Management and Conservation Article

Grizzly Bear Behavior and Global Positioning System Collar Fix Rates

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ABSTRACT Animal locations collected by Global Positioning System (GPS) collars will represent a biased sample of the sites an animal used if some position fixes fail and if those missed locations do not occur randomly. Probability of a GPS receiver obtaining a position fix is known to decline as canopy cover increases, but the impact of forest canopy cover was insufficient to account for the low fix rates we observed for GPS collars on grizzly bears (*Ursus arctos*). We tested the hypothesis that GPS fix rates were related to the interaction between animal activity (active vs. resting) and canopy cover by evaluating the following predictions: 1) grizzly bear activity should follow a circadian pattern similar to the circadian fix-rate pattern, 2) grizzly bear use of canopy cover should follow a circadian pattern similar to the circadian fix rates, 3) grizzly bear activity should be related to canopy cover (i.e., bears should rest in areas with relatively high canopy covers and feed and move in relatively open areas), and 4) collar orientation and canopy cover should interact to affect the fix rates of test collars. The GPS fix rates traced a bimodal circadian pattern that was directly related to the circadian pattern of grizzly bear activity. Fix rates declined when bears were more likely to be using denser cover, and fix rates of test collars demonstrated that collar orientation interacted with canopy cover, such that fix rates declined much more with increasing canopy cover when the collar was on its side than when the collar was upright. We concluded that inferences made about grizzly bear microhabitat use, based on GPS locations, will underrepresent high canopy cover sites, especially when grizzly bears are resting there. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):596–602; 2008)

DOI: 10.2193/2007-175

KEY WORDS activity patterns, behavior, Global Positioning System collar fix rates, grizzly bears, microhabitat use, *Ursus arctos*.

Animal locations collected by Global Positioning System (GPS) collars will be a biased sample of the sites an animal used if some position fixes fail and those missed locations do not occur randomly. Even modest underrepresentation of a site's use can have significant effects on ecological models (Tyre et al. 2003, Frair et al. 2004, Gu and Swihart 2004). Solving the problem of GPS fix bias requires estimating the magnitude of potential bias, identifying variables involved, and understanding the functional relationships between the bias and those variables.

We collared grizzly bears (*Ursus arctos*) in central British Columbia, Canada, with GPS collars as part of a general study of grizzly bear ecology (Ciarniello et al. 2005, 2007; Ciarniello 2006). When our examination of GPS collar fix rates (i.e., proportion of GPS fix attempts that produced a location) from some of those grizzly bears showed a distinct circadian pattern, we examined our data to determine which factors were most likely responsible for that pattern. Environmental factors, such as forest canopy cover, tree density, and terrain ruggedness are known to affect GPS collar fix rates (Remple et al. 1995, Moen et al. 1996, Di Orio et al. 2003, Frair et al. 2004, Cain et al. 2005). Fix rates also are affected by animal behavior (Moen et al. 1996, 2001; Bowman et al. 2000; Graves and Waller 2006), possibly because activities such as feeding and resting affect orientation of the GPS antenna. The GPS antenna would be horizontal for a grizzly bear resting on its side or in the case of a grizzly bear resting on its stomach, if the bear rotated its collar so that the battery case was not below its throat (Graves and Waller 2006, Sundell et al. 2006). In addition, animals typically select different microhabitats for different activities, so GPS fix rates may be related to the interaction between animal activity and environmental factors.

We tested the hypothesis that GPS fix rates were related to the interaction between animal activity and canopy cover, one of the most influential environmental factors affecting fix rates, by evaluating the following predictions: 1) grizzly bear activity should follow a circadian pattern similar to the circadian fix-rate pattern, 2) grizzly bear use of canopy cover should follow a circadian pattern similar to the circadian fix rates, 3) grizzly bear activity should be related to canopy cover (i.e., bears should rest in areas with relatively high canopy covers and feed and move in relatively open areas), and 4) collar orientation and canopy cover should interact to affect the fix rates of test collars.

STUDY AREA

We captured grizzly bears north of Prince George, in central British Columbia, Canada (54°55′N, 122°46′W) within 2 distinct environments, mountains and plateau (Ciarniello et al. 2007). The plateau portion of the study area consisted of rolling hills between 600 m and 1200 m above sea level (asl) where the dominant land cover was hybrid white–Engelmann spruce (*Picea glauca* × *engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests, interspersed with successional stands of lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Clearcut logged openings were mostly <30 years old and 60–100 ha and collectively covered about 12% of the study area (DeLong and Tanner 1996).

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Table 1. Fix-acquisition schedules and performance measures for Global Positioning System (GPS) collars on grizzly bears in central British Columbia, Canada, between 1998 and 2003.

Bear No.	Bear Sex	Age of accompanying cubs (yr)	Landscape occupied	Scheduled GPS fix attempts (no./day)	Dates operational	Days operational (n)[a]	Fixes acquired (n)	Fix rate (%)
4	F		Mountain	6	12 May 2001–7 Aug 2001	89	225	42
7	F		Mountain	6	10 May 2001–28 Jul 2002	324	1,424	73
9	F	2	Mountain	6	28 May 2001–24 Sep 2002	364	1,374	63
11	F	2,3	Mountain	6	11 May 2001–30 Sep 2002	387	1,348	58
15	F		Mountain	6[b]	15 May 1998–1 Oct 1999	384	667	60
16	F		Mountain	6[b]	15 May 1998–21 Nov 1999	435	831	64
17	F		Mountain	6	28 May 2001–2 Jun 2002	250	918	61
21	M		Plateau	6[b]	20 May 1998–9 Sep 1998	112[c]	49	14
26	F	1	Plateau	6	3 Oct 2001–20 Sep 2002	232	754	54
29	M		Mountain	6	26 May 2001–23 Aug 2002	334	1,012	50
34	F		Plateau	6	8 May 2001–13 May 2002	250	855	57
38	F		Plateau	6	18 Sep 2000–12 May 2001	114[c]	53	8
39	M		Plateau	6	19 Sep 2000–6 May 2001	109[c]	105	16
43	F		Mountain	6	10 May 2001–8 Aug 2001	91	308	56
44	F		Plateau	6	11 May 2001–14 Aug 2001	96	367	64
45	M		Mountain	6	12 May 2001–22 May 2001	11	56	85
49	F	1	Plateau	6	21 May 2001–3 Jul 2001	45	79	30
51	M		Plateau	6	27 May 2001–20 Jul 2001	57	139	42
55	M		Plateau	12	12 Jun 2002–8 Aug 2002	58	330	47
56	F		Plateau	12	28 May 2002–4 May 2003	223	1,332	50
57	F	2	Plateau	12	18 May 2002–21 Sep 2002	127	1,050	69

[a] Excluding denning period 1 Dec–31 Mar.
[b] Scheduled to acquire fixes only every second day.
[c] Data not used because technical problems resulted in the collar collecting locations at unscheduled times.

The mountain portion of the study area ranged from 700 m to 2,500 m asl, with hybrid white–Engelmann spruce–subalpine fir forests at lower elevations and alpine parkland and alpine tundra above 1,400 m, the latter constituting about 30% of the area. Logged areas were rare and confined to lower elevations.

METHODS

Between 1998 and 2003 we obtained GPS locations from 21 grizzly bears collared with GPS receivers (Televilt GPS Simplex collars; Televilt International, Lindesburg, Sweden). All bear captures were approved by the University of Alberta Animal Care Committee (Protocol 307204). We scheduled 18 collars to acquire a position fix every 4 hours for 6 fixes per day (e.g., 0115 hr, 0515 hr, 0915 hr), hereafter referred to as 6 fix-per-day collars, and we scheduled 3 collars to acquire a position fix every 2 hours for 12 fixes per day, starting at 0015 hr (hereafter 12 fix/day collars; Table 1). We report all times in Pacific Standard Time. We scheduled collars on bears 15, 16, and 21 to collect fixes only every second day, but we scheduled all other collars to acquire fixes every day. We scheduled GPS receivers in the collars on bears 15, 16, and 21 to remain on for up to 240 seconds versus 180 seconds for all other collars. Collars on bears 21, 38, and 39 malfunctioned and did not collect useful data. Collars on bears 21, 38, and 29 collected fixes on only a small fraction of their scheduled attempts, and most of the position fixes they did acquire occurred at unscheduled times (Table 1). All collars were equipped with a very high frequency (VHF) beacon that transmitted at 60 beats per minute when the bear was moving, switching after about 5 seconds to 40 beats per minute when the bear was still.

We attempted to locate the 21 GPS-collared bears and up to 40 VHF-collared grizzly bears, from 1998 to 2003, up to twice per week during daylight from a fixed-wing aircraft. We arbitrarily varied order of relocation on any given day to reduce potential for temporal bias. We recorded date and time, the bears' location using a GPS in the aircraft, and, starting in 2001, a visual estimate of percentage canopy cover. We took a Polaroid (Polaroid Corporation, Waltham, MA) picture of the site and immediately marked the bear's location on the photograph.

We visited about 20% of nonden locations determined from aerial VHF telemetry (412 of 2,005 locations), usually within 7 days and after the bear had left the area (Ciarniello 2006). We visited a random selection of sites, excluding those that were inaccessible by either foot or helicopter. Using the coordinates and the site photograph, we went to where we located the bear during the VHF telemetry flight and centered our measurements where there was the most bear sign. At each site, we estimated canopy cover and inferred from sign the bear's primary activity, feeding, resting, moving, or scent-marking, at the time we located it. Sign we detected during our site visits was most likely from the collared bear when it was located during the VHF telemetry flight and not subsequently from the same or another bear, because collared bears showed no site fidelity over short time periods, and on the plateau, grizzly bear density was low (Mowat et al. 2005). Further, we have conducted hundreds of site investigations and would have recognized sign if it had been substantially fresher than expected.

We indexed grizzly bear activity patterns for the 3 bears that had 12 fix-per-day collars, by calculating distance moved during the 2 hours between fixes. If a fix was missed we did not calculate a movement rate. We compared cover use to time of day based on aerial telemetry locations and related grizzly bear activity to canopy cover using our site investigation data. We compared afternoon GPS fix rates to air temperatures at 1400 hours, reasoning that if grizzly bears are sensitive to heat stress as suggested by Mattson and Merrill (2002), they may respond to warmer temperatures by resting in the shade. We used the temperature recorded at the Prince George airport (Environment Canada 2002), which was about 100 km southwest of the center of the study area, and assumed those temperatures to be representative of the plateau portion of the study area.

To determine combined effect of canopy cover and the GPS collar's antenna orientation on fix rates we used 16 combinations of 3 stationary collars, 5 areas, and 5 canopy covers ranging from 0% to 75%, in a representative forest stand in flat terrain on the southern edge of our study area. We estimated percentage canopy cover visually. In each area, we suspended a randomly selected collar 60 cm above the ground with its antenna oriented vertically, representing a bear standing on all 4 feet, and we put another collar on the ground with its antenna oriented horizontally to represent a bear lying on its side. We oriented horizontal collars along random azimuths to avoid biasing fix rates, in case fix acquisition was sensitive to variation in the density and proximity of nearby trees. We tested all 3 collars in both the vertical and horizontal positions. We scheduled collars to acquire a fix every hour and left them in each area for between 31 and 345 fix attempts ($\bar{x} = 96$). We conducted tests between 12 September and 19 October 2003. Leaf-off unlikely affected our results because tests were in spruce and subalpine fir stands and the few deciduous trees still retained most of their leaves.

We defined spring, summer, and autumn based on generalized grizzly bear diets, which were related to plant phenology (Ciarniello 2006). Spring lasted from den emergence until 14 July when bears switched from eating green vegetation to ripe summer berries. Autumn lasted from 21 September, when above-ground portions of plants became senescent and bears switched to eating roots, until bears entered their dens. At the midpoints of those 3 bear seasons (22 May, 17 Aug, and 11 Oct), sunrise and sunset times were 0358 hours and 2019 hours, 0453 hours and 1936 hours, and 0631 hours and 1723 hours Pacific Standard Time for spring, summer, and autumn, respectively (National Research Council of Canada 2007).

We fit fix rates and movement rates to a fifth-degree polynomial using Statistica Version 6.0 (Statsoft Inc., Tulsa, OK) and used logistic regression to relate the probability of obtaining a fix at 1415 hours to air temperature at 1400 hours. We looked for variation in canopy cover use (canopy cover = 0 and canopy cover > 0) by resting and active grizzly bears in the 2 landscapes (plateau and mountain), using log-linear analysis.

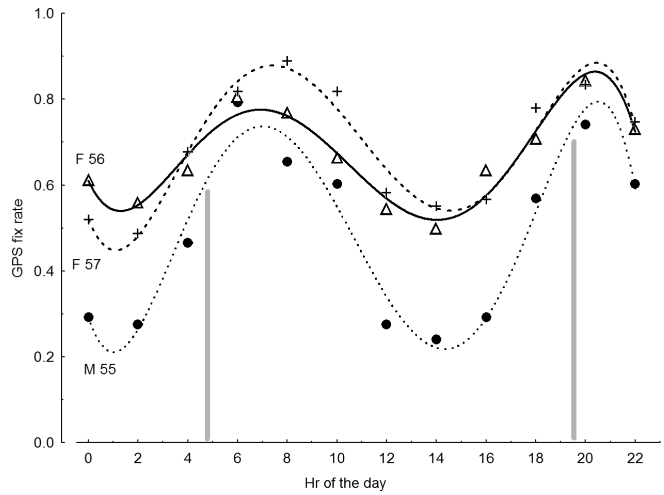

Figure 1. Circadian pattern of Global Positioning System (GPS) collar fix rates from 3 grizzly bears carrying collars that attempted 12 fixes per day, in central British Columbia, Canada, in 2002 and 2003. Curves are fifth-order polynomials. Vertical lines represent midsummer sunrise and sunset times.

RESULTS

Fix rate for the 3 plateau bears with 12 fix-per-day collars (bears 55, 56, and 57; Table 1) followed a bimodal circadian pattern, with minima after noon and after midnight and maxima after sunrise and around sunset (Fig. 1). Potential for location bias was high because minimum fix rates were only about half of the maximum fix rates. Neither sex nor presence of accompanying cubs appeared to be related to the circadian fix-rate pattern, but fix rates for the male (bear 55) were always lower than that for the 2 females, one of which was accompanied by offspring (bear 57). A bimodal circadian fix-rate pattern was evident in the data from all 3 bears in spring and summer. There was no pattern to circadian fix rates in autumn for bear 56, the only animal for which we had autumn data, nor for bear 57 in late summer (1–22 Sep).

Even with only half the number of potential locations per day, the mean fix-rate pattern among the 15 bears carrying the 6 fix-per-day collars also followed a bimodal circadian pattern but with only a small afternoon decline. Mean afternoon fix rate was 95% of the mean maximum fix rate. Of the 15 collars, 13 had their lowest fix rates in the middle of the night (0100 hr). The 2 exceptions (49 and 51) may not have been functioning properly given that they had the lowest overall fix rates, low total number of fixes (Table 1), and were the only 2 plateau bears not to have low afternoon fix rates.

Fix rates varied with canopy cover at the landscape scale, and with air temperature. Global Positioning System collars on bears that lived in the more open mountain environment tended to have higher fix rates than did collars on plateau dwelling bears ($\bar{x}_{\text{mountains}} = 61.2\% \pm 1.18$ SE, $n = 10$; $\bar{x}_{\text{plateau}} = 49.4\% \pm 2.69$ SE, $n = 5$; $t = 1.733$ for arcsine

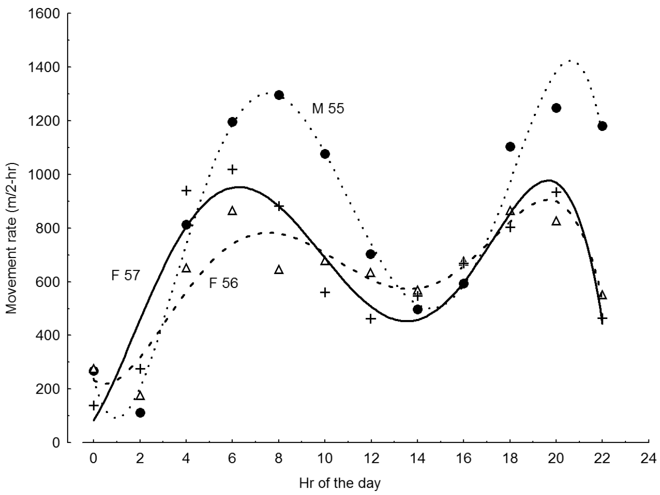

Figure 2. Circadian pattern of movement rates for 3 grizzly bears carrying collars that attempted 12 fixes per day, in central British Columbia, Canada, in 2002 and 2003, where movement was based on the 2-hour interval beginning at the indicated time.

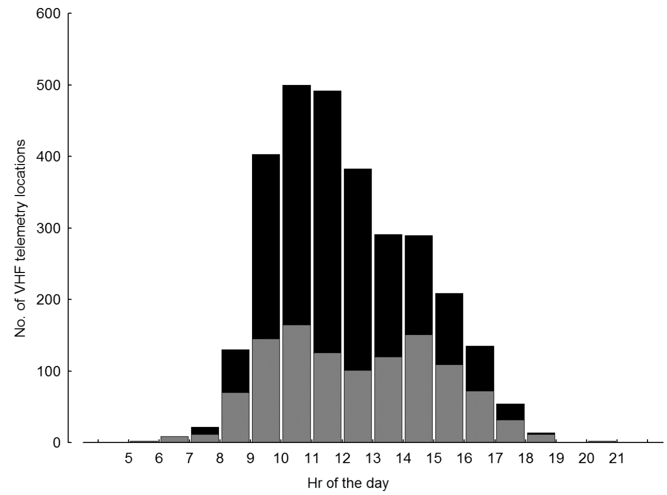

Figure 3. Number of very high frequency (VHF) telemetry locations, by 1-hour intervals throughout the day, for plateau (grey) and mountain (black) grizzly bears in central British Columbia, Canada, between 1998 and 2003.

sq-root transformed percentages, df $= 13$, $P = 0.10$). The probability of a missed fix increased with midday air temperature for all 3 12 fix-per-day bears ($P < 0.002$ in all cases; where P represents the probability that the effect of adding temperature, to an intercept-only model, could have occurred by chance).

Grizzly Bear Activity and Canopy Cover Use

For the 3 bears with 12 fix-per-day collars, movement rates showed a bimodal circadian pattern similar to the fix rates (Fig. 2), and movement rates and fix rates were linearly related (adj$R^2_{\text{bear 55}} = 0.79$, $P < 0.001$; adj$R^2_{\text{bear 56}} = 0.30$, $P < 0.04$; adj$R^2_{\text{bear 57}} = 0.47$, $P < 0.001$). The male (bear 55) had a greater maximum movement rate than the 2 females (1,296 m/2-hr vs. 1,018 and 867 m/2-hr; Fig. 2), but female fix rates averaged 4 times higher than the male for a given movement rate.

Grizzly bear's use of canopy cover varied with time of day. We obtained all aerial VHF telemetry locations between 0535 hours and 2020 hours (Fig. 3), and we obtained 65% between 1100 hours and 1700 hours, the 6-hour period in the middle of the day when GPS fix rates were lowest. For the 753 locations where we recorded canopy cover we located fewer bears in the open during those midday hours (28% of 194 locations) than at other times (33% of 559 locations).

Grizzly bear's use of canopy cover depended on their activity. We classified the primary activity at the 412 bear telemetry locations we visited as resting ($n = 39$) or active ($n = 373$; feeding $n = 336$, moving $n = 33$, at a rub tree $n = 4$). In both landscapes, we observed a smaller fraction of resting sites in the open than active sites (Table 2). The overall log-linear model fit the frequency data (Pearson $\chi^2_1 = 1.88$, $P = 0.39$) and showed that resting sites were less likely to be in the open, after accounting for the landscape effect (marginal $\chi^2_1 = 18.1$, $P < 0.001$). Where canopy cover was present, mean canopy cover at resting sites was higher than where a bear was active ($F_{1,169} = 27.04$, $P < 0.01$, for arcsine-transformed percentages) in both mountain and plateau landscapes ($P = 0.24$).

Fix Rates Versus Collar Orientation and Canopy Cover

Test collar fix rates showed that collar orientation interacted with canopy cover ($F_{3,12} = 10.8$, $P = 0.001$, adj$R^2 = 0.66$) such that fix rates declined much more with increasing canopy cover when the collar was on its side than when the collar was upright (Fig. 4). Inherent variation in fix success rates among test collars was low because all 3 collars obtained between 94% and 97% fixes when oriented upright in the open.

DISCUSSION

Our results suggest that environmental factors and animal behavior can interact to affect GPS collar fix rates. Our data were consistent with all 4 of the predictions we set out as tests of our animal activity—environmental factor interaction hypothesis. The circadian fix-rate pattern we observed could not be the result of bimodal circadian patterns in satellite availability because the satellite configuration changed gradually, occurring 3 minutes later every 24 hours (A. Harrington, Trimble Navigation Limited, personal communication).

Grizzly bear movement rates followed a bimodal circadian pattern similar to the circadian pattern in GPS fix rates both in our study and in Montana (Waller and Serveen 2005, Graves and Waller 2006). Moreover, movement rates appeared to be a good index of general grizzly bear activity patterns, because they correlated with fine-scale activity. McCann (1991) used motion-sensitive collars and chart recorders to determine the fraction of time grizzly bears were active by hour of the day for a sample of free-ranging grizzly bears in the Flathead River valley in southern British Columbia and northern Montana, USA. McCann (1991) showed that grizzly bears of both sexes and 2 age categories followed a bimodal circadian activity pattern that was

Table 2. Canopy cover used by active and resting grizzly bears in mountain and plateau landscapes in central British Columbia, Canada, between 1998 and 2003.

Landscape activity	Sites where canopy cover = 0 *n*	%	Mean canopy cover for sites where canopy cover > 0 *n*	%
Plateau				
Resting	28	11	25	61
Active	237	50	118	36
Mountain				
Resting	11	64	4	63
Active	136	81	26	19

strikingly similar to the circadian movement and GPS fix-rate pattern of the 3 12 fix-per-day bears in our study (Fig. 5). Movement rates of all 3 12 fix-per-day bears in our study correlated with McCann's mean hourly activity measures for spring and summer ($P < 0.04$ in all 3 cases). Data fortuitously recorded during a concurrent study (M. Wood, Peace-Williston Fish and Wildlife Compensation Program, personal communication) showed that fix rate was directly related to grizzly bear activity. A VHF data-logger recorded the pulse rate, indicating collar motion, from bear 57's collar on 11 occasions within 15 minutes (an arbitrary cut-off time) of a GPS fix attempt. Of those attempts, 9 (82%) were consistent with our expectations. Of 8 possible fixes 7 were missed when the bear was inactive, whereas only 1 of 3 possible fixes were missed when the bear was active (Yates corrected χ^2 1-tailed test, $P = 0.15$). Our data showing that grizzly bears rested under higher canopy covers than where they fed was consistent with other studies (McLellan and Hovey 2001, Munro et al. 2006).

Fix Rates Versus Collar Orientation and Canopy Cover

The decline in fix rates of our vertically oriented test collars with increasing canopy cover was almost identical to that shown by Frair et al. (2004) for upright collars made by Televilt International (slope = 0.0016 for this study vs. 0.0015 for Frair et al. [2004]). The decline in fix success for our collar orientation tests for collars in the open was similar to that shown by D'Eon and Delparte (2005), but we are the first to show the interaction between orientation and canopy cover.

Potential Solutions

The most obvious solution to GPS bias is to pursue options that will result in 100% fix rates. Our attempt to increase fix rate by having the receivers on bears 15, 16, and 21 remain on for 240 seconds as opposed to 180 seconds did not result in higher fix rates (Table 1). Leaving the GPS receiver on until it obtains a fix, or scheduling repeated fix attempts until successful, will not remove location bias (even for a fix rate of 100%) if a successful fix was obtained only because the bear moved to a different microsite (i.e., a distance greater than the min. patch size of interest). Perhaps manufacturers could install multiple antennas around the collar so that one antenna is always pointing toward the sky. If behavior could be reliably predicted (e.g., feeding and resting from activity sensors in collars; Coulombe et al. 2006, Gervasi et al. 2006), then each behavior could be analyzed independently.

At a minimum, statistical corrections for GPS bias will require knowledge of both the canopy cover an animal might have used (e.g., Frair et al. 2004) and as we have shown, the behavior of the animal when it was there. Estimating those correction factors was beyond the scope of our study, but even if we had done so those correction factors would be unlikely to have general application for other species and other environments.

Without more direct measures, collar fix rates may be useful metrics for ecological interpretation themselves, or at least suggest areas for further study. For example, the change in the circadian fix-rate pattern in late summer and autumn for bears 56 and 57 suggests a temporal change in foraging strategy. Population differences in foraging strategies and food availability may be reflected in fix rates. Changes in fix rate may be used to index activity changes from diurnal to nocturnal activity because of disturbance (e.g., Gibeau et al. 2002, Nielsen et al. 2004). Data suggest that analysis of grizzly bear behavior by subjective divisions that center on midday, midnight, and crepuscular periods may not be the most efficient way to lump periods of similar activity (e.g., Gibeau et al. 2002, Nielsen et al. 2004, Munro et al. 2006). Our data suggest bears are most active after sunrise (0600 hr to 1000 hr) and least active after noon (1000 hr to 1600 hr) and after midnight (0000 hr to 0400 hr; Fig. 1).

Global Positioning System Bias Relative to VHF Bias

Few, if any, techniques are perfect, so problems associated with GPS location biases need to be considered in relation to alternative methods. Relatively new techniques, like GPS telemetry, are received with enthusiasm, but are then interpreted with caution after field application exposes some problems and limitations. As techniques become more established, critical analysis of their potential problems may be ignored, which appears to be the case with VHF telemetry. Aerial VHF telemetry does not necessarily provide an accurate and unbiased sample of an animal's locations. It is possible, for example, that an animal may move to a different microhabitat in response to the noise or sight of the approaching aircraft. The most obvious and frequently ignored bias is that aerial VHF telemetry

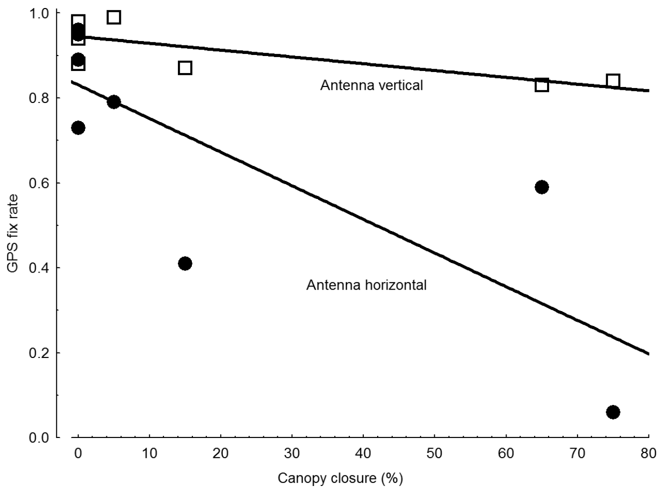

Figure 4. Effect of collar orientation and canopy cover on Global Positioning System (GPS) fix rates using test collars in central British Columbia, Canada, 12 September to 19 October 2003. Fix rate = 0.94 − 0.12 × orientation − 0.0016 × canopy cover − 0.0062 × (orientation × canopy cover), where upright antenna orientation = 0 and horizontal antenna orientation = 1.

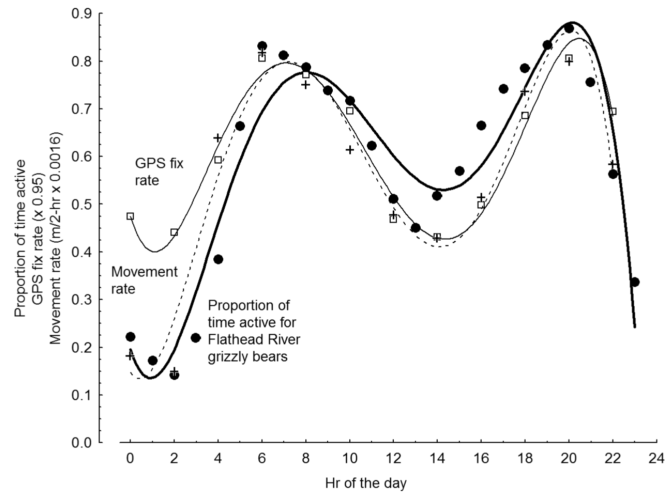

Figure 5. Circadian patterns in the proportion of time active for grizzly bears in the Flathead River, British Columbia, Canada, 1984 to 1988 (McCann 1991), and mean Global Positioning System (GPS) fix rates and mean movement rates of the 3 12 fix-per-day collars in central British Columbia, Canada, in 2002 and 2003. We scaled fix rates and movement rates to provide maximum overlap with activity. Curves are fifth-order polynomials.

locations represent only daytime locations but are sometimes interpreted as if they constitute a representative sample of an animal's locations (e.g., Beyer and Haufler 1994, Mace et al. 1996, Wielgus and Vernier 2003, Beier et al. 2006, Ciarniello et al. 2007). In contrast to ignoring potential behavioral variation between day and night, grizzly bear biologists often appreciate and account for sex and seasonal differences in grizzly bear behavior (e.g., Nielsen et al. 2004). The bimodal pattern of activity we showed for grizzly bears also demonstrates that VHF telemetry (either aerial or ground-based) could be biased by time of day when locations were obtained. We obtained 65% of our VHF locations between 1100 hours and 1900 hours (Fig. 3), daylight hours when bears were in denser cover and more likely to be resting (Figs. 1, 2, 5). That situation was not unusual. Mace et al. (1996:1396) stated that "Most locations were obtained during the morning when flight conditions were best." Wielgus et al. (2002:1598) stated that all bears were located between 0600 hours and 1200 hours, ". . . so interpretation of habitat use is restricted to daytime only," thereby implicitly assuming those morning data were representative of other times of day. Variation within individuals would be underestimated and among individuals overestimated, if animals were located at the same time each day.

MANAGEMENT IMPLICATIONS

We have shown that grizzly bear's microhabitat use, based on GPS collar locations, will underrepresent high-canopy cover sites, especially when grizzly bears are resting there. Managers should recognize that all telemetry methods, including VHF telemetry, are subject to some bias, and if they do not account for that bias they will form incorrect conclusions about the value of different microsites to grizzly bears. Collecting additional information on circadian grizzly bear behavior patterns and behavior in different microsites will help to better understand those biases and account for them during their interpretation of the data. The interactive effect of canopy cover and animal behavior on GPS fix rates is unlikely unique to grizzly bears, but bias will almost certainly vary among species and environmental conditions.

ACKNOWLEDGMENTS

This paper is one of a series resulting from the Parsnip Grizzly Bear Project (http://web.unbc.ca/parsnip-grizzly/), which was funded primarily by Forest Renewal British Columbia (1998–2001) and the Forest Investment Account (2002–2003), through Canadian Forest Products Ltd. Additional support was provided by the Pas Lumber, Slocan Forest Products Ltd., British Columbia Ministry of Environment, British Columbia Ministry of Forests and Range, Natural Sciences and Engineering Research Council of Canada, and University of Alberta. We thank E. Jones, C. Mamo, J. Paczkowski, I. Ross, G. Watts, and M. Wood of the Peace-Williston Fish and Wildlife Compensation Program for providing field and logistical support. We appreciated constructive comments on the manuscript provided by D. Strickland and 2 anonymous reviewers and the superb flying skill provided by G. Altoft, L. Frey, K. Knight, and C. Norment.

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Associate Editor: Strickland.