The effects of sampling regime on the analysis of movements of over-wintering female caribou in east-central Alaska

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Abstract: Global Positioning System (GPS) technology enables research of animal movements at finer levels of spatial and temporal resolution than previous methodologies allowed. A feature of GPS collar technology is the capability to program the dates of (sample period) and time between successive relocations (sample interval). I investigated the effects of sampling regime, the combination of sample period and interval, on analyzing movements of female caribou (*Rangifer tarandus granti*) in the Fortymile Caribou Herd as a case study. Based on hourly relocations throughout the winter, caribou moved 260 meters per hour or 6.2 kilometers per day. Sample period influenced estimates of movement rates, as I detected both diurnal and seasonal variability. Caribou movement rates during daylight and twilight hours were significantly greater than during the nighttime. Movement rates were greater during twilight hours than during daylight, but only slightly. Mid-winter and late winter movement rates were virtually the same, however, both were significantly less than during early winter. As sample interval increased, estimates of movement rates decreased substantially. Estimates based on 2-hour sample intervals were 14% less than those based on one-hour sample intervals, with estimates declining to 65% of the one-hour sample interval estimates at 167-hour (weekly) intervals. Estimates of home range were also affected by using different sampling intervals, however, kernel and MCP estimates responded antithetically to increasing sample interval. Researchers need to be aware that decisions about sampling regime can affect the estimates of ecological parameters that are based on relocations, such as movement rate, habitat selection, and home range.

Key words: Alaska, *GPS*, home range, movement rates, Nelchina, *Rangifer tarandus granti.*

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Introduction

Global Positioning System (GPS) radiotelemetry holds vast potential for increasing our knowledge of spatially explicit, ecological parameters such as movement rates, habitat use, and home range characteristics (Moen *et al.*, 1996). Compared to conventional VHF or satellite telemetry, GPS technology provides distinct advantages, such as automated scheduling of data acquisition at short intervals and improved locational accuracy to within a few meters (Rempel *et al.*, 1995). However, positional accuracy around 30 m is more typical (D'Eon *et al.*, 2002; this study). GPS collars are capable of collecting thousands of locations, regardless of daylight or weather conditions, and at virtually any sample interval (time between successive relocations). In order to take full advantage of this technological advance and meet study objectives, researchers face decisions about balancing sample period (the duration of the study) and sample interval because of finite battery life, collar weight, storage/transmission capacity, and frequency of animal recapture. This is especially true on smaller animals that cannot carry larger battery packs. Standard GPS collars are capable of lasting over long sample periods but not nearly as long as traditional VHF collars. Battery life is decreased the more time the GPS unit is on while gathering locations. Hence, decreasing the sample interval to collect more locations per day will also decrease the maximum sample period.

Movement rates of free-ranging wildlife are of interest because they provide insights into seasonal migration behavior and patterns of home range use (Stuart-Smith *et al.*, 1997; Schaeffer & Luttich, 1998; Poole *et al.*, 2000; Rettie & Messier, 2001), are necessary for estimating energy budgets (Fancy & White, 1987; Johnson *et al.*, 2002b) and modeling animal movements (Bergman *et al.*, 2000), and are integral to evaluating patterns of resource use (Arthur *et al.*, 1996; Hjermann, 2000; Johnson *et al.*, 2002b,c; Joly *et al.*, 2003). Prior to GPS technology, movement rates were often determined using conventional or satellite telemetry data where sample intervals were commonly > 1 day (Fancy *et al.*, 1989; Schaeffer & Luttich, 1998; Bergman *et al.*, 2000; Rettie & Messier, 2001). GPS systems can be programmed to acquire locations every hour or even more frequently (Nelson *et al.*, 2004), though only for a short sample period – due to increased drain on the battery pack.

My goal was to evaluate the influences of sampling regime on the analysis of movement and elucidate variation in results. I evaluated how diurnal and seasonal variability, aspects of sample period, and sample interval, the lengthening times between successive locations, affected the estimation of movement rates and home range of female caribou (*Rangifer tarandus granti*) in east-central Alaska. Caribou are an ideal species to test the effects of sampling regime on the analysis of movements because they are highly mobile and alternate between migratory and relatively sedentary periods.

Material and methods

Study area

During this study, the Fortymile Caribou Herd consisted of approximately 26 000 individuals (Boertje & Gardner, 1997) that ranged over 43 000 km^2 in east-central Alaska (63°30'–65°45'N; 141°–146°W). The area, generally bounded by the Steese Highway to the west, the United States – Canada border to the east, the Yukon River to the north and the Tanana River to the south (Valkenburg *et al.*, 1994), is a mosaic of boreal forest, muskegs, shrub and alpine communities. Elevation ranges 300 to 2000 m above sea level. Open black spruce (*Picea mariana*) forest dominates the lower elevations, giving way to shrub and eventually alpine communities at higher elevations. The continental climate typical of interior Alaska creates extreme weather conditions both in the winter and summer months. Temperatures can range from –50 °C to 30 °C. Snow depth, which peaked in April, was well below normal levels throughout the winter of 1998–1999 (NRCS, 1999) – nearing record lows. Additional details about the range of the Fortymile Caribou Herd can be found elsewhere (Murie, 1935; Skoog, 1956; Boertje *et al.*, 1988).

Data collection

I deployed 1.7 kg GPS collars between 22–26 October 1998 on three adult caribou cows. The collars were manufacture by Advanced Telemetry Systems (Isanti, MN, USA) with Garmin GPS 25LP receivers. I programmed the collars to collect and store locations at one-hour intervals for approximately 6 months. I employed individual caribou as the basic sampling unit. Positional data were downloaded from the collars and imported into a Geographic Information System (GIS). Selective Availability (SA), the intentional degradation of GPS signals, was active during the study. Positional error can be reduced to approximately five m when GPS data is differentially corrected under optimal conditions (Moen *et al.*, 1996; Rempel & Rodgers, 1997; Dussault *et al.*, 2001); unfortunately the manufacturer was unable to develop software to perform these calculations, so SA-induced errors were not corrected.

To address the issue of positional error, I stationed an additional collar at a known location to quantify locational error caused by SA. I defined, for this study, the average location error as the average distance between the recorded and actual (as identified by a military style GPS unit – a Rockwell Precise Lightweight GPS Receiver - able to remove the effects of SA) position of the stationary collar (Rempel *et al.*, 1995). To assess SA-related error on movement rate estimates, I duplicated the locations from the stationary collar, but shifted the points by the mean hourly movement rate (260 m; see Results). In essence, I created a second, identical dataset to the stationary collar but moved each location of the second dataset by 260 m away from the original dataset. I then determined the average distance between sequential true and shifted locations, simulating a movement of average distance, and subtracted 260 m (the distance the two points would be separated by if there were no positional error) to calculate what I define as the index of error. I hypothesize that the random errors induced by SA (Rodgers *et al.*, 1996) have a natural tendency to cancel themselves out when analyzing movement rates.

Movement patterns

I used distances between successive locations over 1-hour intervals, as determined with the ArcView (ESRI, 1998) extension Animal Movement (Hooge & Eichenlaub, 1998), to analyze diurnal and seasonal variation in movement rates. The rates were determined using the individual caribou as the basic sampling unit and then the rates were averaged. I assigned caribou movements to different daylight categories (daytime, nighttime, or twilight) according to sunrise and sunset times for that day as the amount of daylight can vary by more than 10 hours within the study period at this latitude. Twilight was defined as the hour before and after sunrise and sunset (for four total hours of twilight per day). The study period was subjectively categorized into three seasons; early winter (late October, November, and December), mid-winter (January and February), and late winter (March and early April). I calculated the 95% confidence intervals (Gerard *et al.,* 1998; Joly, 2000) to evaluate differences in movement rates among daylight categories and seasons.

I sub-sampled the data at 2, 3, 5, 7, 23, and 167-hour intervals to determine if movement rates differed with sampling interval. I chose these intervals to highlight the potential hazards of sampling at regular intervals. If sampling is conducted at regular intervals, a multiple of some cycle in the animal's behavior should not be employed (Swihart & Slade, 1985b; Aebischer *et al.*, 1993) because certain activities will be over-sampled and others under-sampled. Sampling intervals of every 4, 6, 12, and 16 hours, for example, divide evenly into multiples of 24, thereby creating periods of the day that are never sampled. Intervals of every 1, 5, 7, 11, 13, 15, 17, 19, and 23 hours progress through every hour of the day before repeating. These sampling intervals will reduce the likelihood of cycle–dependent biases. Locations that did not span the sampling interval exactly were omitted from the analysis. I then divided these distances by the sampling interval to estimate hourly movement rates. I calculated the 95% confidence intervals for the movement rates for each of the different sampling intervals.

I employed linear regression to evaluate the relationship between daily movement estimates based on the sum of 24 one-hour movement intervals those based on a 24-hour sample interval. Bias between 24-hour interval and summed hourly interval movement rates was determined by subtracting the fitted value (based on the regression equation) from the summed hourly movement, and then dividing by the summed hourly movement.

To show that sampling regime can also affect ecological parameters, other than movement rates, I analyzed home range estimates. Fixed kernels, created with the Animal Movement extension (Hooge & Eichenlaub, 1998), were used to estimate the 95% and 50% utilization distributions [UD] for each animal at sampling intervals of 1, 7, 24, 168 (once a week), and 720 (once a month) hours. Home ranges were also estimated using Minimum Convex Polygons (MCP) for each of the sampling intervals. An estimate of relative size was calculated by dividing the UD and MCP area estimates for each sub-sampled data set by the area estimate from the entire hourly dataset, employing the respective techniques. The results reflect averages of the 3 cows.

Results

The three collars retrieved from caribou cows successfully acquired location fixes 11 575 times out of 11 618 possible fixes (99.6%, range 99.5 to 99.7%), while the stationary collar deployed to determine positional accuracy successfully acquired locations at a lower rate (3580/3739; 95.7%). The average location error was 33 m (range: 0 to 265 m), which was very similar to the value of 31 m reported by D'Eon *et al.* (2002). The index of error in hourly movement rates averaged only 5 m (range: –165 to 219 m), or < 2% of the mean hourly movement rate.

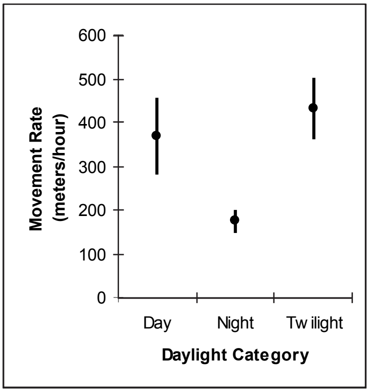

Fig. 1. Average movement rates (meters/hour [m/h]) and 95% confidence intervals of female caribou by daylight categories and season, based on a 1-hour sampling interval, during the winter of 1998–1999, Fortymile Caribou Herd, Alaska.

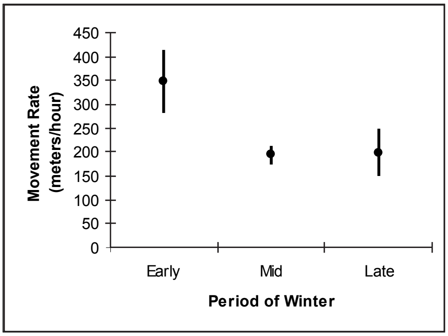

Fig. 2. Average movement rates (m/h) and 95% confidence intervals of female caribou for different periods of the winter, 1998–1999, Fortymile Caribou Herd, Alaska.

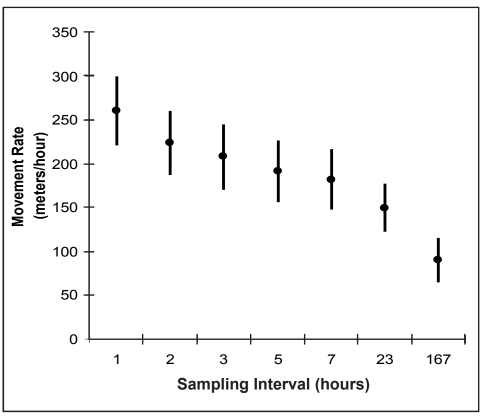

Fig. 3. Average movement rates (m/h) and 95% confidence intervals of female caribou based on different sampling intervals, winter 1998–1999, Fortymile Caribou Herd, Alaska.

The average hourly movement rate for the 3 caribou over the entire winter was 260 m/h (range: 240 to 298 m/h, s = 33), or 6.2 km/day. Movement rates for caribou varied with daylight categories and season. Caribou had significantly greater average rates of movement during the day (368 m/h; range 299 to 445 m/h) than at night (174 m/h; range 155 to 195 m/h), but twilight movement rates (433 m/h; range 394 to 500 m/h) were greater than either of these movement rates (Fig. 1). The caribou had significantly greater hourly movement rates during early winter (349 m/h; range 291 to 402 m/h) compared to the other seasons (Fig. 2). Mid–winter movement rates (194 m/h; range 179 to 209 m/h) were not significantly different from those of late winter (199 m/h; range 153 to 232 m/h; Fig. 2).

Estimates of mean hourly movement rates declined dramatically as sample interval increased (Fig. 3). Estimated daily movements (based on 24-hour intervals) were correlated with daily movements estimated as the sum of hourly movements (r^2 = 0.913, P < 0.001), but consistently lower (Fig. 4A). When the sum of hourly movements did not exceed a daily total of 10 000 m, the mean 24-hour interval movement estimate was 43.1% of summed hourly movements. The mean 24-hour interval movement estimate was 73.2% of summed hourly movements, when the sum of the hourly movements exceeded 10 000 m in a day. Of all the 24-hour interval movement estimates, 13% were less than 500 m and 6% were < 10% of the sum of the associated hourly movements. The bias between the two estimates of daily movement varied widely, ranging from 1.4 when the summed hourly movements were low and caribou movements were localized, to < 0.2 with greater summed hourly movements during migratory periods (Fig. 4B). Due to the negative intercept of the regression equation, fitted values were 0 m (as negative movements are not possible) for summed hourly movement rates as great as 2185 m.

The areal extent of the both 95% and 50% UDs created using sub-sampled data were larger than those created by using the entire hourly dataset (Fig. 5). The 95% UDs for the sub-sampled data were 145.6% (range 111.3 to 173.7%), 192.8% (range 139.7 to 223.8%), 366.3% (range 275.3 to 479.0%) and 659.0% (range 294.0 to 1333.5%; for the 7, 24, 168, and 720 hour sample intervals, respectively) the size of the 95% kernel for the hourly data. The 50% kernels were 152.0% (range 107.1 to 205.5%), 195.8% (range 125.3 to 262.0%), 355.0% (range 215.4 to 429.33%) and 829.1% (range 346.5 to 1390.7; same respective order) of the areal extent of the 50% kernel for the hourly data. MCP estimates of home range decreased with increasing sample intervals (Fig. 5). The MCP estimates were 97.5% (range 94.4 to 99.3%), 96.4% (range 95.5 to 97.6%), 82.6% (range 73.7 to 87.3%), and 38.0% (range 12.1 to 72.1%) of the areal extent of the area of the hourly data (same respective order).

Discussion

Decisions regarding sample regimes for telemetry studies should be based on the understanding of sampling effects relative to research objectives rather than capabilities of the technology. GPS technology provides researchers with a powerful tool that is capable of collecting thousands of relatively precise locations, day and night, within a scheduled sample period at very short sample intervals. However, with this technology comes additional complexity which researchers need to consider, such as spatial auto-correlation (Alldredge & Ratti, 1992), locational error, trade-offs between sample period and sample interval, effects of sampling regime (Schaefer & Mahoney, 2003; this study) and fix rate bias (D'Eon, 2003). Fix rate bias can be affected by habitat and animal behavior (Moen *et al.*, 1996; Moen *et al.*, 2001; D'Eon, 2003), as well as sample interval (location attempt rate by the GPS) I hypothesize. My fix rates were very high, so this should not affect my results. Edenius (1996) showed that fix rates were highest during the winter, while other researchers have reported fix rates 90 - 100% in open areas (Moen *et al.*, 1996; D'Eon *et al.*, 2002) and for wolves in Denali National Park, Alaska, USA (Merrill *et al.*, 1998), so my fix rates are in accordance with previous research. Many other studies have documented the efficiency of GPS collars, as well as their deficiencies (Edenius, 1996; Johnson *et al.*, 2002a; D'Eon, 2003), which is outside the purview of my study.

Researchers estimating movement rates that are based on very frequent sample intervals have to deal with compounding locational errors. The locational error for the fixed GPS collar was 33 m. If 24 hourly relocations were used, one would have to account for locational error for each of the 24 relocations.

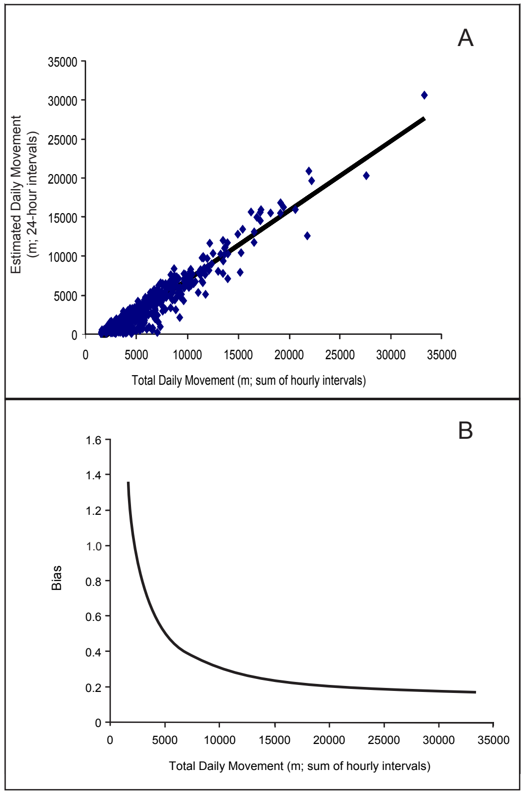

Fig. 4. A) Relationship between total daily movement (TDM; sum of hourly intervals) and estimated daily movement (EDM; 24-hour interval) of female caribou, Fortymile Caribou Herd, Alaska, during winter 1998–1999.
B) Bias is the difference between the total daily movement and fitted regression value for estimated daily movement divided by total daily movement.

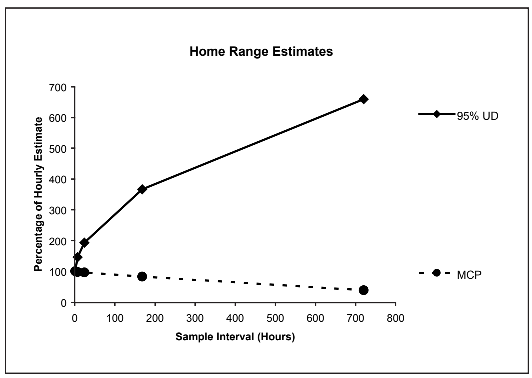

Fig. 5. Mean area of home range estimates (km^2) for the winter of 1998–1999, Fortymile Caribou Herd, Alaska.

Since the errors generated by SA are unpredictable (Rodgers *et al.*, 1996), I expected that some of the errors would cancel each other out. This is, in fact, what I determined when I compared distances between the fixed collar and the locations shifted by the mean hourly movement. The average error was determined to be only 5 m. Thus, locational error is not equivalent to the SA-induced average error in movement rate estimates. Furthermore, this concern is substantially reduced now that SA has been turned off (Dussault *et al.*, 2001).

Estimating movement rates can be important for investigations of migratory behavior, energetics, disturbance and habitat selection. Movement rates of caribou I instrumented varied by daylight categories and segments of the winter, indicating that use of positional data collected only during daylight hours (*e.g.*, Fancy, 1983; Boertje, 1985) should be restricted to inferences about diurnal movements. This may be particularly important for standard telemetry projects that employ fixed-wing aircraft. Similarly, estimates that span different seasons need to be carefully scrutinized. Movement rates can vary significantly within seasons (Russell & Martell, 1984; Fancy *et al.*, 1989; this study) and be highly variable among seasons (*i.e.*, migration versus calving; Fancy *et al.*, 1989; Stuart-Smith *et al.*, 1997; Ferguson *et al.*, 1998; Bergman *et al.*, 2000; Rettie & Messier, 2001; Schaefer & Mahoney, 2003;). It is important to ensure that reported movement rates used in subsequent analyses are applied only to time periods for which they are known to be relevant.

Though I expected estimates of movement rate to decline as sample interval increased (see Fancy *et al.*, 1989; Reynolds & Laundre´, 1990; Ferguson *et al.*, 1998; Schaefer & Mahoney, 2003), I did not predict such dramatic declines with sample intervals as short as two hours. I predict that movement rates will continue to increase with sampling intervals less than one hour as there is no asymptote apparent between the one and two hour sampling intervals (Fig. 3). Other research has also shown that movement rates increase with shorter sampling intervals (Schaefer & Mahoney, 2003).

In accordance with Fancy *et al.*'s (1989) supposition, long movements were generally linear and can be estimated more precisely using a 24-hour sample interval whereas short, localized movements are better characterized when the sample interval is shorter. Estimates determined using large sample intervals tend to have shorter movement rates because of all the non-linear movements between relocations. My analysis of bias revealed that total daily movements < 2185 m resulted in estimated movement rates of 0 m. For movements < 10 000 m/day, movement rates estimated from a 24-hour sample interval were < 50% of daily movement rates estimated with hourly samples.

Home range estimates will vary with different sample intervals (Reynolds & Laundre, 1990; Hansteen *et al.*, 1997; Ballard *et al.*, 1998). The magnitude of the effect of sample interval will be dependent on the ecology of the species under investigation and the sample interval itself (Swihart & Slade, 1985a; Beyer & Haufler, 1994; Hansteen *et al.*, 1997; Rettie & McLoughlin 1999). Species that exhibit constrained movement patterns, such as territorial animals, will likely be less affected by increases in the time between successive locations. Even species like the caribou, which range widely, tend to localize at different times of the year and under certain conditions. The effects of sample interval may be reduced during these periods. My results revealed that the areal extent of sub-sampled MCP home range estimates were smaller than the MCP estimate using the entire database. Home ranges developed from the sub-sampled data using kernels reacted in an opposite manner; their areal extent was greater with increasing sample interval, which has been noted before (Arthur & Schwartz, 1999; Girard *et al.*, 2002). This result may be due to autocorrelation (Swihart & Slade, 1985a, b, Blundell *et al.*, 2001).

Sample regimes, as discussed here, constitute temporal scaling. Identifying appropriate spatio-temporal scale(s) is critical for the robust analysis of biological questions. In my example, perceived movement rates increased with sampling frequency. However maximizing sample interval may not be the most appropriate regime for studying home range and habitat selection, as sample period plays an important role. Researchers must weigh the trade-offs between sample interval and sample period and recognize that both can affect the estimates they are interested in. Comparisons among and within studies must consider differences in each component of the sampling regime. Selection of a sampling regime can have dramatic effects on the estimation of ecological parameters. Each component of a sample regime has a discernable effect.

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