portion of the missed-relocation ellipses where satellites would have likely been obscured by topography (Figure 5). However, daytime GPS relocations indicated greater use of alpine and less use of pine and spruce compared to VHF relocations.

DISCUSSION

Collar Deployment, GPS Data Recovery, and Deployment Success

We found no evidence of collar related health problems on the animals we handled, many of which were followed for more than 5 years and handled multiple times. The one animal that we injured critically was due to an attempt to capture late in the spring when snow conditions were marginal. Many of the reported GPS telemetry studies do not discuss collar related health problems, however, Anderson and Lindzey (2003) reported no injuries on GPS collared cougars. Krausman et al (2004) found that GPS collars placed on mule deer and mountain sheep caused varying degrees of sores depending on the shape of the collar. Our Televilt collars were oval shaped to fit the contour of an ungulates neck which may have helped reduce the likelihood of skin abrasions.

Johnson (2000) and other researchers found that individual collars did not always function as expected. D'Eon and Serrouya (2005) found that 8 out of 20 collars malfunctioned or had unusable data. Gau et al (2004) found that 20 out of 71 collars deployed had some degree of failure, 13 of the 71 had catastrophic failure and a further 10 collars failed pre-deployment. In our case, at least 5 tested collars malfunctioned once deployed and a low-battery coded signal possibly indicated technical issues concerning electrical connectors. Other malfunctioning collars appeared to be powered but still failed to successfully obtain relocations. Cain et al. (2005) forwarded the notion of a trade-off between number of relocation attempts per day and the time-to-fix setting (both battery-life saving decisions) which can likely combine in ways to make it impossible to collect a location. We did not find the number of weekly relocations to be significant in determining deployment success although our study was not specifically designed to properly test this. In general, we also experienced collar failures and concluded that, to verify utility of collected data, individual collars require thorough assessment post-deployment as well as pre-deployment. Understanding bias due to environmental factors presupposes data are collected using reliable, functioning equipment.

Aside from the reliability of the equipment used, deployment success in our study ranged markedly. Factors such as collar identification and study area were found to be important and individual collar performance likely masked our ability to detect other potentially important factors. Gau et al. (2004) found similar results from data collected from collared grizzly bears in BC and Alberta with deployment success ranging between 56–65 %. However, they had higher success with GPS collars on bears in the Northwest Territories and attributed the difference to gentler terrain and lower forest canopy coverage in the northern study. Stotyn et al. (2005) had a relatively low deployment success of 48 % which they attributed to steep terrain, dense canopy cover, and animal behavior. In his study in the Washington Cascade Mountains, Rice (2003) found that 58 % of attempted relocations of mountain goats achieved 3D fixes, 19 % achieved 2D fixes and 23 % completely failed to get a fix. He found that his results were similar to other mountain goat studies in BC and felt the results were related to terrain shielding similar to what we termed viewable sky.

Ellipses of Failed Relocation Attempts

We chose to use ellipses only because we thought the shape more reasonably fit a zone of probable locations for instrumented animals during missed relocation attempts. In hind-sight, a more efficient approach would have been to establish the ellipse minor axis length as an indirect function to the rate of travel. Regardless, ellipses were found to enclose a reasonable number of independently collected VHF relocations and the degree of spatial correlation (~50 % overlap) among ellipses led us to speculate that some environmental factors likely accounted for P_{ULA}.

Decomposing Bias

We considered that data loss from malfunctioning collars (e.g., the lowest success quartile) was likely less biased than data loss due to poor communication with satellites. While the notion that 10 % data loss due to poor satellite communication is acceptable (D'Eon 2003), we concluded that deployment in our highest success quartile was still a significant factor in P_{ULA} (at least for GPS receivers deployed on caribou) and would therefore likely have implications on our subsequent interpretation of movement rates and habitat use.

Most of our GPS receivers were configured to last 1year but many began failing prior to that which is probably why duration since deployment was significant in many of the top-ranked models. The significant effect of season could have been related to collar batteries approaching their longevity (collars were usually changed in late winter) coincident with progressively colder ambient temperature. Similar to other studies (Moen et al. 1996, Moen et al. 1997, D'Eon et al. 2002), we also found that percent and type of canopy cover can negatively affect the probability of successful GPS relocation attempts. In our case, other factors such as tree density, tree height and site index would likely have contributed to our model as others have found (Rumble and Lindzey 1997, Rempel and Rodgers 1997, Dussault et al. 1999) but these variables were strongly correlated with canopy closure and were dropped from further analysis. Rempel and Rodgers (1997) found that GPS receivers were 3 to 8 times less likely to get a location under a forest canopy >15 m in height then in a treeless area. Our modeling would suggest that if instrumented animals were located in less than optimal sky view (e.g., 0.5-.07) and canopy closure exceeding

40 %, GPS relocation attempts would be 2 (moose) to 3 (caribou) times more likely to be unsuccessful than attempts in open canopy areas.

In Mountainous areas, topography and canopy combine to further restrict location acquisition (D'Eon et al. 2002). In our study, where canopy closure was marginal (20-40%), individual relocation attempts were 31 (caribou) to 36 (moose) times more likely to be unsuccessful in terrain with more than 50 % of the sky obscured by adjacent topography. The effect of obscured sky would be similar to the effect reported by others on reduced relocation success due to collar position (D'Eon and Delparte 2005). Our modeling would suggest that relocations would be unlikely (caribou P_{ULA} = 78%, moose P_{ULA} = 94%) in combinations of sky obscured by terrain combined with a dense forest canopy.

Quarter of day did remain as a significant variable in many of our top-ranked models with lowest relocation success occurring at 13:00-19:00 (moose) and 19:00-01:00 (caribou). However, both ungulate activity patterns (Bowman et al. 2000) or satellite constellation (Moen et al. 1997) could explain this variance. We were unable to test for significant effects due to animal activity patterns or satellite constellation because we did not sample sufficiently intense (i.e., we cannot distinguish between effects of satellite constellation and animal activity). We never assessed influence of collar orientation (compass direction) resulting from animal habitat selection behavior as a further potential reason for this daily pattern since others (D'Eon and Delparte 2005) have demonstrated weak to no significant relationships.

Working with Biased GPS Data Sets

Results of our investigation confirmed that: (1) deployment success ranged widely and, in the lower quartile of success, was attributable to malfunction of individual collars and (2) success of individual GPS relocation attempts was biased against sites where the receiver was partially obscured from satellites; the barrier being strongly influenced by topography and, to a lesser extent, by tree cover. Even though we may argue that malfunctioning collars were not biased, the lowest quartile of deployment success only accounted for 9 % of our data and 30 % of our missed relocations leaving the majority of relocations (n = 59,972) biased.

Implications of the GPS relocation bias is expected to be important in studies of animal movement and habitat use since we showed marked differences in commonly used attributes of habitat such as canopy closure and leading or dominant vegetation type. Counter-intuitively, the bias due to sky being obscured by topography, would likely be against selection for low canopy closure and alpine and, or spruce forest areas.

Now that concern over correcting biased data collected using GPS technology has come into focus, various methods are being developed to adjust biased data sets. Various studies have tested the validity of measuring each habitat type within buffers around point locations rather than using only the habitat type at the location itself (Kufeld et al. 1987, Rettie and McLoughlin 1999). Although Rettie and McLoughlin (1999) found it easier to identify selection versus avoidance using this method, sampling error increased. We concur with Frair et al. (2004) that buffering relocations does not adequately deal with bias in these data. Frair et al. (2004) suggest 2 bias correction methods; sample weighting and iterative simulation. Which of these methods to use depends on the design used to assess resource selection; for example sample weighting will not work where location accuracy is a concern as the weighting is based on GPS locations rather than an actual location of an animal. Frair et al. (2004) also state that further testing under various conditions and locations should be done in order to understand the stability of these methods.

Although we have demonstrated bias in retrieved GPS relocation data and potential covariates that can explain some of this bias, we remain skeptical about the precision and accuracy with which the bias can be corrected. Rather, by decomposing the bias, we have gained an appreciation for the level of interpretation that can be obtained from the data in subsequent analyses. Relocation data obtained from VHF samples are also biased (Beyer and Haufler 1994) but in different ways than GPS samples. Combined interpretations of the two types of data samples, with knowledge of spatial patterns in missed relocations, may persist as the most reliable approach to determining less biased estimates of animal site selections and activity patterns.

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Associate Editor:

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Figure 1. Study area names and relocations of radio-collared caribou and moose in north-central British Columbia. Relocations were based on Global Positioning System technology and were observed between March 1996 and March 2002 in north-central British Columbia.

Figure 2. Average (diamonds) and standard deviation (error bars) of relocation success, number of successful relocations (n_l), number of missed relocations (n_m), and number of deployments (grey histograms) made for Global Positioning System collars used in a study of caribou and moose between March 1996 to March 2002 in north-central British Columbia.

Figure 3. Ellipses used to characterize the probable location of radio-collared animals during failed relocation attempts by Global Positioning System collars. Information was collected between March 1996 and March 2002 in north-central British Columbia.

Figure 4. Frequency of observations for (A) the minor axis of ellipses used to describe probable locations of radio-collared animals during failed relocation attempts by Global Positioning System receivers and (B) the number of failed relocation attempts contained within each ellipse. Information was collected between March 1996 and March 2002 in north-central British Columbia.

Figure 5. (A) Average percent canopy closure and (B) percent of leading forest species found in the following areas: outside ellipses, inside pooled ellipses, sum individual ellipses, GPS relocations, <0.5 viewable sky, daytime relocations, and VHF relocations, during a study of caribou and moose between March 1996 to March 2002 in north-central British Columbia.

Table 1. Numbers of caribou and moose captured, collars used, and deployments made to study animal movements using Global Positioning System technology between March 1996 and March 2002 in north-central British Columbia.

		Species		
	Study	Caribou	Moose	Totals
Animals	Johnson (2000)	23	0	57
	ONCP[a]	26 + 8[b]	8	
	Subtotal	49	8	
Collars	Johnson (2000)	12	0	48
	ONCP[a]	28	8	
	Subtotal	40	8	
Deployments	Johnson (2000)	31	0	107
	ONCP[a]	60	16	
	Subtotal	91	16	

a – where ONCP is the Omineca Northern Caribou Project.

b – where 8 of the Johnson animals were also used on the ONCP.

Table 2. A summary of duration in the field, number of relocations collected, and percent of possible relocations for Global Positioning System collars used in a study of caribou and moose between March 1996 to March 2002 in north-central British Columbia.

Species	Gender		Study Areas and GPS Receiver Type				Total
			Finlay	Chase	Wolverine		
			Televilt	Televilt	Lotek	Televilt	
Moose	Female	Duration in Field	1,014	893		708	2,615
		Relocations Collected	2,048	1,261		1,064	4,373
		Percent Possible Relocations	70%	34%		48%	53%
	Male	Duration in Field	1,065	621		587	2,273
		Relocations Collected	1,814	1,386		1145	4,345
		Percent Possible Relocations	51%	56%		66%	57%
Caribou	Female	Duration in Field	3,814	3,868	6,071	3,728	17,481
		Relocations Collected	6,827	7,092	28,888	5,664	48,471
		Percent Possible Relocations	60%	52%	57%	48%	55%
	Male	Duration in Field	1,232	1,982		1,968	5,182
		Relocations Collected	2,143	4,416		2,378	8,937
		Percent Possible Relocations	58%	63%		38%	53%
Total		Duration in Field	7,124	7,364	6,071	6,991	27,551
		Relocations Collected	12,832	14,155	28,888	10,251	66,126
		Percent Possible Relocations	60%	53%	57%	47%	55%

Table 3. Descriptive statistics (number, total area (ha), average size (ha), and standard error of the mean size) for ellipses used to describe the probable location of radio-collared animals during failed relocation attempts by Global Positioning System receivers. Information was collected between March 1996 and March 2002 in north-central British Columbia.

Parameter	Number of Missed Relocation Attempts				Total
	1	2	3	4	
Number	8,736	5,036	2,529	3,583	19,884
Total Area (ha)	2,040,451	1,234,851	3,744,386	5,359,733	12,379,421
Average Size (ha)	234	245	1,481	1496	623
SE	103	123	938	868	204

Table 4. Comparison of the highest ranked logistic regressions modeling the probability of failure to successfully achieve a GPS relocation for marked caribou and moose in north-central British Columbia. Decreasing model rank was assessed using Akaike's information criterion for small sample sizes (AICc), AICc difference from the model with lowest AICc (Δ_n), AIC weight (W_m), area under the receiver operating characteristics curve (AUC), Wald c^2, and number of independent parameters estimated (df). Models of all possible combinations of six, non-correlated independent variables were assessed.

Model[1]	AICc	Δ_n	W_m	AUC	Wald c^2	df
Moose						
VQCLS	3846	0	0.4313	0.819	197	11
VCLS	3847	1	0.2616	0.822	196	10
VQCS	3848	2	0.1586	0.818	194	10
VCS	3849	3	0.0962	0.821	192	9
VQDCLS	3852	6	0.0215	0.817	198	14
VDCLS	3853	7	0.0130	0.820	196	13
VQDCS	3853	7	0.0130	0.816	194	13
VDCS	3855	9	0.0048	0.819	191	12
QDL	6533	2687	<.0001	0.542	8	5
QD	6533	2687	<.0001	0.540	6	64
QL	6532	2686	<.0001	0.546	3	2
Q	6532	2686	<.0001	0.529	<0	1
DL	6531	2685	<.0001	0.532	8	4
D	6531	2685	<.0001	0.530	6	3
L	6530	2684	<.0001	0.537	2	1
Caribou						
VQDCS	15899	0	0.3875	0.762	5019	13
VQDCLS	15900	1	0.2350	0.762	5020	14
VQCS	15900	1	0.2350	0.763	5019	10
VQCLS	15901	2	0.1425	0.762	5020	11
VQDCL	15946	47	<.0001	0.770	5016	11
VQC	15946	47	<.0001	0.771	5017	7
VQCL	15948	49	<.0001	0.771	5017	8
VQDC	15948	49	<.0001	0.771	5017	8
VDCS	15956	57	<.0001	0.748	5009	12
VDCLS	15958	59	<.0001	0.747	5008	13
VCS	15959	60	<.0001	0.748	5008	9
VCLS	15960	61	<.0001	0.748	5008	10
VDCL	15999	100	<.0001	0.758	5007	10
VC	16000	101	<.0001	0.758	5008	6
VCL	16002	103	<.0001	0.759	5008	7

---

1 – Variables for models were: proportion of viewable sky (V - <0.50, 0.51-0.70, 0 .71-0.90, >0.90), deployment success (Q - %), percent canopy closure (C – 0, 1-20, 21-40, >40), time since deployment (L - days), and season (S). See text for further description.

Table 5. Logistic regression models estimating the probability of failure to successfully achieve a GPS relocation for marked caribou (N = 71,825, Wald c^{2} = 5017, P<0.001, AUC = .771) and moose (N = 12,072, Wald c^{2} = 192, P<0.001, AUC = .821) in north-central British Columbia. See text for variable descriptions.

Variable		Parameter Estimate	SE	Wald c^{2}	P
Caribou					
Intercept		-1.5397	0.0885	303	<0.001
Viewable Sky	>0.9	Reference			
	0.71-0.9	-1.1724	0.0380	951	<0.001
	0.51-0.7	-0.7366	0.0703	110	<0.001
	<=0.5	3.3611	0.0528	4052	<0.001
Canopy Closure	0	Reference			
	1-20	-0.0826	0.0650	2	0.2036
	21-40	0.2475	0.0469	28	<0.001
	>40	0.5147	0.0404	162	<0.001
Deployment		-0.0108	0.0014	56	<0.001
Moose					
Intercept		-0.6576	0.2562	7	0.0103
Viewable Sky	>0.9	Reference			
	0.71-0.9	-2.3927	0.2580	86	<0.001
	0.51-0.7	-1.6932	0.2678	40	<0.001
	<=0.5	6.7787	0.7525	81	<0.001
Canopy Closure	0	Reference			
	1-20	-0.6422	0.1464	19	<0.001
	21-40	0.3855	0.0813	22	<0.001
	>40	0.4854	0.0871	31	<0.001
Season	0	Reference			
	1-20	-0.0577	0.0780	1	0.4593
	21-40	0.3124	0.0848	14	0.0002
	>40	0.2211	0.0822	7	0.0071

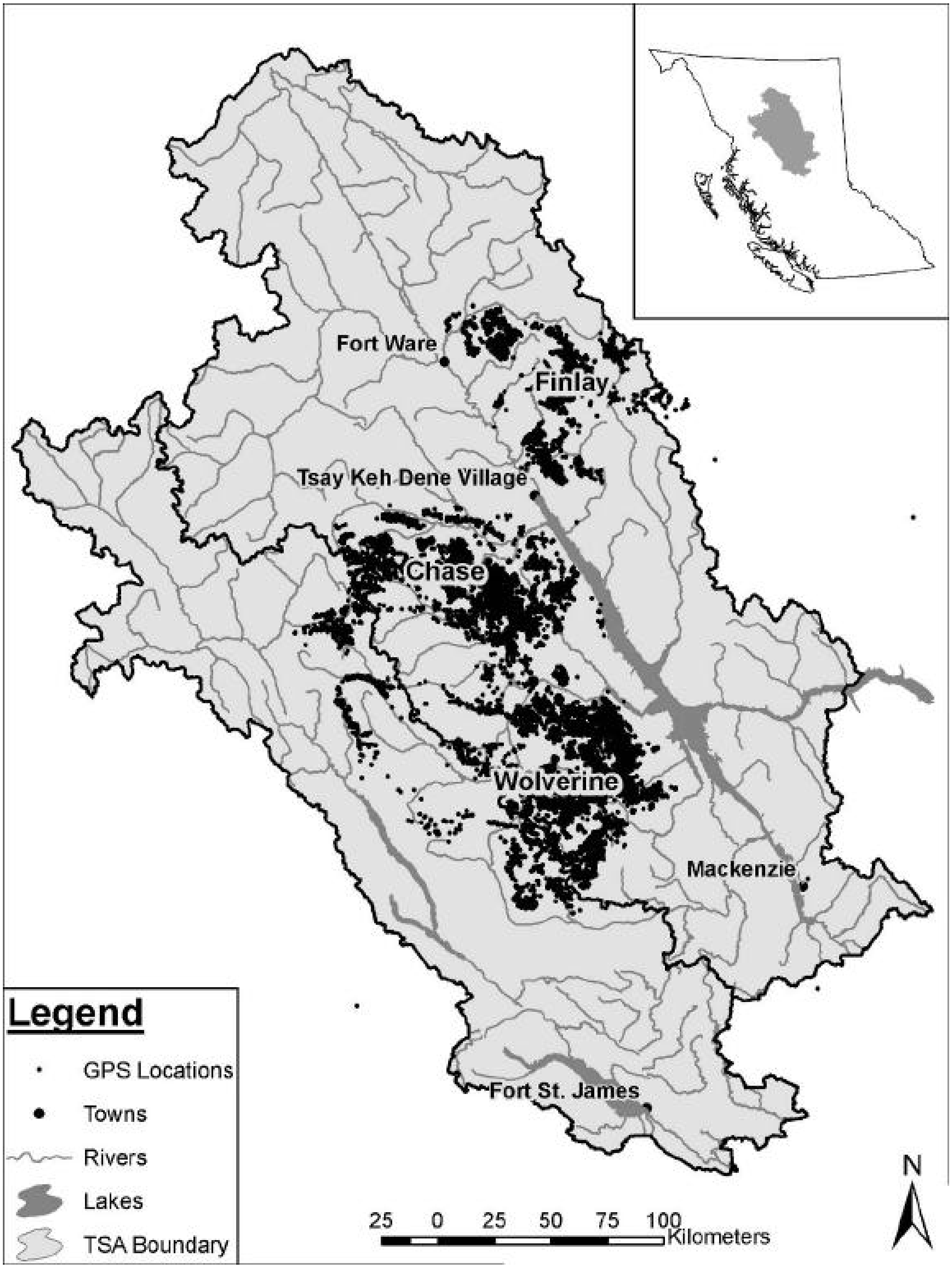
Fort Ware
Finlay
Tsay Keh Dene Village
Chase
Wolverine
Mackenzie
Fort St. James
Legend
GPS Locations
Towns
Rivers
Lakes
TSA Boundary
25 0 25 50 75 100 Kilometers
N

Figure 1

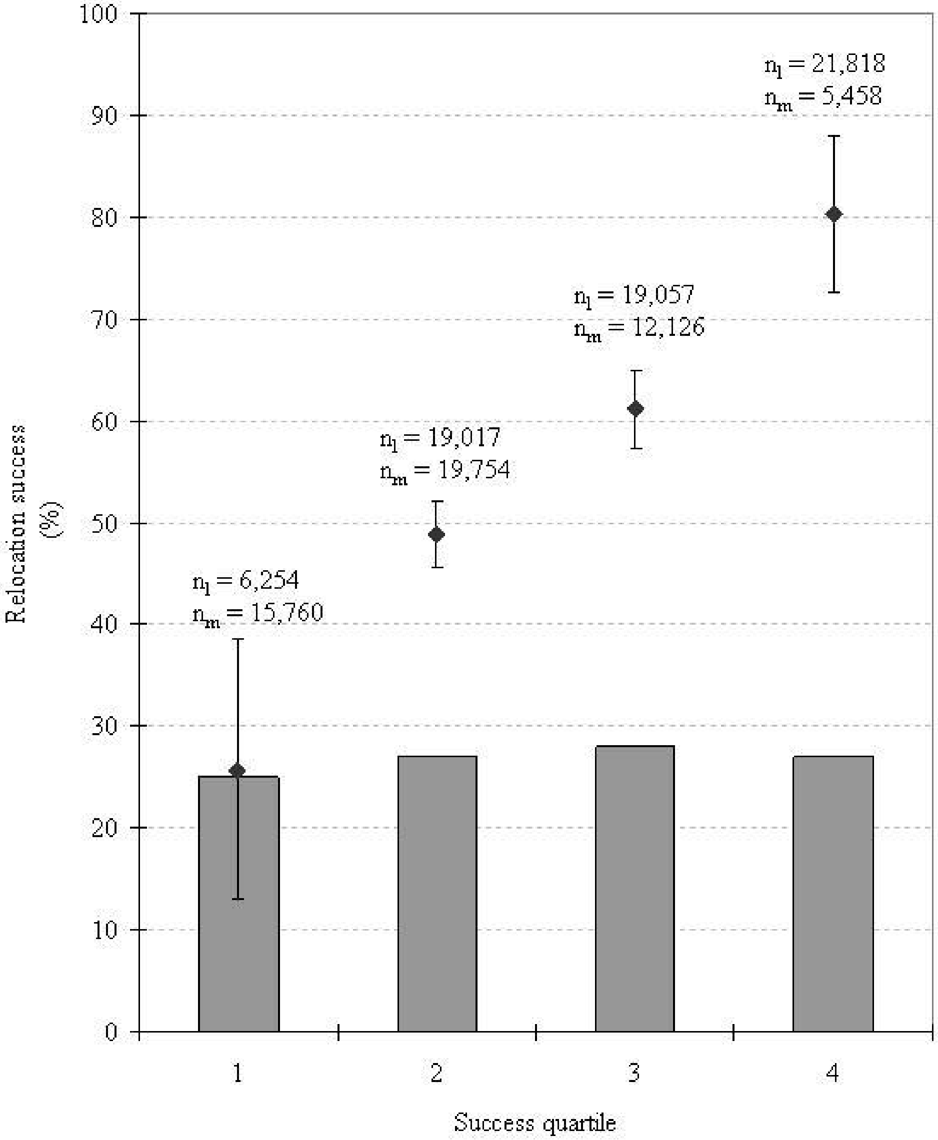
100
90
80
70
60
50
40
30
20
10
0
Relocation success (%)
n_l = 6,254
n_m = 15,760
n_l = 19,017
n_m = 19,754
n_l = 19,057
n_m = 12,126
n_l = 21,818
n_m = 5,458
1
2
3
4
Success quartile

Figure 2

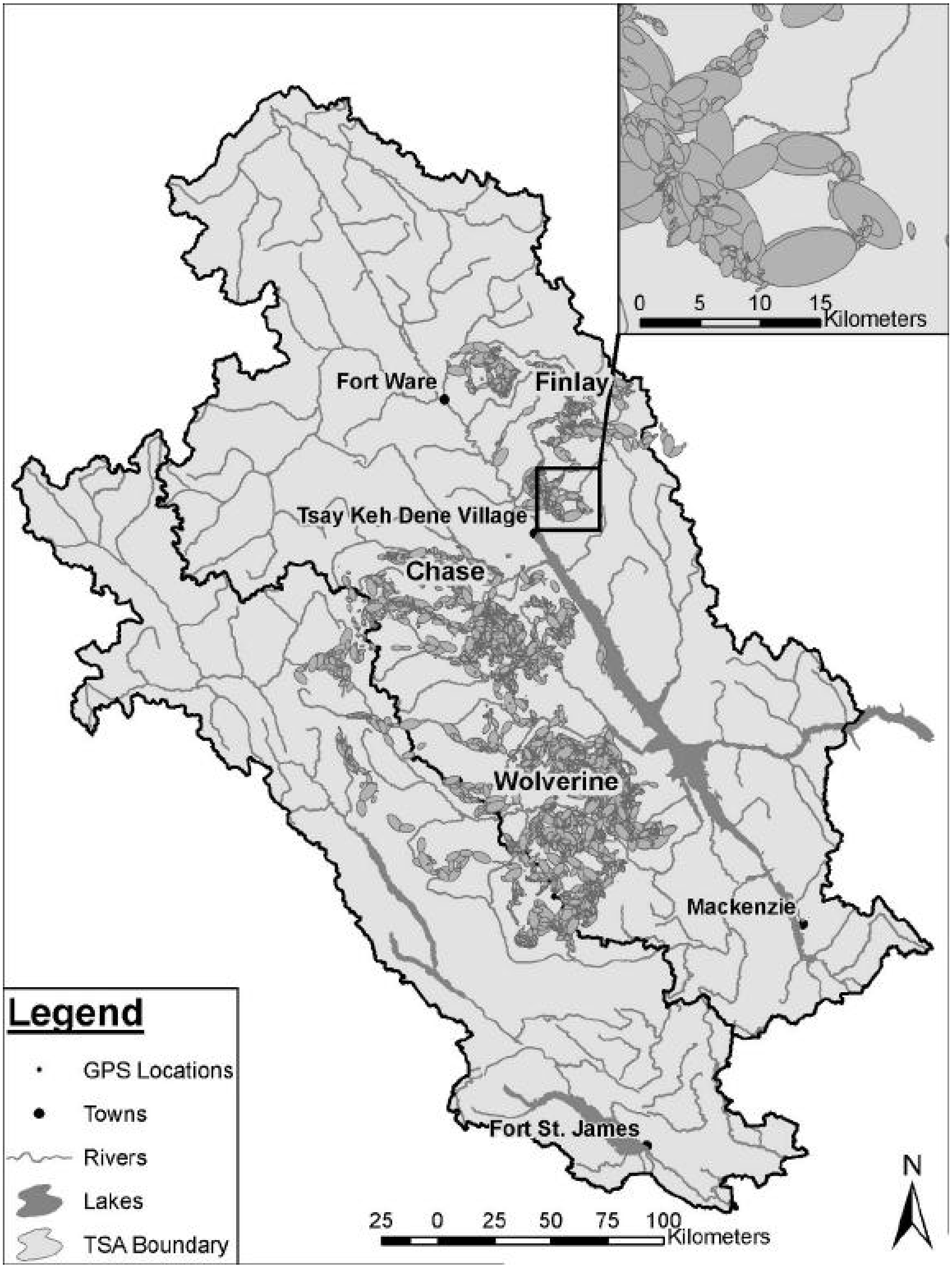
0
5
10
15
Kilometers
Fort Ware
Finlay
Tsay Keh Dene Village
Chase
Wolverine
Mackenzie
Fort St. James
Legend
GPS Locations
Towns
Rivers
Lakes
TSA Boundary
25
0
25
50
75
100
Kilometers
N

Figure 3

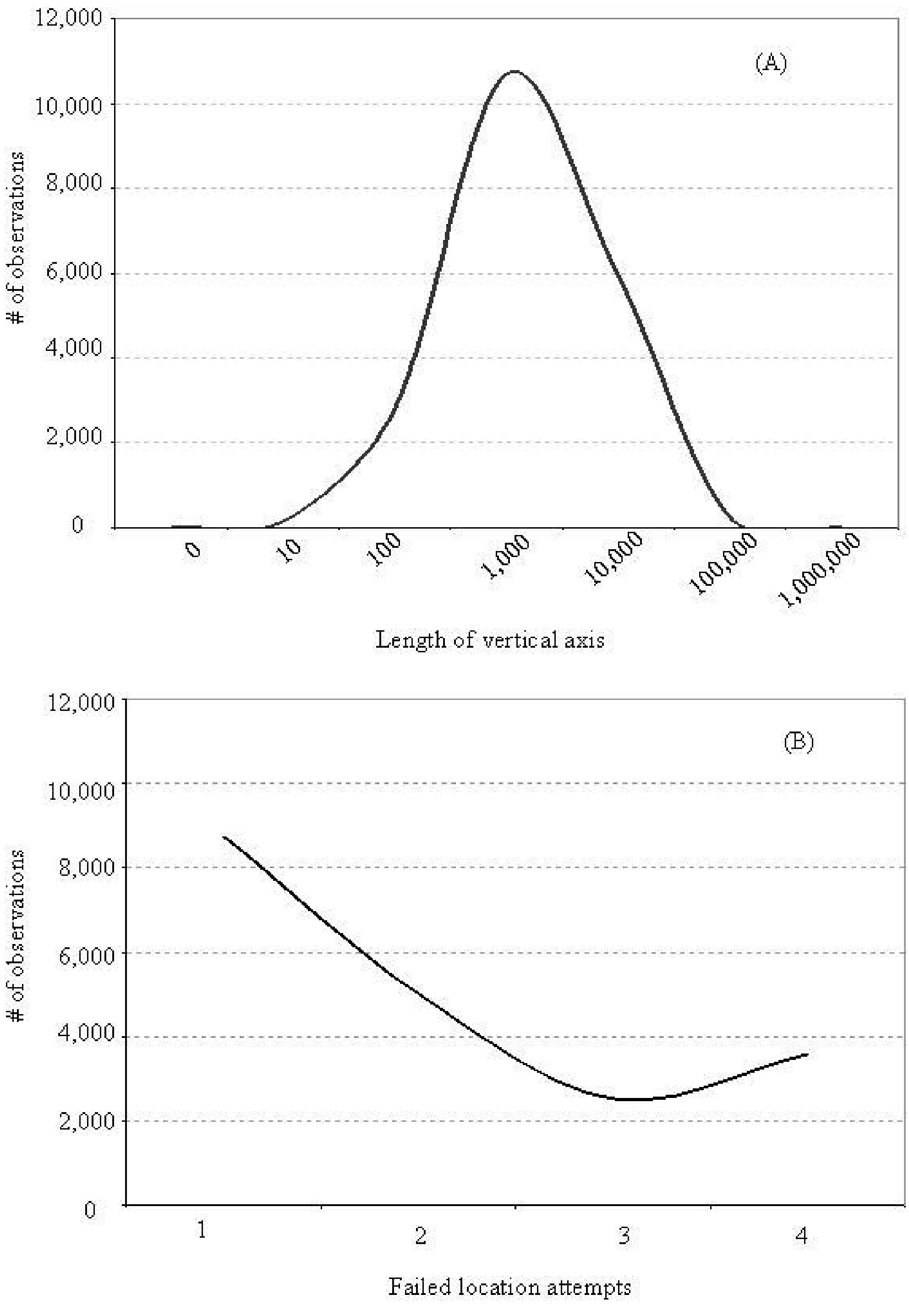
(A)
12,000
10,000
8,000
6,000
4,000
2,000
0
# of observations
0
10
100
1,000
10,000
100,000
1,000,000
Length of vertical axis
(B)
12,000
10,000
8,000
6,000
4,000
2,000
0
# of observations
1
2
3
4
Failed location attempts

Figure 4

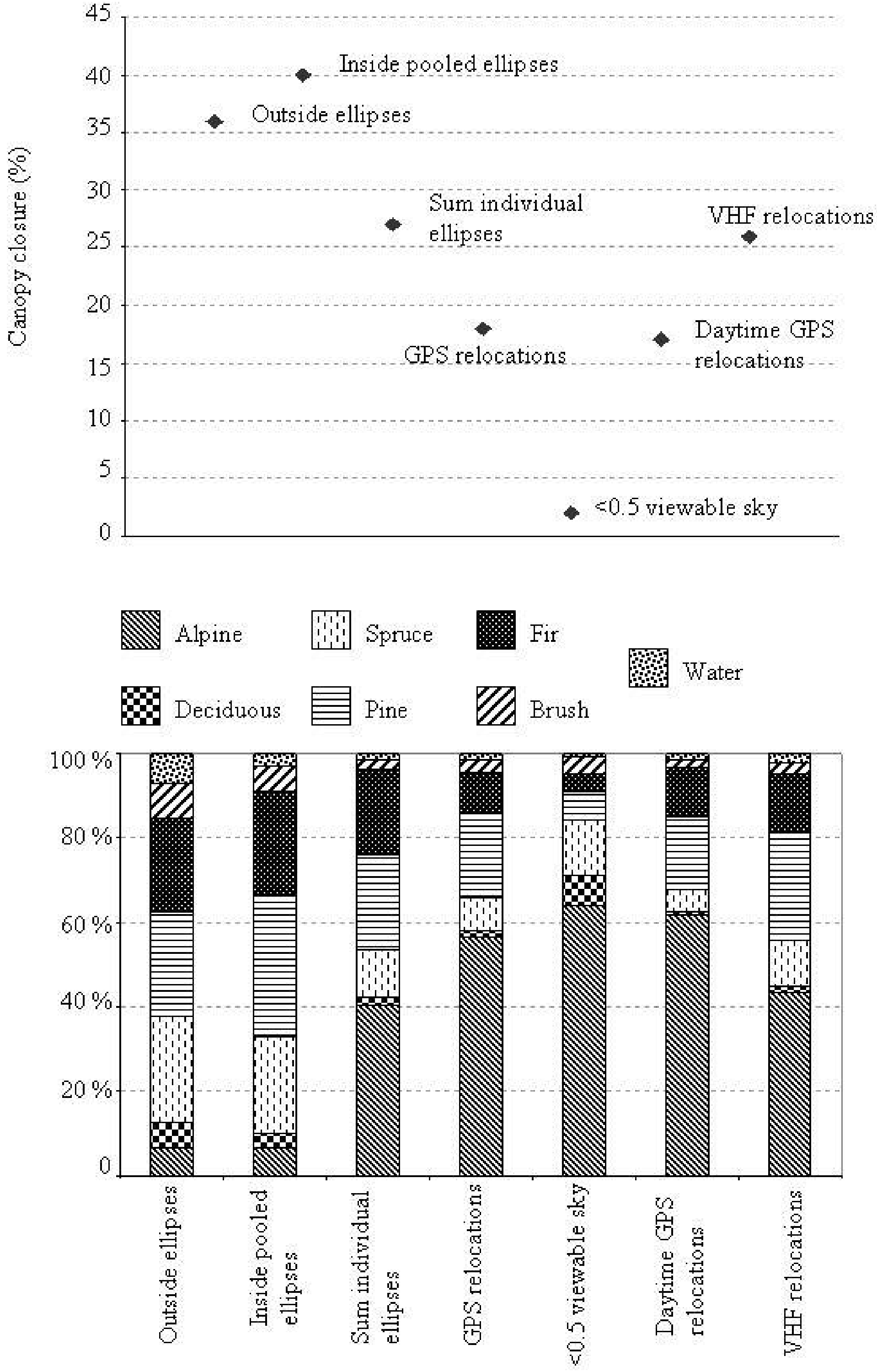
Canopy closure (%)
45
40
35
30
25
20
15
10
5
0
Inside pooled ellipses
Outside ellipses
Sum individual ellipses
VHF relocations
GPS relocations
Daytime GPS relocations
<0.5 viewable sky
Alpine
Spruce
Fir
Water
Deciduous
Pine
Brush
100 %
80 %
60 %
40 %
20 %
0
Outside ellipses
Inside pooled ellipses
Sum individual ellipses
GPS relocations
<0.5 viewable sky
Daytime GPS relocations
VHF relocations

Figure 5