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Accuracy and performance of low-feature GPS collars deployed on bison *Bison bison* and caribou *Rangifer tarandus*

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Recently, a new generation of global positioning system (GPS) collars has become available that provides limited daily location fixes, a relatively long battery life, and are low-cost, compared to full-featured GPS collars. However, their performance is untested, and assessing these biases is needed to inform study designs and data analysis protocols. We used stationary tests of 15 Lotek LifeCycle GPS collars – an example of low-feature GPS collars – to measure the accuracy of location fixes. In addition, we deployed Lotek Lifecycle GPS collars on 153 caribou *Rangifer tarandus* and 24 bison *Bison bison* in Yukon and Alaska, to assess their field performance. We examined differences among species, sex, location fix schedule, and latitude, on four performance metrics (FSR, 3D-V FSR, DOP and DSR). Stationary trials indicated that mean precision (4.3 ± 4.0 m [SD]) and accuracy (6.0 ± 4.7 m) of location fixes was excellent, and FSR was good (87.2%), albeit both were slightly affected by forest canopy cover. Field performance varied by species and sex. Notably, the mean DSR for male bison was dismal (27.4 ± 24.2%) likely because of their behaviour, and the mean FSR, 3DV-FSR and DOP, for male caribou was poor (FSR = 57.3 ± 2.0%), compared to collars deployed on female caribou (72.2 ± 1.7%) or female bison (77.9 ± 1.4%). We also observed that the VHF transmitters often failed when the collar malfunctioned. Biases in the accuracy and performance of these low-cost GPS collars should be taken into account when designing studies. Researchers contemplating investing in low-feature GPS collars require information on their 'real-world' performance so that they can decide whether they are appropriate for their intended application. Moreover, researchers need to consider biases in their GPS collar data prior to embarking on field studies and when conducting analyses with the data collected from them.

In recent decades, global positioning system (GPS) transmitters have revolutionized wildlife monitoring and research. With technological advances, researchers have been able to address an increasingly broad range of behavioural, ecological, and management questions using GPS transmitters (Hebblewhite and Haydon 2010, Latham et al. 2015), on an increasingly diverse range of species (Adams et al. 2013, Glasby and Yarnell 2013). Indeed, the array of GPS technology available to researchers will likely continue to increase in the foreseeable future, facilitating continued expansion of this technology in animal studies. For projects employing GPS transmitters to provide reliable data that may help advance our understanding of animals and their management, two things are required: 1) well-designed projects that capitalize on the advantages of GPS technology (Hebblewhite and Haydon 2010, Latham et al. 2015), and 2) field location data obtained from GPS transmitters that are robust to errors (Frair et al. 2010).

With regards to reliable data from GPS transmitters, two main sources of error are a cause for concern, namely, measurement error and failure to obtain a location fix (Frair et al. 2010). Measurement error is the spatial error in obtained locations (i.e. accuracy), and this poses obvious complications in data analyses; whereas a failure to obtain a location fix occurs under certain environmental or study-specific conditions, and creates biases in the data. Collectively, Frair et al. (2010) termed these as 'GPS errors', and a number of studies have examined errors in GPS collar data (Yamazaki et al. 2008, Swanepoel et al. 2010, Uno et al. 2010, Glasby and Yarnell 2013, Jung and Kuba 2015).

Recently, a new generation of GPS collars has become commercially available for large mammals that, generally, provides limited daily location fixes and claims a relatively long field life, compared to more 'full-featured' (i.e. programmable) GPS collars. These 'low-feature' GPS collars offer limited programming or options. Yet, they may be attractive to researchers because they are relatively economical (≤ $1000 USD), enabling the application of GPS technology where project budgets would otherwise not allow for full-featured GPS collars, or providing an opportunity to increase sample sizes by deploying a larger number of low-cost GPS collars. An example of this class of GPS collar is the Lotek LifeCycle collar (Lotek Wireless Inc., Newmarket, Ontario, Canada), which was originally designed and marketed for survival studies (Latham et al. 2015), and is linked to the Globalstar satellite network. These collars are not programmable by the user, but can be programmed at the factory to obtain 1 or 2 daily location fixes and have a purported battery life of 3–5 years (M. Henriques pers. comm.). Because of the relatively low cost of this type of GPS collar, they may also be attractive to researchers for monitoring broad-scale distribution and movements, as well as survival and other questions that do not require fine resolution movement data. Researchers are likely to use this class of collars for a myriad of studies where they value monitoring animals for multiple years, without recapturing animals, over more detailed location data, and require just a few remotely-sensed locations weekly, providing they contain few GPS errors. However, a critical question remains – how well do low-feature GPS collars work? Information on their performance is not currently available, and potential cost-savings may not be realized if the accuracy or field performance of these low-cost GPS collars are poor. Researcher's contemplating investing in GPS collars require information about the 'real-world' collar performance in order to make evidence-based decisions on whether certain types or models are a sound choice (Johnson et al. 2002, Gau et al. 2004, Uno et al. 2010, Jung and Kuba 2015).

Here, we provide a short-term (6–18 months) assessment of the performance of Lotek LifeCycle GPS collars deployed on free-ranging caribou *Rangifer tarandus* and bison *Bison bison* in northwestern North America, focusing on GPS errors. Notably, only Johnson et al. (2002) examined the performance of any model of GPS collars on caribou, despite likely hundreds of devices being deployed on caribou annually in Canada, Alaska, and Fennoscandia. GPS collar performance had been previously reported for bison (Jung and Kuba 2015). Neither of these studies, however, evaluated the performance of low-feature GPS collars deployed on caribou or bison.

To assess measurement error, we conducted trials with stationary GPS collars and report on the precision and accuracy of location fixes and elevation. Additionally, we measured the effect of forest canopy cover on precision, location accuracy and fix success rate (FSR). Several studies (Rempel et al. 1995, Edenius 1996, Sager-Fradkin et al. 2007) have reported that earlier GPS collar models performed poorer under a forest canopy than at sites with an open canopy. We predicted that forest canopy cover would result in poorer accuracy and FSR of stationary collars. One of the relocation quality metrics produced for each location fix is the dilution of precision (DOP). DOP is a measure of the satelite configuration, or geometry, relative to the GPS collar at the time the location fix is obtained, and is often used as an indicator of the accuracy of a location fix (D'Eon and Delparte 2005, Ironside et al. 2017). In a real-world setting, with collars deployed on live animals, DOP may be the only metric available to assess the accuracy of a location fix. Thus, a key question is whether there is a relationship between DOP and relocation accuracy. We predicted that increasing DOP values would result in poorer accuracy.

We also examined four performance metrics (FSR, 3D-V fix success rate [3DV-FSR], DOP, and deployment success rate [DSR]; Table 1) on Lotek LifeCycle GPS collars deployed on free-ranging caribou and bison. We tested for treatment effects of species and sex, as well as their interaction, the effect of programming for one or two locations per day, as well as small-scale latitudinal differences, on performance metrics. Previous studies have investigated the percentage of malfunctioning collars providing evidence that the fix schedule (number of location fix attempts per day) is positively related to FSR and 3DV-FSR, and negatively related to DOP (Cain et al. 2005, Yamazaki et al. 2008).

Table 1. Description of metrics used to assess the field performance of GPS collars deployed on free-ranging bison *Bison bison* (n = 24) and caribou *Rangifer tarandus* (n = 153) in northwestern Canada and Alaska.

Acronym	Description	Calculation
FSR	Fix succes rate. The percent of location fix attempts by the GPS collar that result in successfully obtaining a location fix. FSR is expressed as a percent of location fix attempts. See D'Eon and Delparte (2005) for further details.	FSR = fix1/fix2 ×100 Where fix1 = the number of location fixes obtained by the GPS collar; and fix2 = the total number of attempts the collar made to obtain a location fix.
3DV-FSR	3DV Fix success rate. For this metric the value is the percent of all location fix attempts that resulted in obtaining a 3DV location—the most accurate class of location available from our GPS collars. 3DV-FSR is expressed as a percent of location fix attempts. See D'Eon and Delparte (2005) for further details.	3DV-FSR = 3DV-fix1/fix2 ×100 Where 3DV-fix1 = the number of 3DV class location fixes obtained by the GPS collar; and fix2 = the total number of attempts the collar made to obtain a location fix.
DOP	Dilution of precision. The strength of the satellite configuration, or geometry, on the accuracy of the location fix obtained by the GPS collar. Low DOP values (e.g. <1) indicate favourable, and higher DOP values indicate increasingly poor, satelite geometry at the time of the location fix. See D'Eon and Delparte (2005) for further details.	Not applicable. (As reported from the GPS collar.)
DSR	Deployment success rate. The percent of time that a GPS collar successfully worked, relative to the amount of time that the device was expected to work (e.g. 2 years). Essentially, this is the percentage that the realized life span is of the expected lifespan, with the latter being that as reported by the manufacturer. DSR is expressed as a percent of time the collar provided data, relative to the time it should have worked. See Jung and Kuba (2015) for further details.	DSR = days1/days2 ×100 Where days1 = the number of days the GPS collar worked (i.e. its realized lifespan); and days2 = the number of days the collar was expected to function (i.e. it's expected lifespan).

As such, we predicted that our GPS collars with a fix schedule of one location per day would perform poorly on our four metrics, compared to GPS collars with a fix schedule of two location per day. Species (Mattisson et al. 2010) and sex (Recio et al. 2010, Jung and Kuba 2015) influence GPS collar performance; yet, this appears to be rarely taken into account in studies of GPS collar performance. For bison, Jung and Kuba (2015) reported generally poor GPS collar performance because animals, particularly males, damaged the collars. Thus, we predicted that our four performance metrics would be better for 1) caribou than bison, and 2) females than males. We believed that GPS collars would perform better on caribou than bison, because wallowing behaviour by bison has been implicated in poor performance of GPS collars on bison (Jung and Kuba 2015), and caribou do not wallow. We expected that fighting behaviour among males of both species would result in damaging some GPS collars (Brooks et al. 2008, Jung and Kuba 2015) and be responsible for sex differences in collar performance. Finally, we predicted that our GPS collars – which used the Globalstar satellite network – would achieve poorer FSR in the northern part of our study area, which was close to 70°N. Based on our experience with other GPS devices using the Globalstar satellite network, we suspect that the satellite geometry of that network is not favourable for GPS location fix acquisition at that latitude.

Material and methods

Study area

Our study occurred across much of Yukon, Canada, extending eastward into the Northwest Territories, and westward into interior Alaska (Fig. 1), and spanned about 10° in latitude (60°–70°N). The study area was predominantly composed of mountainous terrain, with several mountain ranges intersecting the study area. Elevations of prominent peaks were often >2000 m a.s.l. Much of the landscape inhabited by caribou and bison was composed of broad alpine

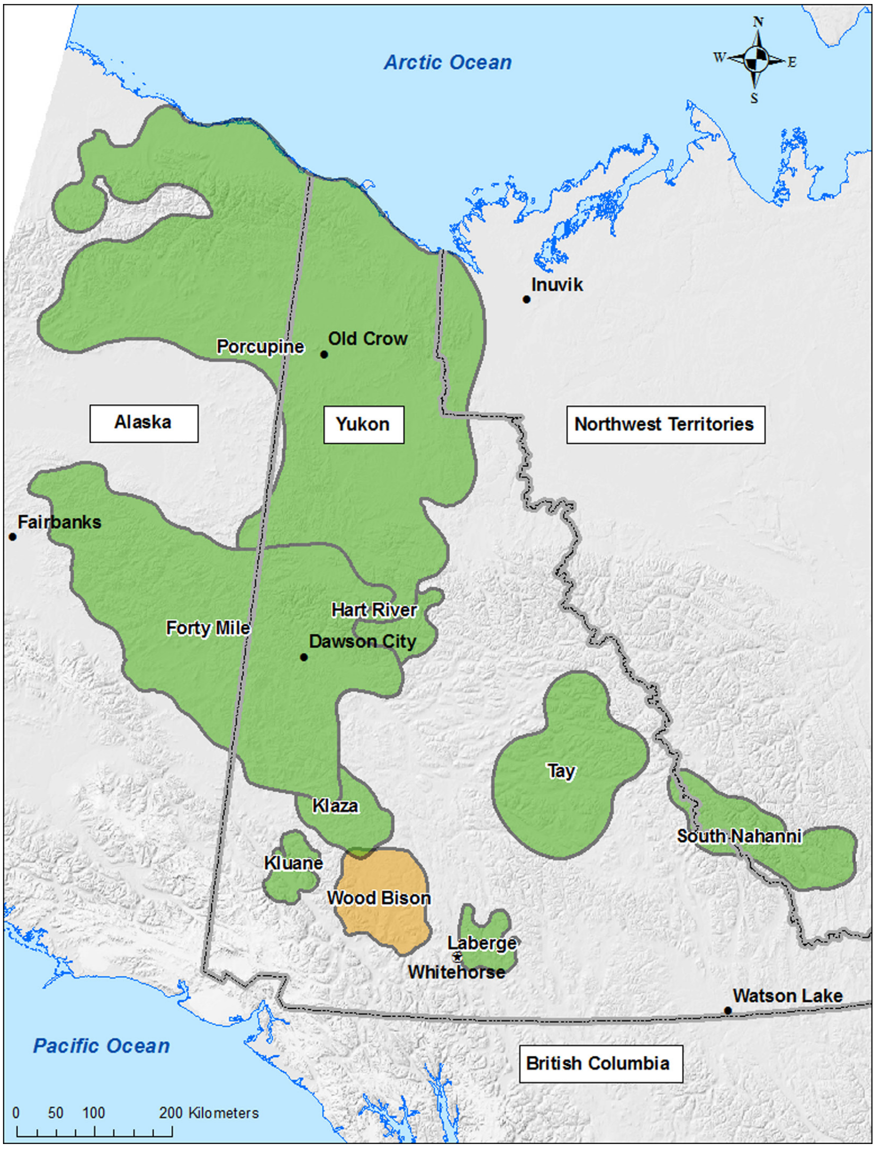

Figure 1. Location of the eight populations of caribou *Rangifer tarandus* and the population of bison *Bison bison* in Yukon, Alaska, and Northwest Territories, which were used in our study on the field performance of Lotek LifeCycle GPS collars.

plateaus interspersed by lakes, rivers, and open-canopied boreal forests, found at lower elevations (≤900 m a.s.l.). Closed-canopied boreal forest was often found along river corridors and lake shores. Spruce *Picea* spp. and poplar *Tremuloides* spp. were the dominant tree species in forested areas. Caribou in the most northern reaches of the study area (~68–70°N) seasonally occurred on the Beaufort Coastal Plain, an area of arctic tundra. Stationary trials occurred ≤20 km from Whitehorse, Yukon, Canada, at the southern edge of our study area (~60°N).

Stationary trials

During February–March 2016, we performed small-scale trials with stationary collars (i.e. not deployed on an animal) to provide an initial assessment of their performance: specifically, the precision and accuracy of location fixes, the effect of forest canopy cover on the accuracy of location fixes, and the accuracy of elevation values, as well as the relationship between DOP and accuracy. We used 15 new Lotek LifeCycle GPS collars for our stationary trials. We placed three collars together at each of 13 different sites for 4–8 consecutive days ($\bar{x} = 6.2 \pm 1.1$ [SD] days) to collect location fixes. GPS collars were programmed at the factory to collect one location daily. The three GPS collars at each site were placed within 0.5 m of each other with their antennas oriented toward the sky. Sampling sites were classified as open (0–15% canopy cover; n = 7) or closed (31–52% canopy cover; n = 6) based on visual estimates of canopy cover immediately above the collars, which were all taken by the same observer. Our stationary trials were short-term in nature and we did not consider variation in weather or topography on GPS collar performance.

Field trials on ungulates

Using a staggered entry design (Pollock et al. 1989), we captured and GPS-collared 153 adult caribou and 24 adult bison. Caribou were captured during collaring sessions between November 2014 and April 2016, using a helicopter to deliver either a net (Barrett et al. 1982) or dart containing a chemical immobilant (Lian et al. 2016). GPS-collared caribou were distributed among eight populations (Fig. 1): the Hart River, Klaza, Kluane, Laberge, South Nahanni, Tay River, Fortymile and Porcupine caribou herds (Hegel and Russell 2013). All bison were captured from a reintroduced population in southwestern Yukon (Jung et al. 2015, 2018; Fig. 1) using chemical immobilants delivered via a dart fired from a helicopter (Harms et al. 2018) during capture sessions in March and July 2015. We affixed Lotek LifeCycle GPS collars to captured caribou and bison.

About half of the GPS collars (54%) worn by caribou, and all those worn by bison, were programmed to attempt one location fix per day. The remainder (46%) of the GPS collars worn by caribou were programmed to obtain two location fixes per day. Each GPS collar was expected to function for 3–5 years, depending on the number location fix schedule (one or two location fixes per day), at which time the battery was expected to expire. As such, we expected our GPS collars to operate for the 6–18 month duration of our trials. Our GPS collars were equipped with a VHF transmitter to facilitate relocating the collar in the field.

Data analysis

We used ArcGIS 10.3 to plot the locations obtained from stationary collars and assessed the precision and accuracy of location fixes. First, we calculated the geometric mean location from the combined locations from all three collars deployed at a sampling site during the same deployment, which we used as a reference location for the sampling site. We then measured the difference between each location fix and the geometric mean of the combined locations, and determined this to be the precision of the location fix. To assess accuracy of location fixes, we obtained the coordinates of the sampling site with a handheld GPS (GPS76SCx, Garmin Inc.) and assumed this to be a true measure of the location of the sites. We then measured the accuracy as the difference between each location fix obtained by the GPS collars at that site, and the location of the site obtained by the handheld GPS.

To measure the accuracy of the elevation reported by the GPS collars we derived the elevation for each location from a digital elevation model (DEM) in ArcGIS 10.3. We then calculated the difference between the elevation reported by the GPS collar and that from the DEM, and recorded this as the elevation accuracy. We assumed that the elevation derived from the DEM was the apparently true elevation.

We assessed the relationship between DOP, as reported from the stationary GPS collars for each location fix, and the accuracy of each location fix, relative to that obtained from the handheld GPS. To assess for non-linearity in the relationship we fitted an additive mixed model, with radio-collar as a random effect. The model was fitted using the 'gamm4' package (ver. 0.2-5; Wood and Scheipl 2017, Wood 2006) for the statistical software R (ver. 3.4.1, <www.r-project.org>).

Data remotely downloaded from the GPS collars deployed on free-ranging ungulates included the date, time, latitude, longitude, elevation, fix status (2D, 3D-V and no fix) and DOP. Malfunctioning GPS collars were screened before analyses, as per D'Eon et al. (2002). When the collar stopped acquiring location fixes for ≥10 consecutive days we considered that it was malfunctioning and did not use subsequent fix attempts in our analyses.

We examined four metrics of GPS-collar performance: FSR, 3DV-FSR, DOP and DSR (Table 1). FSR of each collar deployed was calculated by dividing the number of successful location fixes by the total number of location fix attempts. Three-dimensional location fixes (3D-V) are more accurate than are two-dimensional fixes (D'Eon and Delparte 2005, Uno et al. 2010) and, hence, more desired by researchers. We calculated the 3DV-FSR by dividing the number of 3D location fixes by the total number of location fix attempts. The closer the DOP values are to 1, the greater the confidence in the accuracy of the location. We recorded the fate of each GPS collar deployed at the end of our 18 month study period, and assessed the performance of GPS collars in collecting location fix data by calculating a DSR. As per Jung and Kuba (2015), the DSR was the percentage of time (in days) that the collar successfully collected location fix data, relative to the estimated time that the collar was to be deployed and should have been collecting data. In our case, this was variable due to a staggered entry design, and ranged between 6–18 months. We censored the DSR to 100% in cases where the animal died before the end of the study, but the GPS collar was functioning at the time of removal.

We tested for differences in the precision and accuracy of stationary GPS collars in open and closed forest canopy sites with a *t*-test using Bonferroni-adjusted p-values. A likelihood ratio chi-square test was used to compare the FSR of stationary collars at sites with an open and closed canopy. We used a general linear model to test for the effect of species, sex, and their interaction on our four performance metrics (FSR, 3DV-FSR, DOP and DSR). To test for an effect of the number of location fixes per day (1 or 2) on our four performance metrics we performed a *t*-test, using only female caribou (in order to control for species and sex effects). Similarly, to test for an effect of latitude on our four performance metrics we used a *t*-test, using only males (no females from the Porcupine herd were available) from the Fortymile and Porcupine caribou populations separated by 4°–6° of latitude (Fig. 1). FSR may differ between location fix attempts taken during day and night due to animal behaviour (Bowman et al. 2000, Zweifel-Schielly and Suter 2007, Jung and Kuba 2015), so we calculated the FSR of a subsample of GPS-collared females with a fix schedule of two locations per day (n = 15) and used a *t*-test to examine differences between FSR during the day and night. Because of dramatic changes in the seasonal light regime at northern latitudes, we used locations from 11:00–15:00 and 23:00–03:00 as day and night locations, respectively (Jung and Kuba 2015). Statistical tests were conducted using SYSTAT (ver. 13; Systat Software Inc.).

Results

Stationary trials

We obtained 212 location fixes from 243 location fix attempts (FSR = 87.2%) by 15 stationary Lotek LifeCycle GPS collars deployed at 13 sites in southwestern Yukon. All location fixes were 3D-V, the highest category of location quality provided. We found a significant difference ($X^2_1 = 14.888$, $p < 0.001$) in the FSR at sites with an open canopy (94.7%) compared to those with a closed canopy (78.4%).

Mean precision of the location fixes was 4.3 ± 4.0 m (SD; range = 0–24.0 m) based on the geometric mean of all locations at a site, and mean accuracy was 6.0 ± 4.7 m (range = 0.2–37.9 m) based on the apparently true location measured by a handheld GPS. Precision was significantly better at open versus closed canopy sites ($t_{210} = 2.358$, $p = 0.019$), as was accuracy ($t_{210} = 2.808$, $p = 0.005$); however, the difference in the mean precision and location accuracy between open and closed canopy sites was relatively small (≤2 m; Fig. 2). Regardless of canopy openness, the precision (92.9%) and accuracy (90.1%) of the vast majority of location fixes was ≤10 m (Fig. 3).

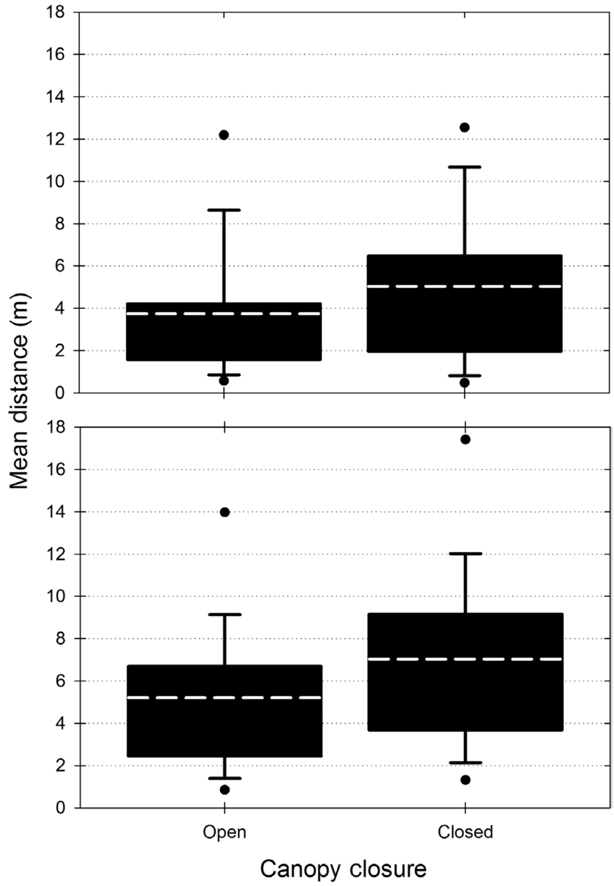

Figure 2. Box plots of the precision (upper panel) and accuracy (lower panel) of location fixes (n = 212) obtained from 15 stationary Lotek LifeCycle GPS collars in sites with an open (0–15%; n = 6) and closed canopy (31–52%; n = 7). Dashed lines represent the mean. All sample sites were located in southwestern Yukon, Canada.

The mean difference between the elevation from individual location fixes and the apparently true site elevation from a DEM was 5.6 ± 4.3 m asl (SD; range = 0.1–56.2 m asl). Close to two-thirds (63.9%) of location fixes were ≤20 m asl, and almost all were ≤40 m asl (97.7%), of the apparently true site elevation (Fig. 4).

The relationship between relocation accuracy and DOP was non-linear (Fig. 5) with an intercept estimate of 6.0 (SE = 0.41) and the effective degrees of freedom of the smoothing function was 2.9. Variance estimates of the model were 1.1 for the collar, 34.4 for the smooth term of DOP, and the residual variance was 18.6. Generally, locations with a DOP <4 were accurate to 10–15 m, but those with a DOP ≥4 had increasing variability in their accuracy (Fig. 5).

Field performance

We deployed 177 Lotek LifeCycle GPS collars on free-ranging ungulates, with 153 (110♀, 43♂) on caribou and 24 (20♀, 4♂) on bison (Table 2). All GPS collars were deployed for ≥6 months before our analyses, with 109 GPS collars being deployed for ≥18 months. Mean tracking duration was 354.9 ± 197.2 [SD] days, and was highest for female bison and lowest for male bison (Table 2). We observed 22 mortalities (21 caribou, 1 bison; Table 2) before the scheduled end of our GPS collar deployments and right censored

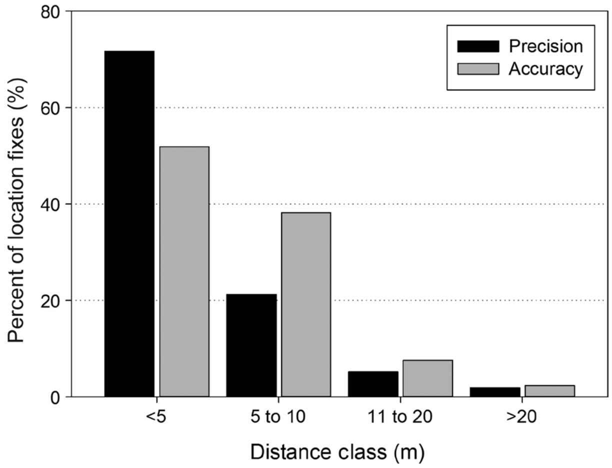

Figure 3. Distribution of the percentage of location fixes (n = 212) obtained from 15 stationary Lotek LifeCycle GPS collars in four distance classes representing their precision and accuracy.

(Pollock et al. 1989) these animals when calculating FSR, 3DV-FSR, and DSR. We found that 19 of 177 (10.7%) GPS collars malfunctioned during our study. GPS collar malfunctions were greater for bison (7 of 24 [29.2%]) than caribou (12 of 153 [7.8%]), with differences for sex being prominent for bison but not caribou (Table 2). Overall, the GPS collars we deployed transmitted 68 962 of 105 020 scheduled location fixes (65.7%).

Performance metrics were variable across species and sex (Table 3). There was no difference in FSR or 3DV-FSR based on sex ($p \geq 0.559$). The interaction term (Species × Sex) was significant ($p \leq 0.006$) for all four performance metrics based on our general linear model (Table 4). Specifically, FSR and 3DV-FSR were greatest for male bison and lowest for male caribou; those for female caribou and female bison were similar. DOP was greater for male caribou than for female caribou or either sex of bison, and DSR was lowest for male bison and similar for female bison and both sexes of caribou (Table 3). Our general linear model found a significant difference for all four performance metrics based on species, and for DOP and DSR for sex ($p \leq 0.001$; Table 4).

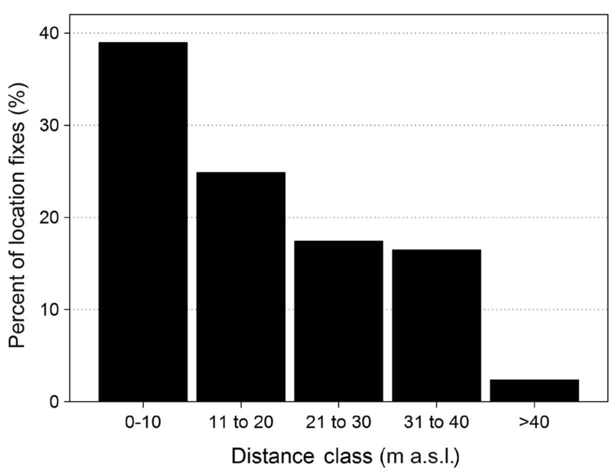

Figure 4. Distribution of the percentage of elevation measures reported from location fixes (n = 212) obtained from 15 stationary Lotek LifeCycle GPS collars in four distance classes that represent the difference between the reported altitude and the apparently true altitude, as measured by a digital elevation model.

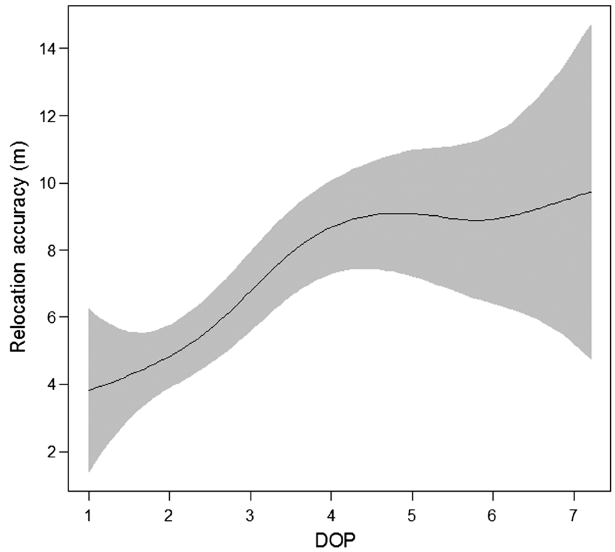

Figure 5. Relationship between DOP (dilution of precision) and GPS collar relocation accuracy, based on 212 location fixes from 15 Lotek LifeCycle GPS collars placed at 13 stationary sites in southwestern Yukon, Canada. The shaded area represents 95% confidence intervals.

To assess the effect of latititude on GPS collar performance, we compared our 4 performance metrics between adult male caribou in a population in central Yukon/Alaska (~64°N) with one from northern Yukon/Alaska (~68°N) and found no difference in DOP or DSR (Table 4). FSR and 3DV-FSR, however, were different among populations at different latitudes, with those at higher latitudes (Porcupine caribou) being significantly lower ($p \leq 0.001$; Table 5).

We tested the effect of the fix schedule on our four performance metrics for female caribou and found that collars scheduled to obtain one location fix per day had significantly ($p \leq 0.002$) higher FSR and 3DV-FSR values than those scheduled to obtain two location fixes per day (Table 6). Conversely DOP performance was significantly poorer ($p = 0.002$) for one versus two location fixes per day (Table 6). We found no difference ($p = 0.491$) in DSR among GPS collars on female caribou scheduled to obtain one or two location fixes per day (Table 6). For GPS collars scheduled to obtain two location fixes per day, mean FSR did not differ ($t_{14} = 0.923$, $p = 0.923$) between location fix attempts during the day (59.3% ± 0.2 [SD]) from those at night (59.9% ± 0.2).

Discussion

Stationary trials

One of our main findings was that the precision and accuracy of Lotek LifeCycle GPS collars was high (>90% of location fixes were both precise and accurate to ≤10 m), based on stationary trials. Our measure of accuracy of Lotek LifeCycle collars compares favourably to similar stationary trials done

Table 2. Sample sizes of the number of male and female bison *Bison bison* and caribou *Rangifer tarandus* wearing Lotek LifeCycle GPS collars in an assessment of the field performance of these collars. Number of apparently malfunctioning GPS collars, number of mortalities during field trials, and the mean (± SE) tracking duration of GPS-collared animals, are reported.

			Fate of GPS-collared animals		Tracking duration	
Species	Sex	n	Apparently malfunctioning GPS collars	Mortalities	$\bar{x}$ ± SE (days)	Range (days)
Bison	female	20	4 (20%)	0 (0%)	488.4 ± 26.1	175–551
	male	4	3 (75%)	1 (25%)	55.5 ± 41.2	14–179
Caribou	female	110	9 (8%)	14 (13%)	362.2 ± 19.2	12–687
	male	43	3 (7%)	7 (16%)	302.0 ± 26.4	122–560

on other, earlier models of GPS collars that reported a mean accuracy of about 5–20 m (Cargnelutti et al. 2007, Hebblewhite et al. 2007, Zweifel-Schielly and Suter 2007, Yamazaki et al. 2008). Indeed, the accuracy of GPS collars has increased substantially since the first generation commercially available over 20 years ago, when accuracy was about 40–180 m (Edenius 1996). Our results indicate that DOP values of <4 were usually accurate to within 10–15 m, but DOP values ≥4 increased variability and decreased location accuracy.

Accuracy of the elevation reported by our GPS collars was mediocre, with <40% of location fixes being <10 m of the elevation obtained from a DEM. In >20% of location fixes elevation accuracy was >30 m. Previous studies have found that GPS collars perform poorly on steep, densely forested slopes (Hebblewhite et al. 2007, Jiang et al. 2008), compared to in flat, open areas. Because the accuracy of elevation reported from our GPS collars was often >10 m, we suggest that researchers working in topographically-variable areas use altitudes derived from a DEM, rather than use the elevation data from Lotek LifeCycle GPS collars.

As reported by earlier assessments of GPS collar performance, and in support of our prediction, we found that Lotek LifeCycle GPS collars located under a forest canopy performed poorer than those in more open sites (Edenius 1996, D'Eon 2003, Graves and Waller 2006, Hebblewhite et al. 2007, Sager-Fradkin et al. 2007, Yamazaki et al. 2008). GPS collars at sites with more canopy cover were less precise, less accurate, and had lower FSR values, than those in open habitats. Differences in accuracy between our GPS collar trials in open and closed canopy sites, even though statistically different, were quite small (<2 m), and probably not of critical concern for studies of ungulate movement ecology or habitat selection. Similarly, we found that canopy closure had a significant impact on FSR, with GPS collars under a relatively open canopy (0–15% closure) having a FSR 16.3% higher then those under a closed forest canopy). This difference in FSR between open and closed canopy sites may warrant consideration of FSR bias when modeling habitat selection (Hebblewhite et al. 2007, Sager-Fradkin et al. 2007, Frair et al. 2010). Of note, a limitation of our study was that boreal forests at high-latitudes are generally not structurally complex and do not have canopies as closed as those in more coastal or southern locations. Thus, the small differences we observed in accuracy and FSR may not reflect differences that may be observed in forested ecosystems characterized by a more closed canopy than in our study, such as in coastal rainforest of the Pacific Northwest (Sager-Fradkin et al. 2007).

Differences in GPS collar performance in relation to the accuracy of location fixes and FSR can create important biases in habitat selection studies that researchers need to be aware of and possibly address in their analyses (D'Eon 2003, Lewis et al. 2007, Bourgoin et al. 2009, Nielson et al. 2009, Frair et al. 2010). Our stationary trials were limited in scope in this regard, with the main of aims being to assess accuracy and supplement data on the influence of habitat (i.e. canopy cover) on FSR acquired during our field trials on free-ranging ungulates. Earlier studies have amply shown that topography (Cain et al. 2005, Hebblewhite et al. 2007, Zweifel-Schielly and Suter 2007) and weather (Bourgoin et al. 2009, Ensing et al. 2014, Aguado et al. 2017), for instance, can also potentially effect the FSR of GPS collars. While it was beyond the scope of this study to investigate the influence of these environmental conditions on FSR, we acknowledge that varied topography and inclement weather may have had an unmeasured impact on GPS collar performance in our study. We note, however, that our field trials covered a wide variety of topographic and weather conditions, and represent 'real-world' trials for ungulates in our vast study area. Regardless, researchers contemplating using GPS collars should assess through stationary trials how variation in topography and weather in their study areas will impact performance of the GPS collars in their studies.

Field performance on ungulates

Our analyses of a large sample (n = 177) of instrumented animals, across a large geographic area, and for up to 18 months, allowed us to robustly assess the field performance

Table 3. Mean (± SE) for four performance metrics of Lotek LifeCycle GPS collars deployed on free-ranging bison *Bison bison* and caribou *Rangifer tarandus* in Yukon, Alaska, and Northwest Territories.

			Performance metric			
Species	Sex	n	FSR ($\bar{x}$ ± SE) (range)	3DV-FSR ($\bar{x}$ ± SE) (range)	DOP ($\bar{x}$ ± SE) (range)	DSR ($\bar{x}$ ± SE) (range)
Bison	female	20	77.9 ± 1.4 (67.9–87.5)	74.7 ± 1.4 (65.7–85.7)	3.2 ± 0.1 (2.5–3.5)	90.6 ± 4.8 (32.4–100.0)
	male	4	98.1 ± 2.7 (91.6–100.0)	91.3 ± 4.3 (82.1–100.0)	3.4 ± 0.4 (3.5–4.5)	27.4 ± 24.2 (3.1–100)
Caribou	female	110	72.2 ± 1.7 (24.4–97.9)	70.9 ± 1.7 (23.0–97.9)	3.4 ± 0.1 (2.3–7.4)	95.9 ± 1.6 (2.1–100.0)
	male	43	57.3 ± 2.0 (22.4–80.4)	55.7 ± 1.9 (21.8–79.9)	5.2 ± 0.3 (2.8–8.6)	95.6 ± 2.5 (29.2–100.00)

Table 4. General linear model results of the effect of species, sex, and their interaction, on the performance of Lotek LifeCycle GPS collars deployed on free-ranging bison *Bison bison* (n = 24) and caribou *Rangifer tarandus* (n = 153) in Yukon, Alaska, and the Northwest Territories.

	Model effect[1]					
	Species		Sex		Species × Sex	
Performance metric	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
FSR	25.725	<0.001	0.343	0.559	14.591	<0.001
3DV-FSR	18.870	<0.001	0.021	0.884	12.389	0.001
DOP	14.227	<0.001	11.939	0.001	7.633	0.006
DSR	49.824	<0.001	37.135	<0.001	36.473	<0.001

[1]all with 1 df.

of our GPS collars on free-ranging ungulates. Overall, FSR was moderate (65.7%) and the percentage of GPS collars that malfunctioned within 6–18 months of deployment was also moderate (10.7%). The apparent quality of location fixes was high, with 97.8% of the location fixes obtained being 3DV fixes, the highest quality class of location fixes, and over 88.4% of location fixes reported a DOP ≤4.

We observed that, for the most part, our four performance metrics also varied between bison and caribou, and, in some cases, males and females, providing support for our predictions. While all of our performance metrics were similar for female caribou and female bison, they differed substantially between males and females of both species and between male caribou and male bison. For instance, the mean FSR and 3DV-FSR was high for male bison (≥91.3%) and comparatively low for male caribou (≤57.3%); yet it was moderate for female caribou and female bison (~71–78%). Our data for male bison provide further support for that of Jung and Kuba (2015) who also reported high FSR (99.5%) for male bison. Others have attributed high FSR to those animals spending more time in open habitats (D'Eon 2003, Nielson et al. 2009), and this may be the case for male, compared to female, bison (Jung and Kuba 2015). Mean DOP was comparatively low for bison and female caribou (3.2–3.4) but higher for male caribou (5.2), indicating that not only FSR was poorer for male caribou but so too was DOP. Why Lotek LifeCycle GPS collars performed comparatively poorly for male caribou is not known, but the most plausible reason is likely related to habitat selection choices of males compared to females. Perhaps, with less energy demands than pregnant or nursing females, males may spend more time resting in forests with denser canopy cover. Notably, the FSR of Lotek LifeCycle GPS collars on the male caribou we observed was no better than early generation GPS collars (Lotek GPS1000) deployed in 1996–1999 (Johnson et al. 2002); however, the percentage of malfunctioning collars has improved substantially, as well as FSR for female caribou, since the earlier GPS collars used by Johnson et al. (2002). Mean DSR was high (≥90.6%) for female bison and caribou, but very low (27.4%) for male bison. Jung and Kuba (2015) also found a very low (19.1%) DSR for male bison and, upon their inspection of the damage to the collars, attributed this to bison behaviour leading to broken GPS electronics, particularly the top-mounted antennas.

Another main finding of our study was that the field performance of Lotek LifeCycle GPS collars varied for caribou and bison, and males and females, in support of our predictions. The percentage of GPS collars malfunctioning before the end of our study was 3.4 times greater on bison than caribou, a finding that confirms the results of a previous study that bison behaviour likely results in terminal damage to GPS collars (Jung and Kuba 2015), which was apparently not the case for caribou. Bison in wallows will often roll on their backs, sometimes forcefully, which likely resulted in critical damage to the GPS collar antenna (Jung and Kuba 2015), while caribou do not wallow. In particular, most of the GPS collars placed on adult male bison (75%) malfunctioned within ≤30 days of deployment, while those on adult female bison that malfunctioned (20%) did so over a wider range of times after deployment (175–469 days). Interestingly, we did not observe any difference in the percentage of GPS collars that malfunctioned in the field between male (7%) and female (8%) caribou, suggesting that no similar sex-specific bias occurs for caribou. A caveat is that our study reports on the short-term (6–18 months) field performance of Lotek LifeCycle GPS collars, and these devices are designed to operate for 3–5 years in the field, depending on the location fix schedule (M. Henriques pers. comm.). As such, our observations of the percentage of collars that malfunction in the field is conservative, and would be expected to increase somewhat over the remainder of their deployment in the field, particularly for bison. Further research on

Table 5. Mean (± SE) and test statistics (*t*-test) of differences in four performance metrics for Lotek LifeCycle GPS collars affixed to 43 male caribou *Rangifer tarandus* from two different populations. GPS-collared Fortymile caribou (n = 19) were found at lower latitudes (~64°N) than Porcupine caribou (n = 24; ~68–69°N).

	Caribou population		Test statistic[1]	
Performance metric	Fortymile ($\bar{x}$ ± SE)	Porcupine ($\bar{x}$ ± SE)	*t*	p-value[2]
FSR	66.0 ± 2.2	50.5 ± 2.4	4.762	<0.001
3DV-FSR	63.3 ± 2.1	49.7 ± 2.3	4.196	0.001
DOP	5.4 ± 0.3	5.1 ± 0.4	0.415	1.000
DSR	100 ± 0.0	92.2 ± 4.4	1.589	0.479

[1]all with 41 df.
[2]Bonferroni adjusted p-values.

Table 6. Mean (± SE) and test statistics (*t*-test) of differences in four performance metrics for Lotek LifeCycle GPS collars affixed to 110 female caribou *Rangifer tarandus* using location fix schedules of one per day (n = 47) versus two per day (n = 63).

	Fix schedule		Test statistic[1]	
Performance metric	1 per day ($\bar{x}$ ± SE)	2 per day ($\bar{x}$ ± SE)	*t*	p-value[2]
FSR	84.8 ± 1.9	62.9 ± 2.0	7.838	<0.001
3DV-FSR	83.4 ± 1.9	61.9 ± 2.0	7.730	<0.001
DOP	3.7 ± 0.1	3.3 ± 0.1	3.525	0.002
DSR	98.7 ± 0.9	93.8 ± 2.6	1.555	0.491

[1]all with 109 df.
[2]Bonferroni adjusted p-values.

their long-term performance, specifically the DSR, would be informative.

Our analysis provides a preliminary assessment of the impact of small-scale differences in latitude (4–5°N) on the performance metrics of Lotek LifeCycle GPS collars. While limited to only male caribou (n = 43), we found that these GPS collars performed significantly poorer on male caribou that occurred predominately north of the Arctic Circle, than those that were south of it. FSR observed for male caribou in the most northern population in our study (50.5%) were substantially lower than those reported (99.7%) during stationary trials of Telonics Generation 3 GPS collars (Telonics, Mesa, AZ, USA) at the most northern fringe of our study area (Swanlund et al. 2016). The difference observed between FSR in our study and that of Swanlund et al. (2016) is difficult to reconcile. This may be because the two studies used different models of GPS collars, or the differences between stationary trials and those on free-ranging animals, topography in the two study areas, or that collars used in the two studies linked to different satellite networks (i.e. Globalstar versus Iridium), or a combination thereof. Regardless, the differences in these two studies point to the need to assess the 'real world' performance of GPS collars on free-ranging animals when trying to understand differences in collar performance metrics (Johnson et al. 2002, Gau et al. 2004, Frair et al. 2010). Further studies are needed to assess the effect of latitude, and hence, satellite positioning on GPS collar performance metrics.

Perhaps the most perplexing result of our study was that the Lotek LifeCycle GPS collars that we deployed on adult female caribou performed better when they were scheduled to obtain one versus two location fixes per day. This is contrary to our prediction. Other studies have reported that shorter intervals between location fix attempts result in better FSR and other performance metrics (Cain et al. 2005, Yamazaki et al. 2008). Although some studies have found that FSR can vary between location fix attempts taken during day versus night (Zweifel-Schielly and Suter 2007, Heard et al. 2008, Jung and Kuba 2015), we found no such difference among female caribou with GPS collars scheduled to obtain two location fixes per day. Thus, potential diel changes in animal behavior (i.e. bedding, activity level, habitat selection) does not account for the difference in performance of our GPS collars based on fix schedule. While the reason for difference in GPS collar performance based on fix schedule is unknown, the implication to researchers is that a shorter interval between location fix attempts may not result in more successful (FSR) or higher quality (3DV-FSR and DOP) location fixes. We encourage others using these or similar GPS collars with variable fix schedules to report their results, so that researchers contemplating one or two fixes per day will have better information from which to base their choice of fix schedule.

A significant concern observed in our study was that VHF transmitters often failed when the GPS collars malfunctioned and retrieval of these collars from animals in the field was not possible because they could not be found. These were not catastrophic failures in the sense reported by others (Gau et al. 2004, Jung et al. 2015) because we remotely obtained location fixes up until the collars malfunctioned, which is not possible with GPS collars that solely store data onboard. However, not being able to locate animals in the field with malfunctioning VHF transmitters seriously compromised our ability to take action after a GPS collar malfunctioned, such as retrieving the collar for a diagnostic inspection, determining if the malfunction was related to a mortality event, placing a new collar on the same animal, or repairing the collar and redeploying it on an another animal. This may be a limitation when using these collars to study survival or cause-specific mortality. More importantly, we ancedotally found that, in a subsample of five GPS collars retrieved from dead caribou, location fix data was stored onboard that was not transmitted via satellite transmission. However, not being able to locate the collar via the VHF signal or a satellite-transmitted mortality signal severely limits researchers' ability to locate malfunctioning collars and download data that may have been solely stored onboard. Additionally, although VHF beacon signal strength was not specifically evaluated for this study, we found that the VHF signal tended to be weak on Lotek LifeCycle GPS collars even when they were functioning correctly, compared to other GPS or VHF collars we have collectively used. The weak VHF signal strength of these collars often made it difficult to visually locate collared animals in the field when observations were required to facilitate population estimates, group composition counts, or similar monitoring activities.

Conclusions

Our stationary trials of Lotek LifeCycle GPS collars indicated that location fixes from these collars were highly precise and accurate, and FSR was moderate-high, albeit precision, accuracy, and FSR were affected by low-moderate forest canopy cover. The field performance of these GPS collars varied by species and sex. Sex-specific biases in the field performance of GPS collars should be taken into account when designing studies (Brooks et al. 2008, Recio et al. 2010, Jung and Kuba 2015). We found evidence that the fix schedule and latitude affected the performance of GPS collars in our study area, and recommend that these are areas of further research with respect to GPS errors.

A good understanding of the performance of various models of GPS transmitters is needed so that investments in the technology represent a good use of limited resources for wildlife management and translate to reliable knowledge (Johnson et al. 2002, Gau et al. 2004, Hebblewhite et al. 2007, Uno et al. 2010, Jung and Kuba 2015, Latham et al. 2015). Despite low-feature GPS collars, such as the Lotek LifeCycle model, having been on the market since 2013, to the best of our knowledge no other studies have reported on their accuracy or field performance. Yet, this type of GPS collar should be of particular interest to researchers and managers because their relatively low cost may allow for the use of GPS technology where project budgets are limited and the use of full-featured GPS collars is not feasible or necessary. Our stationary and field trials of Lotek LifeCycle GPS collars provide information on their accuracy and field performance, which should help researchers determine if this type of GPS collar might work for their intended purposes.

Regardless of the type of GPS collar chosen, we recommend that researchers using GPS collars examine the biases created by conditions in their study area (e.g. forest cover, latitude, topography, climate, etc.) and behavior of the species studied, prior to embarking on large-scale GPS collaring campaigns. Understanding these biases is necessary to ensure that the data collected using GPS collars will be sufficient to answer the intented question (Hebblewhite and Haydon 2010, Latham et al. 2015), and inform data analysis protocols (Hebblewhite et al. 2007, Ironside et al. 2017). Moreover, understanding GPS collar performance allows researchers to make study design decisions that can optimize the use of GPS technology to provide reliable knowledge for wildlife management.

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