**Tools and Technology Article**

**Effects of Species Behavior on Global Positioning System Collar Fix Rates**

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**ABSTRACT** Use of Global Positioning System (GPS) telemetry is increasing in wildlife studies and has provided researchers and managers with new insight into animal behavior. However, performance of GPS collars varies and a major concern is the cause of unsuccessful fixes. We examined possible factors causing missed fixes in GPS collars on sympatric free-ranging Eurasian lynx (Lynx lynx) and wolverines (Gulo gulo) in northern Sweden. We tested for effects of species, activity, habitat, individual, and collar on fix rate. Species was the most important factor affecting fix rate. Fix rate of GPS collars on lynx (80%) was almost twice as high as on wolverines (46%). Fix rate decreased during periods of low activity (day beds) for both species. Fix rate also decreased for females (both lynx and wolverine) for a period after they gave birth. We found no effect of proportion of forest within individual home range on fix rate. We conclude that species behavior, characteristics, and activity pattern are important factors affecting fix rate that we recommend be taken into consideration prior to analyzing GPS location data.

**KEY WORDS** activity pattern, behavior, fix rate, Global Positioning System, *Gulo gulo*, *Lynx lynx*.

Use of Global Positioning System (GPS) telemetry is increasing in wildlife studies and the technology is constantly developing (Rodgers 2001). Global Positioning System telemetry has provided researchers and managers with new insights into animal behavior. However, use of this technology also raises new issues for consideration. Accuracy and precision of GPS locations have been discussed extensively, particularly in relation to studies of habitat selection (Rempel et al. 1995, Edenius 1997, Moen et al. 1997, Hansen and Riggs 2008). Today, with improved GPS technology, accuracy and precision are less critical because location error of high-quality fixes is often less than the error of most habitat maps (Rempel and Rodgers 1997, Hulbert and French 2001). Another major concern is instead the cause, and the extent of, unsuccessful fixes (Frair et al. 2004, Graves and Waller 2006, Hebblewhite et al. 2007). If fix rate is influenced by behavior or habitat type, analyses can be biased and lead to misinterpretation of habitat selection, for instance.

Effect of collar model, terrain, and vegetation on fix rate and quality of fixes has been studied extensively, but recently more studies have focused on the importance of animal behavior on GPS collar performance (Bowman et al. 2000, Moen et al. 2001, Graves and Waller 2006, Heard et al. 2008). Studies on stationary test collars have shown a lower fix rate when collars are placed horizontally compared to vertically, mimicking standing and bedded animals, respectively (D’Eon and Delparte 2005, Heard et al. 2008, Jiang et al. 2008).

Studies on white-tailed deer (Odocoileus virginianus), red deer (Cervus elaphus), and grizzly bears (Ursus arctos) have shown a decrease in fix rate when animals are inactive or bedded (Bowman et al. 2000, Graves and Waller 2006, Zweifel-Schielly and Suter 2007, Heard et al. 2008). In contrast, a study on moose showed an increase in fix rate when animals were inactive (Moen et al. 2001). Furthermore, no difference was observed between standing or moving white-tailed deer (Bowman et al. 2000). Several authors have discussed the possibility of species-specific influence on fix rate (D’Eon 2003, Hebblewhite et al. 2007), but to our knowledge no study has confirmed species-specific differences in fix rate.

Most studies have tested performance of GPS collars weighing >500 g on medium-sized to large mammals. Little information is available for collars <300 g on small and medium-sized mammals (but see Cargnelutti et al. 2007). One specific concern with smaller collars is battery life. It is therefore important when planning a GPS study to consider factors influencing battery use (e.g., search time and fix interval) to optimize longevity of the collar (Cain et al. 2005, Jiang et al. 2008).

Our objective was to examine factors affecting performance of GPS collars fitted interchangeably on free-ranging individuals of 2 sympatric medium-sized carnivore species, Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*). We focused on the influence of species and their activity pattern on fix rate but included habitat and individual differences.

**STUDY AREA**  
We conducted our study in and around Sarek National Park in northern Sweden (Kvikkjokk: 67°00’N, 17°40’E). The study area was characterized by deep valleys, glaciers, and high plateaus with peaks up to 2,000 m. Vegetation was primarily alpine tundra at higher elevations, sparse mountain birch forest (*Betula pubescens*) in higher valleys and

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hillsides, and mixed conifer forest with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) at lower elevation. Mountain birch formed the tree line at 600–700 m and elevation ranged from 300 m to 2,000 m. In addition, we studied lynx in the lowland of the counties Norrbotten, Västerbotten, and Jämtland (ranging 61°80’–66°80’N, 12°50’–23°80’E). This area was dominated by mixed conifer forest scattered with wetlands and some alpine tundra. Both areas had medium-warm summers and cold winters with snow-covered ground for approximately 6 months.

**METHODS**

From 2002 to 2006, we equipped 28 lynx (13 lynx in the Sarek area and 15 lynx in the forested lowland) and 20 wolverines with 20-channel store-on-board GPS collars weighing approximately 300 g (Televilt PosrecTM C300, TVP positioning AB, Lindeberg, Sweden). Global Positioning System fixes were stored within the collar and were accessible after retrieval of the collar. We captured animals by darting from a helicopter or from the ground. We immobilized animals with a mixture of ketamine and medetomidine, following preestablished protocols (Arnemo and Fahlman 2008). Handling protocols were examined by the Animal Ethics Committee for northern Sweden and fulfilled the ethical requirements for research on wild animals.

We used 41 GPS collars, 12 of which were lost in the field and 5 of which were lost when used the first time (see below). Thus, in the analyses we used 36 collars and 42 individuals (lynx: 22 F, 3 M; wolverine: 13 F, 4 M). We defined a GPS period as a unique combination of one collar and one individual during one battery-life length. We equipped the same individual with a GPS collar ≤7 times resulting in 82 GPS periods (26 individuals for 1 period, 5 individuals for 2 periods, 4 individuals for 3 periods, 3 individuals for 4 periods, 3 individuals for 5 periods, and 1 individual for 7 periods). We removed one GPS period from analyses because of collar malfunction.

We programmed all collars to acquire a GPS fix every third hour (8 fixes/day). We set maximum search time to acquire a fix to 90 seconds. Fixes were classified, by the manufacturer, into 4 categories depending on number of satellites used: 1) 1-dimensional (1D) using 1–2 satellites, 2) 2-dimensional (2D) using 3 satellites, 3) 3-dimensional (3D) using 4 satellites or 4) 3-dimensional (3D+) using ≥5 satellites. One-dimensional is an inaccurate, low-quality fix and 2D is often an inaccurate fix, whereas 3D and 3D+ are usually accurate fixes (Moen et al. 1996, Dussault et al. 2001, D’Eon et al. 2002). Elevation and dilution-of-precision values (values for possible error of GPS fixes) were not available. Geographic coordinates were transformed to the Swedish national grid, RT90, by the manufacturer.

We fitted all collars, except one, with a drop-off function programmed to release when the battery of the GPS unit was depleted. However, in 35% of GPS periods, release mechanisms failed. We fitted all lynx and wolverines in Sarek with an intraperitoneally implanted very-high-frequency (VHF)-transmitter to facilitate long-term monitoring of individual animals, which made it possible to recapture the animal and remove the collar manually when drop-off failed. Still, 11 collars vanished because we lost contact with the collared animal (n = 6) or the collar after it fell off the animal (n = 5). In one case the collar dropped where we could not reach it.

We reused collars, after refurbishment and battery replacement, up to 5 times (8 collars refurbished once, 16 collars twice, 7 collars 3 times, 3 collars 4 times, and 2 collars 5 times). Until 2006, 6 of the collars we used 2–4 times were too damaged to be refurbished.

**Statistical Analyses**

We analyzed differences in search time in relation to species and fix quality using a 2-way analysis of variance (ANOVA). We tested the effect of shortening search time on quality and quantity of acquired fixes. We grouped fixes into accurate fixes (3D and 3D+) and inaccurate fixes (1D and 2D). Although we set collars to a maximum search time of 90 seconds, 2.2% of all fixes had search times >90 seconds. The manufacturer explains this to be the result of a malfunction in an older version of the firmware used in the GPS receivers. We included only positions with a search time of ≤90 seconds in the analyses.

We calculated 3 types of fix rate by dividing the acquired fix number by the expected fix number (i.e., operational days ∗ 8): 1) a total fix rate per GPS period, 2) a monthly fix rate per GPS period using month with >7 operational days, and 3) a circadian fix rate for each programmed hour per GPS period.

To test if the number of GPS periods for which we used a collar influenced its performance, we used analysis of covariance (ANCOVA) with number of GPS periods as a covariate and collar as a random factor. We used only 28 collars multiple times (wolverine: ≤5, lynx: ≤4) for a total of 73 GPS periods. We used 12 of these collars on both wolverine and lynx. We used Wilcoxon Signed Rank test to test the effect of species on fix rate independent of collar while controlling for order of use.

To analyze fix rate in relation to habitat we created separate home ranges for each GPS period using the 100% minimum convex polygon (MCP) method in ArcView 3.2a. We used a broad-scale vector map (overview map, geographic data of Sweden, scale 1:250,000; Swedish National database for geographic information and maps [Lantmäteriet], Gäve, Sweden) to calculate habitat composition for each home range. The map categorized habitat into tundra, forest, wetland, open land, or water. Forest included both birch and conifer forest. One GPS period had fix data in Norway and was not covered by the available habitat map. We excluded these fixes (16%) before estimating home range. We used general linear models to analyze the effect of proportion of forested area within the MCP on fix rate.

We estimated animal activity as movement rate (m/hr) by calculating the straight-line distance between 2 fixes (3 hr in
between). If a fix was missed we did not calculate movement rate. Movement rate is not an exact measure of activity but has been shown to be a good index of general activity patterns in grizzly bear (Heard et al. 2008). We related movement rate to fix rate for every programmed fix time (n = 8) in each GPS period. In addition, we related all fixes to a specific habitat type using the same map as above. We calculated the proportion of fixes in forest at each programmed fix time for each GPS period to get an index of diurnal changes in habitat use. We performed a separate ANCOVA for lynx and wolverine with fix rate as the dependent variable, activity as the covariate, and GPS period as a random factor. In this analysis we only used GPS periods from the Sarek area (n = 65), because the lynx and wolverine overlap spatially in this area and we collared no wolverine outside it. Thus, some effect of variation in available habitat between the species was excluded.

We used monthly fix rate to test for seasonal variation in fix rate. In addition, we defined a denning period for each species: February–May for wolverine and June–August for lynx. Within the denning period we classified months depending on presence (F only) or absence of offspring (F + M). Females of both species stay close or nearby one spot for an extended time after giving birth (Land et al. 1998; J. Mattisson, Grimso Research station, unpublished data) so we expected that fix rate would be affected by an altered activity pattern of females with dependent offspring during the first months after birth. We used ANOVA with monthly fix rate as the dependent variable, month and offspring as fix factors, and GPS periods as a random factor. Because lynx and wolverine denning periods differ in both length and time of year we performed separate analyses for each species. We conducted all analyses using SPSS 14.0 for Windows (SPSS Inc., Chicago, IL).

**RESULTS**

Average search time for a fix was 51.5 seconds (median 43 sec). Search time increased when fix quality decreased (F3,51928 = 120.6, P < 0.001). Collars on wolverines had longer (4-sec) search time than collars on lynx (F1,51928 = 27.1, P < 0.001) and this pattern was consistent for each quality type (F3,51928 = 4.58, P = 0.003; Table 1). Collars on both lynx and wolverines had a high proportion of 3D fixes (lynx: \( \bar{x} = 0.86, SE = 0.005, n = 45 \); wolverine: \( \bar{x} = 0.78, SE = 0.019, n = 36 \)). Decreasing maximum search time from 90 seconds to 80 seconds resulted in a loss of only 1% of accurate fixes and 5% of inaccurate fixes (Fig. 1). Further decrease in maximum search time did, however, result in a rapidly decreasing number of fixes.

Mean fix rate for GPS collars on lynx (80%) was almost twice as high as mean fix rate for GPS collars on wolverines.
(46%; Table 2). Fix rate was always higher for collars on lynx than on wolverine, independent of internal order of use or individual collar (lynx to wolverine: $Z = 2.52, P = 0.012$, $n = 8$; wolverine to lynx: $Z = 1.83, P = 0.068$, $n = 4$). Fix rate decreased on average 47% when moved from lynx to wolverine and increased 33% when moved from wolverine to lynx. Species, when included as a factor in the analysis, always had a strong effect ($P < 0.001$).

Performance of collars declined continuously with number of times used on wolverines but not on lynx (species: $F_{1,69} = 5.44, P = 0.023$; species $\times$ time used: $F_{1,69} = 3.19, P = 0.079$). We estimated a 31% decrease in fix rate from first to fourth time used on wolverines. In contrast, the effect of times used was none or slightly negative on collars used on lynx (3% from first to fourth time used).

Proportion of forested area within home ranges did not influence fix rate on either species (forest: $F_{1,77} = 1.96, P = 0.17$; forest $\times$ species: $F_{1,77} = 1.17, P = 0.28$) even though proportion of forested area ranged from 6% to 86% for lynx and from 0% to 76% for wolverine (Fig. 2).

Fix rate for both lynx and wolverine followed a circadian pattern with a minimum fix rate during midday to afternoon (Fig. 3A). The movement rate showed a similar pattern with a minimum fix rate during midday to afternoon and from 0% to 76% for wolverine (Fig. 2).

Most variation in monthly fix rate was explained by GPS performance (offspring: $F_{1,239} = 72.7, P < 0.001$; lynx: $F_{2,208} = 55.4, P < 0.001$), whereas there was no effect of use of forest (wolverine: $F_{1,239} = 0.17, P = 0.68$; lynx: $F_{1,208} = 2.95, P = 0.09$). Altogether, this implies that fix rate is influenced negatively by low activity but not by use of forest. However, most variation in fix rate was explained by GPS period (wolverine: $F_{34,239} = 30.8, P < 0.001$; lynx: $F_{29,208} = 15.6, P < 0.001$).

We observed a seasonal difference in fix rate for both species. The highest monthly fix rate for wolverine (Aug: $\bar{x} = 61.2 \pm 2.40\%$ [SE]) matched the lowest monthly fix rate for lynx (Jun, all lynx pooled: $\bar{x} = 61.3 \pm 3.73\%$). Months with lowest fix rates coincided with denning months for each species (Fig. 4). For lynx, fix rate was lowest in June and July ($F_{1,161} = 16.4, P < 0.001$). Presence of offspring only influenced fix rate in June, decreasing fix rate from 71 ± 3.87% without offspring to 45 ± 3.94% with offspring (offspring: $F_{1,161} = 4.039, P = 0.046$; month $\times$ offspring: $P < 0.001$).

**DISCUSSION**

Species was the most important factor affecting fix rate of GPS collars fitted on lynx and wolverines. Fix rate for collars on wolverines (46%) was at the lower end of fix rates reported in the literature on wild animals, whereas for lynx (80%) it was at the upper end (Cain et al. 2005), similar to fix rate of collars on Canada lynx (*Lynx canadensis*; Burdett et al. 2007). The lower fix rate of GPS collars on wolverines could not be explained by collar brand or individual collar, because the same collars have been used on lynx. The difference in fix rate is most likely affected by species behavior and physiology.

Lynx and wolverines in our study area occupy similar habitat and regularly use steep terrain, but wolverines generally show a much stronger preference than lynx for dwelling underneath large boulders (P. Segerström, Grimsö...
Figure 4. Monthly fix rate (proportion of successful fix attempts) for Global Positioning System collars on (A) Eurasian lynx and (B) wolverines in northern Sweden during 2001–2006, presented as means with 95% confidence intervals. We classified denning periods, (A) June–August and (B) February–May, into females with offspring (circles) or individuals without offspring (stars). Sample sizes vary between months (n = 2–34).

Figure 3. Circadian pattern of (A) fix rate (proportion of successful fix attempts), (B) movement rate (mean straight distance travelled between Global Positioning System [GPS] fixes 3 hr apart), and (C) forest use (proportion of successful fixes in forested habitat) for Eurasian lynx (stars) and wolverines (open circles) in northern Sweden during 2001–2006. We calculated mean values for each programmed hour (n = 8) of each GPS period (lynx: n = 46, wolverine: n = 35) and present them with 95% confidence intervals.
Wildlife Research Station, personal observation). This behavior may decrease available sky for the GPS receiver (Cain et al. 2005). Furthermore, collars fitted on wolverines will be closer to the ground than those fitted on lynx because wolverines are short-legged (ht: 36–43 cm) compared to lynx (ht: 60–75 cm; Pasitschniak-Arts and Larivière 1995, Liberg 1998). Collars placed near the ground are more likely to be obstructed visually, causing lower fix rate (Bowman et al. 2000, Graves and Radant 2004). Collars fitted on wolverines often show external damage on retrieval (e.g., scrape marks, beaten edges, worn belt), whereas such damage is rarely seen on collars fitted on lynx. Thus, when reusing collars they may be more sensitive to physical stress, explaining the decreasing performance of collars fitted on wolverines but not on lynx. Altogether, these factors contribute to longer search time, a higher proportion of unsuccessful fixes, and shorter battery life. Hence, species-specific differences may be an important factor affecting the GPS collars' ability to obtain successful fixes.

We documented a marginal increase in forest use during periods of low activity in accordance with previous studies (Bowman et al. 2000, Graves and Waller 2006, Zweifel-Schielly and Suter 2007, Heard et al. 2008). Fix rate followed both a circadian and a seasonal pattern but was less pronounced for wolverines than for lynx. During the daytime when animals were resting, fix rate was low compared to the active period at night (Fig. 3A, B). Temporal variation in satellite availability (Cain et al. 2005) may cause the circadian pattern in fix rate (cf. Sager-Fradkin et al. 2007) but could be neglected in our data because circadian patterns in fix rate differed in time between lynx and wolverine (Fig. 3A).

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We conclude that low activity per se will influence fix rate negatively independent of habitat characteristics, which is supported by previous studies observing decreased fix rate in bedded, compared to standing, animals (Bowman et al. 2000); static test collars placed horizontally compared to vertically (D’Eon and Delparte 2005, Heard et al. 2008, Jiang et al. 2008); or mimicking bedding behavior (Sager-Fradkin et al. 2007). The lack of effect from forest cover, in contrast to previous research (e.g., Di Orio et al. 2003, Frair et al. 2004, Hebblewhite et al. 2007), may be a result of improvement in GPS technology (e.g., better receivers with more channels) in later years (Rodgers 2001). However, we cannot exclude that microhabitat during bedding or denning influence fix rate, but it is hard to distinguish between effects of small-scale habitat and behavior. If fix rate is lower in resting habitat (i.e., low activity) than during other activities, it can result in misinterpretation of the importance of resting habitats when activity is not considered in analyses. Low fix rate will have less effect on movement rates, home range analyses, and predation studies.

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A limiting factor when using GPS telemetry is battery life. Adjusting the preprogrammed search time is one way to preserve battery power. A short search time will increase battery life but decrease precision and lower fix rate (Hansen and Riggs 2008). The optimal search time will vary depending on species, habitat, and design of study, because search time is influenced by activity and fix interval (Jiang et al. 2008) as well as collar model and habitat characteristics (Hansen and Riggs 2008). We recommend not using a maximum search time <90 seconds because the gain in battery life is little and, although decreasing search time will primarily leave out a few low-quality fixes, these could be the only clue to rare habitat use or behavior.

**MANAGEMENT IMPLICATIONS**

Information on individual behavior, such as habitat selection, movement, and activity patterns, are often important for management of wildlife populations. The development and constant improvements of GPS wildlife telemetry offer unique opportunities for researchers and managers to reveal such information. Compared to traditional VHF telemetry, GPS telemetry is less biased through greater sample sizes and higher precision, independent of weather, time of day, or year. Although GPS telemetry is valuable there is still a need for caution. Specific conditions (e.g., behavior or habitat) that decrease the ability of GPS
collars to acquire successful fixes could result in an increased risk of error in analyses. We therefore recommend researchers explore their GPS data in search of patterns in fix rate and adjust for these to improve further analyses (e.g., only use similar proportions of fixes throughout the day if fix rate shows a circadian pattern). By adjusting for patterns in fix rate, uneven representation is minimized. There is still a risk of missing or underestimating rare but important behaviors, but by being attentive to details and combining GPS data with fieldwork and previous knowledge, the risk of misinterpretation will decrease.

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LITERATURE CITED


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