

EFFECTS OF A STATIONARY GPS FIX-RATE BIAS ON HABITAT-SELECTION ANALYSES

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Abstract: Global Positioning System (GPS) radiotelemetry, as a data collection technique, currently suffers from largely unknown fix-rate biases that result in lost data due to environmental factors, which could lead to wrongful research conclusions. Estimates of bias within uncorrected data from free-ranging animals have not been reported. I tested the effects of a known fix-rate bias model on habitat-selection conclusions by correcting habitat-use data for mule deer (*Odocoileus hemionus*) and random data, and comparing outcomes to those of the original uncorrected data. In all cases, corrected and uncorrected data yielded similar habitat-selection conclusions. I attributed this to the model, which accounted for <10% data loss in all cases. Due to this small amount of explained data loss, I suggest that animal behavior (e.g., bedding vs. moving) is a large source of unexplained data loss from free-ranging animals and must be accounted for to best overcome biases in GPS radiotelemetry data.

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Global Positioning System radiotelemetry is gaining popularity in wildlife research because of its obvious advantages of automated tracking of animal movements (Rodgers et al. 1996). However, as a scientific method of data collection, GPS radiotelemetry is arguably still in its infancy due to unknown and unquantified sources of error and bias in collected data, including radiocollar malfunctions, location errors, and fix-rate biases (Rempel et al. 1995, Moen et al. 1996, D'Eon et al. 2002). Of these, fix-rate bias is likely the most problematic; radiocollar malfunctions should decrease as technological advancements in radiocollar construction are made, and location errors have been shown to be relatively small for many wildlife research applications ($\pm 31\text{m}$ 95% of the time; D'Eon et al. 2002).

Fix-rate bias can be defined as the inverse of fix success rate or observation rate, which is the likelihood of obtaining a GPS fix given a multitude of environmental factors including terrain, habitat, and animal behavior. Terrain and habitat, particularly thick forest, have been demonstrated to affect fix success rate, and therefore impose biases on data collected by GPS radiotelemetry systems (Rempel et al. 1995, Dussault et al. 1999, D'Eon et al. 2002). These biases manifest themselves as omissions in data collected by GPS radiotelemetry systems and potentially translate into wrongful research conclusions, especially those concerning habitat selection. As an example: if thick forest

cover imposed a negative bias on fix-rate success (i.e., the likelihood of obtaining a fix is lower in thick forest than in an opening), a GPS radiotelemetry data set from an animal using thick forest heavily would contain a set of locations describing habitat use that was disproportionate to actual use (i.e., openings would be overrepresented, thick forest sites would be underrepresented). If the bias was severe enough, habitat analyses of these data could lead to the conclusion that this animal preferred openings and avoided thickly forested sites, when the opposite was actually true. The problem is no doubt exacerbated by animal movement, which results in much lower fix rates on free-ranging animals than on stationary radiocollars (Merrill et al. 1998, D'Eon et al. 2002) and likely represents additional unknown biases in resulting data (Moen et al. 2001).

To my knowledge, estimates of fix-rate bias within uncorrected data have not been reported (but see Moen et al. 2001). This is probably due to the extreme difficulty of knowing exactly why data are missing from GPS radiotelemetry data. To best overcome the problem of fix-rate bias, researchers using GPS radiotelemetry require knowledge of the unique biases in the data they collect and methods to correct them—knowledge and methods that are currently unknown or underdeveloped (Johnson et al. 1998, Rettie and McLoughlin 1999). I investigated the effects of a known fix-rate bias for stationary GPS radiocollars on habitat-selection analyses in a mountainous, forested landscape in southeast British Columbia, Canada. I used a fix-rate bias model derived from previous work in this

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landscape (D'Eon et al. 2002) to correct data collected on wintering mule deer. I compared the corrected data to uncorrected data to test the effects of this data correction on habitat-selection conclusions. I also used a Monte Carlo approach to test for Type I errors in random data by testing a null hypothesis that biases inserted into random data representing hypothetical animals would have no effect on habitat-selection conclusions.

METHODS

Study Area

I obtained mule deer use and random locations within the Lemon Creek drainage (49°42'N, 117°25'W), a 21,924-ha mountainous, forested landscape within the Selkirk Mountains of south-eastern British Columbia, Canada. The area lies approximately 23 km northwest of Nelson and is described by D'Eon et al. (2002).

Radiotelemetry Data

Deer Capture and Radiocollaring.—Between 18 and 27 February 1999, field crews captured 3 male and 3 female adult mule deer in clover traps baited with alfalfa and salt (Clover 1954, D'Eon et al. 2003). We fitted deer with GPS radiocollars, obtained from Advanced Telemetry Systems (Isanti, Minnesota, USA) that contained Garmin GPS 25LP receivers (Wildlink 1990) and remote release mechanisms. Radiocollar battery life was limited to approximately 1 year. We therefore removed and retrieved radiocollars, fitted them with new batteries, and redeployed them on 6 different mule deer (5 males, 1 female) between 4 and 18 March 2000. We retrieved radiocollars within 1 year of the second deployment. The radiocollars were set to attempt GPS fixes every 4 hr. Fix success rates were determined by calculating the proportion of possible fixes obtained for the time span of a deployed radiocollar.

Habitat-selection Analyses.—I downloaded data from retrieved radiocollars and deleted obvious anomalies and impossible data (D'Eon et al. 2002). Neither real-time nor post-processing differential correction was used because location accuracy of these data was sufficient for most broad-scale applications. I created 100% minimum convex polygon annual home ranges for each deer (White and Garrott 1990). Within each deer home range, I generated a number of random locations equal to the number of radiotelemetry locations for that individual. I considered random locations to represent habitat availability within individual home ranges for analytical purposes (White and Garrott 1990).

I derived habitat attributes for each radiotelemetry and random location using British Columbia forest cover and terrain resource information mapping in digital format. Because of their strong influence on mule deer winter habitat selection in this area (D'Eon 2001), I focused analyses on the following habitat variables: elevation, slope gradient, crown closure, stand age, solar radiation, and habitat type. I extracted elevation, slope, crown closure, and stand age directly from digital map information. Solar radiation was calculated as the amount of direct solar radiation (kW/m³) for each location during winter (Kumar et al. 1997) and was considered a surrogate for aspect because of its high correlation with aspect class ($r = 0.834$). I assigned a habitat type to each location based on forest attributes: 1 = western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) forest, 2 = Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forest, 3 = Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) forest, 4 = forest opening and shrub communities, and 5 = alpine.

I then stratified locations of individual deer into winter and all other seasons combined by inspecting spatial distribution of locations and elevational movements (Apps et al. 2001). Mule deer in this drainage display a consistent migratory pattern from low-elevation winter ranges near the mouth of Lemon Creek to high-elevation summer ranges (similar to mule deer migration patterns described by Garrott et al. 1987). For the purposes of data analyses in my study, I concentrated on winter because of the strong habitat relationships displayed by deer at this time of year in my study area (D'Eon 2001). I identified winter locations based on an obvious localized congregation of locations at the lowest elevation in the annual migration, usually occurring between February and April.

Because I had many locations for a few individuals, I considered individual mule deer the experimental unit. I calculated mean values for individual deer and corresponding random locations, rather than pooling all locations, as suggested by White and Garrott (1990) and Aebischer et al. (1993). Doing so avoided both pseudoreplication and inflated sample-size problems (Hurlbert 1984). I then performed habitat-selection analyses in 2 ways. For continuous data, I used *t*-tests with Bonferroni multiple-test corrections (Zar 1984, SPSS 1998) to compare mean deer use to the available mean (n = number of deer, α = 0.05). For analysis among habitat types, I tested selection and avoidance of habitat types by each

deer by comparing the proportional use of each habitat type to its corresponding availability and calculating the associated Bonferroni confidence intervals ($\alpha = 0.1$, $k = 5$; Neu et al. 1974, White and Garrott 1990). In this way, I compared habitat used by individual mule deer in winter to available habitat within their corresponding annual home range (design 3 from Thomas and Taylor 1990).

Simulated Data

I constructed 30 sets of random location data to simulate 30 hypothetical animals using the landscape in a random fashion. Locations were selected within the entire study area (D'Eon et al. 2002). To investigate the influence of the number of locations obtained per animal in GPS radiotelemetry, I constructed 10 sets each of 100, 1,000, and 10,000 random locations. I then derived habitat data for each location similar to radiotelemetry data.

Data Correction and Bias Effect

Radiotelemetry Data.—To investigate the effect of GPS fix-rate bias on radiotelemetry data in my study area, I corrected individual deer-use data by inserting data representing assumed missing data as a result of GPS fix-rate bias. I did this by classifying all locations into 1 of 9 bias classes with an associated bias rate ranging from 89.99 to 100.00% (i.e., a bias rate of 89.99% means 89.99% of fix attempts are recorded, or 10.01% of locations are missing). Bias rates were calculated from D'Eon et al.'s (2002) fix-rate bias model for this study area:

$$FR = 0.098 \times AS - 0.076 \times CC + 95.363,$$

where FR = fix rate, AS = available sky (see D'Eon et al. 2002), and CC = crown closure. I assigned bias classes using a 3-cell \times 3-cell matrix with 3 AS classes (0–30%, 40–70%, 80–100%) along the x-axis and 3 similar CC classes along the y-axis. I then calculated the number of assumed missing locations in each bias class by multiplying the bias rate by the number of locations in each class. I added data by randomly selecting a number of locations within each bias class equal to the number of calculated missing locations. I then duplicated selected locations, along with associated habitat data, and added them to the data set. To correct corresponding available data sets for each deer, I added a number of random locations to the available data equal to the number of additional deer-use locations. In this way, I generated corrected use and random data for each deer that compensated for the predicted GPS fix-rate bias from D'Eon et al. (2002). To investigate

the effect of the bias on conclusions about habitat selection, I then performed habitat analyses on corrected data similar to those described for uncorrected data and compared the results.

Simulated Data.—I used random data to test the null hypothesis that 1 set of random locations will not differ from another set of random locations that have been corrected for GPS fix-rate bias. If the bias affects habitat-selection conclusions, then I predicted differences should occur between corrected and uncorrected random data, assuming that 2 sets of uncorrected random data have similar data distributions. To test this, I assumed that the data contained all locations of a hypothetical animal, and I thus included locations that would not be recorded given a fix-rate bias. To correct for the bias, I again assigned a bias class to each location from D'Eon et al.'s (2002) fix-rate bias model. I then randomly removed locations from each bias class as predicted by the model.

To investigate the bias effect on habitat-selection conclusions, I repeated habitat-selection analyses similar to those performed on radiotelemetry data. For continuous variables, I compared the means from 5 uncorrected data sets to the means from 5 corrected data sets, within each of the 3 groups of data (100, 1,000, 10,000 locations). For habitat types, I first paired each uncorrected data set with a corrected data set of the same number of locations (100, 1,000, 10,000). I then tested a hypothetical selection and avoidance of habitat types by comparing the proportional distribution of habitat types to the corresponding corrected distribution and calculating the associated Bonferroni confidence intervals, similar to analyses of radiotelemetry data. In this way, any differences between corrected and uncorrected data could be attributed to the effect of the GPS fix-rate bias.

Prior to correcting random data sets for fix-rate bias, I tested all random data sets for similarity (i.e., to ensure no pre-existing differences were in the data). I performed habitat-selection analyses with the prediction that no significant differences should occur in uncorrected random data.

RESULTS

Radiotelemetry Data

Of the 12 radiocollars deployed, 5 malfunctioned and provided unusable data. The remaining 7 collars (4 males, 3 females) had fix success rates ranging from 27 to 63% ($\bar{x} = 50$, SE = 4.6). The number of recorded locations within winter ranged from 75 to 409 ($\bar{x} = 186$, SE = 51.3).

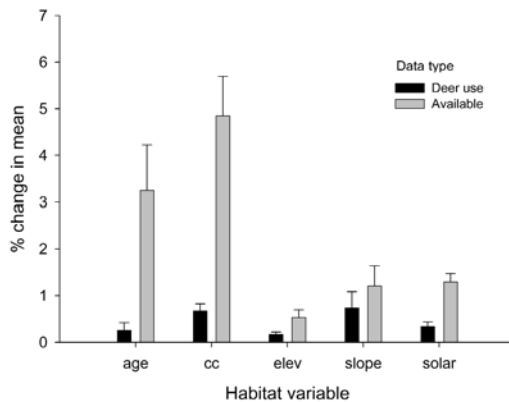


Fig. 1. Change in the mean (± 1 SE) among 5 habitat variables from uncorrected to corrected data by inserting a Global Positioning System (GPS) fix-rate bias to deer use and random data for 7 mule deer in winter in Lemon Creek, British Columbia, Canada. Habitat data were derived from digital mapping information for each location, where age = forest stand age, cc = crown closure, elev = elevation, slope = slope gradient, and solar = direct solar radiation. Available habitat was derived from random locations within annual home ranges.

Habitat-selection analyses of uncorrected data resulted in the following: 6 of 7 deer used lower elevations, and 1 used elevations similar to available (combined \bar{x} : use = 945 m, available = 1,333 m; $t = 4.981$, $df = 12$, $P < 0.001$); 4 of 7 deer used higher slopes, and 3 used slopes similar to available (combined \bar{x} : use = 57%, available = 48%; $t = -2.746$, $df = 12$, $P = 0.018$); 5 of 7 deer used older stands, and 2 used stand ages similar to available (combined \bar{x} : use = 116 yr, available = 82 yr; $t = -2.301$, $df = 12$, $P < 0.040$); 4 of 7 deer used higher crown closures, 1 used lower crown closures, and 2 used similar crown closures to available (combined \bar{x} : use = 41.8%, available = 25.9%; $t = -1.755$, $df = 12$, $P = 0.105$); 4 of 7 deer used areas of higher direct solar radiation, 1 used lower solar radiation, and 2 used areas of similar solar radiation to available (combined \bar{x} : use = 102,521 kW/m², available = 82,441 kW/m²; $t = -2.082$, $df = 12$, $P = 0.059$).

Among habitat types using uncorrected data, all 7 deer preferred habitat type 3 and avoided type 2; 5 of 7 deer avoided type 1, and 2 deer used type 1 in proportion to availability; 5 of 7 deer avoided type 4, 1 deer preferred type 4, and 1 deer used type 4 in proportion to availability; 5 of 7 deer avoided type 5, and 2 deer used type 5 in proportion to availability.

Data corrections resulted in the addition of between 5 and 25 locations, representing a range in increased data from 4.8 to 7.7% ($\bar{x} = 6.2$, $SE = 0.38$, $n = 7$). Mean differences between uncorrect-

ed and corrected data ranged from 0.17 to 0.74% for deer use, and 0.53 to 4.85% for availability data (Fig. 1). Changes in individual deer use of habitat types between uncorrected and corrected data were <5% of uncorrected data in all cases.

Habitat-selection analyses on corrected data yielded unchanged conclusions between uncorrected and corrected data. All deer displayed similar trends (significantly higher or lower than available mean) with continuous variables, and all habitat types were preferred, avoided, or used in proportion to availability similar to uncorrected data.

Simulated Data

In 3 cases, pre-existing differences were detected in random data (i.e., significantly different mean between 1 data set and an associated data set). I replaced these data sets with other random data that I then tested for similarity. I detected no significant differences among means of continuous variables (all $P > 0.05$) or habitat-type distributions (all Bonferroni CIs nonsignificant) in habitat-selection analyses of ensuing uncorrected random data.

Data corrections resulted in the deletion of 6.0–7.0% of locations for data sets of 100 locations ($\bar{x} = 6.8$, $SE = 0.42$, $n = 10$); 4.6–4.8% ($\bar{x} = 4.7$, $SE = 0.03$, $n = 10$) for data sets of 1,000; and 4.2–4.3% ($\bar{x} = 4.3$, $SE = 0.005$, $n = 10$) for data sets of 10,000. I detected no differences among means of continuous data between corrected and uncorrected data (all $t < 2.292$, all $P > 0.255$). Mean differences between corrected and uncorrected data were highest for data sets of 100 locations and least for data sets of 10,000 locations. Differences varied from 9.18% of the uncorrected mean for stand age within the 100-location data to 0.69% for elevation within the 10,000-location data (Fig. 2).

Among habitat types, I detected no avoidance or preference for any habitat types, with the exception of 1 corrected 10,000-location data set displaying a preference for habitat type 4 (corrected use = 18.86%, uncorrected = 19.89%). Differences between corrected and uncorrected habitat type use were largest in the 100-location data and least in the 10,000-location data (range = 0–13%).

DISCUSSION

The number of locations used in simulated data had no effect on habitat-selection conclusions between uncorrected and corrected data in my study, despite the somewhat predictable outcome of smaller differences and variances between means of larger paired data sets. But because data were not pooled among individual data sets,

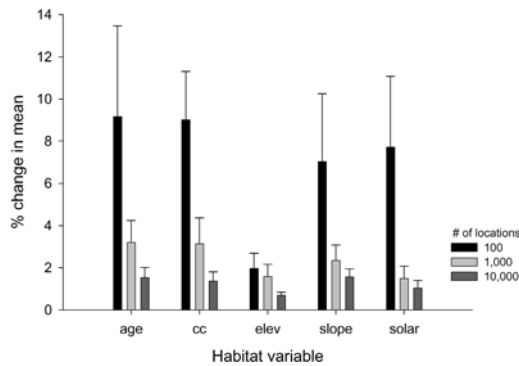


Fig. 2. Change in the mean (± 1 SE) between sets of uncorrected data and data corrected for a Global Positioning System (GPS) fix-rate bias in Lemon Creek, British Columbia, Canada. Ten sets each of 100, 1,000, and 10,000 random locations were generated. Habitat data were derived from digital mapping information for each location, where age = forest stand age, cc = crown closure, elev = elevation, slope = slope gradient, and solar = direct solar radiation. Five sets within each group were corrected and compared to the corresponding 5 uncorrected data sets.

sample sizes remained the same (n = number of animals or data sets representing hypothetical animals) for habitat-selection tests regardless of the number of locations in a data set.

The fix-rate bias considered in my study resulted in small changes to mean values of continuous habitat variables and proportional use of habitat types between uncorrected and corrected data. The changes were not large enough to change conclusions about habitat-selection analyses. Issues of statistical power did not likely cause the lack of detectable differences, since power of these data was demonstrated to be adequate in a similar habitat analyses (D'Eon 2002). Rather, the lack of detectable difference most likely was due to the relatively small amounts of data additions (in the case of deer-use data) or removals (in the case of simulated data), which in all cases were <10%. My results are consistent with J. Friar (University of Alberta, unpublished data) who found similar results at this level of data removal.

Data removals and additions of this magnitude are not surprising given the model used in my study. The model accounts for data losses that ranged from zero to about 20% on individual radiocollars, depending on environmental conditions (D'Eon et al. 2002). These rates, however, reflect stationary radiocollars placed in an optimal position for satellite acquisition. Since fix success rates generally are much lower than 80% on free-ranging animals (e.g., Merrill et al. 1998,

Bowman et al. 2000) and can be as low as 27% (1 case in my study), models derived from stationary radiocollars do not account for most missing data. To assume that the remaining data losses are randomly distributed and therefore unbiased would likely be wrong. Rather, I suggest that much of the remaining data loss could be attributed to animal activity that will vary with terrain, species, and perhaps even individuals. Indeed, Bowman et al. (2000) found 19% fewer locations for bed deer than moving deer. In turn, if different activities occur in different habitats, which is likely the case in most species, animal activity imposes additional biases in GPS radiotelemetry data sets.

My results illustrate the magnitude of biases found from GPS radiocollars deployed on mule deer in this particular landscape. While I believe these results are useful for comparison with other future studies and the methods I explored for correcting these data are useful elsewhere, I caution against direct extrapolation of these data into other situations. Due to the unique nature of bias resulting from unique combinations of vegetation, terrain, and individual animal movement, determining the relative magnitude of my results will be difficult, if not impossible, until more studies of this nature are performed.

MANAGEMENT IMPLICATIONS

In my study, I demonstrated that biases accounting for <10% data loss did not change habitat-selection conclusions. On this basis, I suggest that GPS radiotelemetry data sets with <10% data loss can be safely analyzed without the need for correction. However, I caution against simply scaling a bias model based on stationary radiocollar data to account for additional data loss (i.e., scaling the model equal to the amount of data loss without changing the slope of the model). While intuitively appealing, this ignores that most data loss may be attributed to biases related to animal activity and therefore does not reflect true biases in the data. The challenge for future work is therefore clear. To best account for fix-rate biases in GPS radiotelemetry data, biases attributable to animal activity in free-ranging environments must be explored—in addition to biases attributable to terrain and habitat variables—and perhaps form the emphasis, if not the focus, of future research on this topic.

A first step in this direction is quantifying the bias associated with the position and orientation of the GPS antenna on radiocollars. Conventional wisdom dictates that a vertically oriented radiocollar

(i.e., GPS antenna is flat and directly facing the sky) will have the most success in obtaining GPS fixes (due to best satellite acquisition rate), and therefore the lowest bias (if any). However, the degree to which this bias increases with angle away from vertical (and lower satellite acquisition rate) and in combination with compass direction is unknown.

Radiocollar position and orientation are critical factors related to animal activity, since activity and movement of free-ranging animals determines the position and orientation (and therefore bias) on deployed radiocollars in wildlife studies. Bias related to animal activity will no doubt vary among species and perhaps even individuals (e.g., Moen et al. 2001). For example, a radiomarked animal that often digs while foraging (e.g., grizzly bear [*Ursus horribilis*]) may have a different fix-rate success (due to a different radiocollar position) than an animal that keeps its head more horizontal while foraging (e.g., moose [*Alces alces*]). These issues present a second challenge and requirement for studies involving observed radiomarked animals, where specific movement and behavioral observations must be directly linked to fix-rate success.

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LITERATURE CITED

- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radiotracking data. *Ecology* 74:1313–1325.
- APPS, C. D., B. N. MCLELLAN, T. A. KINLEY, AND J. P. FLAA. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management* 65:65–77.
- 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.
- CLOVER, M. R. 1954. A portable deer trap and catch-net. *California Fish and Game* 40:367–373.
- D'EON, R. G. 2001. Deer winter distribution and habitat use using snow-track surveys. *Wildlife Society Bulletin* 29:879–887.
- . 2002. Landscape spatial patterns and forest fragmentation in managed forests in southeast British Columbia: perceptions, measurements, and scale. Ph.D. dissertation, University of British Columbia, Vancouver, British Columbia, Canada.
- , G. PAVAN, AND P. LINDGREN. 2003. A small drop-net versus clover traps for capturing mule deer in southeast British Columbia. *Northwest Science* 77:178–181.
- , R. SERROUYA, G. SMITH, AND C. O. KOCHANNY. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.
- DUSSAULT, C., R. COURTOIS, J.-P. OUELLET, AND J. HUOT. 1999. Evaluation of a GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin* 27:965–972.
- GARROTT, R. A., G. C. WHITE, R. M. BARTMANN, L. H. CARPENTER, AND A. W. ALLDREDGE. 1987. Movements of female mule deer in northwest Colorado. *Journal of Wildlife Management* 51:634–643.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- JOHNSON, B. K., A. A. AGER, S. L. FINDHOLT, M. J. WISDOM, D. B. MARX, L. W. KERN, AND L. D. BRYANT. 1998. Mitigating spatial differences in observation rate of automated telemetry systems. *Journal of Wildlife Management* 62:958–967.
- KUMAR, L., A. K. SKIDMORE, AND E. KNOWLES. 1997. Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographic Information Science* 11:475–497.
- MERRILL, S. B., L. G. ADAMS, M. E. NELSON, AND L. D. MECH. 1998. Testing releasable GPS radiocollars on wolves and white-tailed deer. *Wildlife Society Bulletin* 26:830–835.
- MOEN, R., J. PASTOR, AND Y. COHEN. 2001. Effects of animal activity on GPS telemetry location attempts. *Alces* 37:207–216.
- , ———, ———, AND C. C. SCHWARTZ. 1996. Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* 60:659–668.
- NEU, C. W., C. R. BYERS, J. M. PEEK, AND V. BOY. 1974. A technique for analysis for utilization-availability data. *Journal of Wildlife Management* 38:541–545.
- 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.
- RETTIE, W. J., AND P. D. MCLOUGHLIN. 1999. Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology* 77:1175–1184.
- RODGERS, A. R., R. S. REMPEL, AND K. F. ABRAHAM. 1996. A GPS-based telemetry system. *Wildlife Society Bulletin* 24:559–566.
- SPSS 1998. SYSTAT 8.0 for Windows. SPSS, Chicago, Illinois, USA.
- THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322–330.
- WILDLINK. 1990. Wildlink data acquisition system. Reference manual. Advanced Telemetry Systems, Isanti, Minnesota, USA.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

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