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Research Article

Individual activity interacts with climate and habitat features in influencing GPS telemetry performance in an Alpine herbivore

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Abstract

Global Positioning System (GPS) telemetry allows to monitor large herbivores in Alpine habitats that are difficult or impossible to access by humans. However, little is known about the factors influencing the performance of GPS telemetry in these habitats. We used stationary test collars and a data set of over 90000 attempted locations from 11 collared free-ranging Alpine ibex (*Capra ibex ibex*) females to quantify the loss of scheduled locations and accuracy of GPS telemetry at the high-elevation habitats of the Marmolada massif (eastern Italian Alps). In both tests the fix acquisition rates and proportions of 3D fixes averaged near 90%. After removing outliers, the estimated location error in stationary collar tests was within 10 m for 75% of 3D locations and within 20 m for 75% of 2D locations. In both tests, sky view determined by terrain morphology was the main habitat feature influencing the performance of GPS telemetry, while forest had only minor effects compared to open ground. Both fix acquisition rates and proportions of 3D fixes in free-ranging ibexes were lowest (close to 85%) in winter and highest (close to 95%) in summer, and exhibited contrasting seasonal diel patterns, being lowest during the night and highest at midday in winter, and lowest at midday and highest at dawn and dusk in summer. Fix acquisition rates and proportions of 3D fixes were positively influenced by individual activity, warm temperatures in winter, absence of precipitation in all seasons, and shallow snow depth in winter. These effects could explain the seasonal and diel patterns. The performance of GPS telemetry of large herbivores at Alpine habitats can be as good as or better than in forested habitats at low elevations. However, acquired locations underestimate inactive periods in sheltered habitats, especially in winter and in adverse weather conditions.

Introduction

Global Positioning System (GPS) telemetry has enormously increased the possibility of locating animals where traditional VHF methods are hindered by weather conditions and accessibility to study areas (Cagnacci et al., 2010). However, GPS location data can be biased because missing and inaccurate locations are not random but instead increase where terrain topography and thick canopy cover obstruct satellite signals (D'Eon et al., 2002; Cain et al., 2005; Hansen and Riggs, 2008; Sager-Fradkin et al., 2007; Zweifel-Schielly and Suter, 2007). Data screening and modeling techniques have been proposed to correct for bias in fix acquisition probability and accuracy (Frair et al., 2010; Montgomery et al., 2010; Wells et al., 2011; Webb et al., 2013; Laver et al., 2015). However, implementation is problematic (Augustine et al., 2011), mainly because GPS failures are highly influenced by the animals' behaviors and habitat selection (Heard et al., 2008; Bourgoin et al., 2009), which are species-specific and influenced by seasonal and climatic conditions (Bourgoin et al., 2009; Mattison et al., 2010; Ensing et al., 2014).

Large herbivores in mountainous habitats have evolved adaptations to the strong seasonality in resource availability and climatic constraints (Grignolio et al., 2004; Festa-Bianchet and Côtè, 2007; Signer et al., 2011). These habitats are difficult or even impossible for humans to access, especially in winter, and only GPS telemetry can provide movement data for detailed analyses of behavioral responses to the seasonality in available resources and climate. However, it is also necessary to identify those animal behaviors, habitat features, and climatic conditions that might introduce bias into the performance of GPS telemetry.

In this study, we took Alpine ibex (*Capra ibex ibex*) as a model species to identify the habitat, individual and climatic factors influencing GPS telemetry performance in Alpine habitats. The Alpine ibex is a large herbivore inhabiting the European Alps at high elevations, mostly above the tree line (Grignolio et al., 2003; Scillitani et al., 2012). Adult males select Alpine grasslands (Grignolio et al., 2003; Scillitani et al., 2012), while females prefer safer habitats, such as cliffs and rocky slopes (Villaret et al., 1997; Grignolio et al., 2007). In winter, ibex select small, steep areas (Grignolio et al., 2004; Scillitani et al., 2012) and greatly reduce activity and movement (Signer et al., 2011). The habitats it uses and the seasonality in its behavioral patterns make the Alpine ibex an interesting species not only per se, but also as a model for a wide range of Caprinae and other herbivore taxa living in high mountain areas.

We combined stationary collar tests with analysis of a database of over 90,000 attempted GPS locations of female ibex over three years. Stationary collar tests may overestimate GPS performance compared with collars deployed on animals, but they can quantify the potential impact of habitat factors (Cagnacci et al., 2010) and estimate location errors that may otherwise be quantified only with domestic animals (Cargnelutti et al., 2007; Forin-Wiart et al., 2015). Therefore, we used stationary collars to assess the effects of land morphology and cover on the probability of acquiring a scheduled location (PFix), the probability of an acquired location to be classified as 3D (P3D), and the

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location error (LE). We expected (H1) sky view as a function of terrain topography to have a positive influence (D'Eon et al., 2002; Cain et al., 2005; Bourgoin et al., 2009) and forest cover to have a negative influence (Frair et al., 2004; Janeau et al., 2004; Sager-Fradkin et al., 2007).

On the other hand, only tests with free-ranging animals can reveal temporal patterns of GPS performance in relation to animal behavior and environmental conditions. In these tests we examined PFix and P3D, which we used as a proxy for LE that cannot be measured with free-ranging animals. In addition to verifying whether sky view and forest cover in the areas used daily by free-ranging ibex females had similar effects as in stationary tests, we wanted to determine whether PFix and P3D in free-ranging ibex exhibited temporal patterns (H2). We expected an uneven performance of GPS telemetry on both yearly and daily temporal scales (Janeau et al., 2004; Wells et al., 2011; Stache et al., 2012; Zweifel-Schielly and Suter, 2007; Mattison et al., 2010). However, we could not predict a priori the shape of these patterns. Since temporal patterns derive from behavioral responses to seasonality in resource availability and climatic conditions, we explored the effects of individual activity and climatic conditions. Alpine ibex females tend to feed in open areas but to rest in steep, rocky areas where there is greater obstruction to satellite signals. We therefore expected PFix and P3D to improve when ibex were more active, in all seasons (H3). We expected high temperatures to have a negative effect on PFix and P3D during summer (H4), because wild herbivores select shaded habitats and reduce feeding activity when they are under heat stress (Bourgoin et al., 2011; Melin et al., 2014; Aublet et al., 2009). We expected instead a positive effect during winter, when animals are more likely to use open habitats during warmer days. We also hypothesized that precipitation would reduce PFix and P3D (H5) as animals may seek cover in microhabitats where the satellite signal is weaker (rock shelters, forest). We expected this effect to be greater in winter than in summer, as fresh snow may considerably limit movement (Grignolio et al., 2004; Richard et al., 2014). Finally, and for the same reason, we also expected deep snow to reduce PFix and P3D (H6).

Materials and methods

Study area

The study area was the Marmolada massif (46°25′13″ N, 11°51′54″ E) in the eastern Italian Alps. Rocky cliffs and peaks reach the highest elevations (the highest being "Punta Penia", 3343 m a.s.l.), rising above steep slopes that delimit narrow valleys. The vegetation is clearly stratified. At the foot of the cliffs, scree slopes with sparse patches of Alpine grasslands predominate, while below these, where the gradient decreases, Alpine grasslands interspersed with isolated rocks provide the growing conditions for shrubs, mainly dwarf pine (*Pinus mugo*), rhododendron (*Rhododendron ferrugineum*), and blueberry (*Vaccinium* spp.). The arboreal stratum, which predominates below 1800 m and at the bottom of the valleys, consists primarily of European larch (*Larix decidua*) followed by Norway spruce (*Picea abies*).

The local ibex colony ranges over an area of approximately 60 km^2 at elevations between 1700 m and 2800 m (Scillitani et al., 2011). Ibex females mostly make use of open habitats, and less so of forest. During the study period, the proportions of use of open habitats by the monitored ibex females were 0.89 (SD=0.12) during summer, and 0.65 (SD=0.22) during winter. We obtained average daily temperature (°C), precipitation (mm), and snow depth (cm) from two meteorological stations located within 11 km of the study area (one at 2,250 m a.s.l and the other at 2,032 m a.s.l). We used Terrain Analysis algorithms for SAGA Systems 2.0.8 (Free Software Foundation, Inc., Boston, MS, USA) to obtain maps of the percentage of visible sky as a Sky View factor from a Digital Elevation Model with 5 m resolution provided by the Veneto Region. We used a land cover map of the study area (Scillitani et al., 2013) to re-classify land cover into "forest" (>30% tree or shrub cover) and "open" (rocks, scree, and grasslands) using the GIS software ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

Stationary Tests

Using the sky view and land cover maps of the study area, we identified a priori sub-areas potentially accessible to operators while representing the different land morphologies and covers. We placed GPS-GSM collars (GPS PLUS, Vectronic Aerospace GmbH, Berlin, Germany) at approximately 40–60 cm from the ground in random sites within the identified sub-areas. Two collars were positioned in each of 117 sites and scheduled to attempt a position recording every 5 minutes for periods of 1.5 hours, and four collars were placed in each of 64 sites and scheduled to attempt a position recording every 30 minutes for at least 24 hours. We recorded the "true" position of each site as the centroid of 20 positions recorded by a portable GPS receiver (Garmin eTrex 10 with high-sensitivity, WAAS-enabled and HotFix satellite prediction, Garmin, Schaffausen, Switzerland) with an accuracy of 2.0±2.8 (SD) m. We associated each collar position site to the sky view (%) and the land cover category (forest or open) of the pixel in which it was located. We classified each scheduled location attempt as successful if it resulted in the acquisition of location coordinates, and unsuccessful if it did not. We calculated LE as the Euclidean distance in meters between each acquired position and the "true" collar position.

The LE values had a highly skewed distribution (Fig. S1), with most acquired positions having a very small LE, and a few having a large or very large LE. In identifying outlying locations we wanted to mimic the editing of a database from free-ranging animals. To do this, we excluded as outliers LE values larger than 270 m, which was the threshold including 95% of step lengths in the trajectories of free-ranging ibex females after removing outliers using the screening method of Bjørneraas et al. (2012). Since the remaining 5% of longer step lengths were mostly steps of directional movement paths, which are easily recognizable, we assumed that the probability of accepting a location as good with an error greater than 270 m was very small. We log-transformed LE as log(1+x) to obtain a normal distribution, and categorized sky view values into 5 classes: 100–90%; 89–80%; 79–70%; 69–60%; <60%.

We conducted statistical analyses in R (R Version 3.2.1, www.r-project.org). We modeled PFix and P3D using generalized linear mixed models with a binomial error distribution using the glmer function of the lme4 package (Bates et al. 2015), while LE was modeled with linear mixed models using the function lme of the nlme package (version 3.1–120). We constructed an a priori set of models that included the collar position site as random factor, and different combinations of sky view class, land cover category, fix interval and navigation code (2D or 3D, only for LE) as fixed effects (Table S2). We performed model selection based on the Akaike information criterion (AIC) (Burnham and Anderson, 2004). When two candidate models had a ΔAIC<2, we selected the most parsimonious one.

Tests on Free-Ranging Ibex

Our database consisted of 90966 GPS location attempts on 11 Alpine ibex females (estimated age at capture 2 to 12 years) from September 2010 to October 2013. Animals were captured from late July to early October using a tele-injection of xylazine (Rompun©, Bayer, Leverkusen, Germany) (Dematteis et al., 2008) with veterinary assistance and in compliance with Italian laws. Capture and handling protocols were approved by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale, ref. n. 9097–9501/2012) and were similar to those described by Brivio et al. (2015), which have a low impact on this species. All captured individuals were fitted with GPS-GSM collars (GPS PLUS, Vectronic Aerospace GmbH, Berlin, Germany) programmed to attempt recording a location every hour over 54 weeks. Each attempted location was associated to the average of the X and Y activity values of the motion sensors of the collars during the 5 minutes preceding and following the scheduled acquisition time, as well as to the hour (0001–2400), week of the year (1–52, beginning December 21st), and season (summer: weeks 23–42; winter: weeks 43–22). We identified seasons using a clustering approach (Basille et al., 2013) that grouped Julian dates on the basis of elevation, slope, land cover, activity level, and step lengths between the animals' locations (Parraga, 2015). Since we did not have hourly temperature, precipitation, and snow depth values, each attempted location within a single day was associated with the corresponding daily values. Similarly, as we did not have the true position of attempted locations, we associated them with the sky view values and land cover features of the corresponding individual daily minimum convex polygons. We shaped polygons for days with at least 8 successful locations (accounting for 98% of individual days), and grouped sky view values into intervals of 10 deciles. We then assigned a unit score (5, 6, ...10) to each interval class starting with the lowest, and calculated a sky view index for each polygon as $\Sigma(Si * Pi)$, where Si is the score of interval class i, and Pi is its proportion of the polygon area. In addition, we associated to each polygon the proportion covered by forest or open areas. Each attempted location within a single day was classified with the features of the corresponding polygon.

We expressed the daily mean temperature and snow depth as deviations from the corresponding weekly average values during the study period in order to index stochastic variability. We categorized the values of sky view, residual temperature, residual snow depth and activity as "lower than average" ($\leqslant 25^{th}$ percentile), "average" ($>25^{th}$ and $\leqslant 75^{th}$ percentile), and "higher than average" ($>75^{th}$ percentile). Daily total precipitation was classified as "absent" or "present" (>0 mm), due to the very high frequency of days without precipitation. Land cover was classified as either "forest" or "open", according to the land cover type predominating (>50%) in the daily polygons.

We analyzed PFix and P3D with generalized additive mixed models with a binomial error distribution in R using the gam function of the mgcv package (Wood, 2011) to account for intra-annual and circadian trends. We first checked our expected seasonal and diel patterns (H2) by comparing a constant model (including only the random individual effect) with three models including also: 1) the cyclic cubic spline of week, 2) the cyclic cubic spline of hour, 3) the interaction between the cyclic cubic spline of hour and the season, and 4) the cyclic cubic spline of week plus the interaction between the cyclic cubic spline of hour and the season. The cyclic cubic spline is suitable for modeling nonlinear effects of circular covariates, as the annual week, as it constrains the first and last values of the covariates to be continuous.

We then constructed a priori sets of models (Tables S3 and S4) to analyze the factors affecting PFix and P3D with regard to our hypotheses (H1, H3, H4, H5, H6). We conducted separate analyses for each season in order to include the effect of stochastic snow in winter. All models included individual identity as random factor, the spline of week and the cyclic cubic spline of hour to account for temporal variation and diel patterns, and different combinations of factors indexing physical obstruction (sky view and proportion of forest), climatic variability (temperature, precipitation, and, in winter only, snow depth), and animal behavior (index of activity). We performed model selection based on AIC (Burnham and Anderson, 2004). When two candidate models had a ΔAIC<2, we selected the most parsimonious one.

Results

Stationary Tests

We recorded 6283 locations from 6736 attempts, corresponding to an average acquisition rate of 0.933. Of these, 5806 locations were classified as 3D, corresponding to an average proportion of 0.924 of acquired locations. Using a threshold of 270 m for outliers we removed 322 fixes. Therefore the database used for LE analysis contained 5961 locations. Probability of acquiring a location was most parsimoniously modeled by sky view only, P3D by sky view in combination with interfix interval, and LE by the full model including the effects of sky view, land cover, navigation and fix interval (Tab. 1). Notably, PFix, P3D and LE patterns in response to sky view were very similar, remaining fairly constant for sky view classes equal to or wider than 70%, then either declining (PFix and P3D) or increasing (LE) with narrower sky views (Tab. 2; see also Fig. S5, S6, and S7 for observed data). Location error was also higher in forest than in open ground, for the 30 minute than for the 5 minute fix interval, and, of course, in the 2D than the 3D fixes. The median LE was 4.5 m with 3D and 13.2 m with 2D fixes (see also Fig. S7 for observed location errors). These results were in agreement with our expectation (H1) regarding the influence of sky view, but our expectation regarding the influence of land cover was confirmed only for LE.

Tests on Free-Ranging Ibex

During the study, daily average temperatures (Fig. S8) were lowest in January and February ($-6\,^{\circ}$C to $-8\,^{\circ}$C) and highest in August ($10\,^{\circ}$C). Precipitation was scarce in winter, but rose in spring, summer (with the exception of August) and autumn (Fig. S8). Snow cover lasted from November to early June, accumulating to more than 150 cm from February to April (Fig. S8). For all the variables, stochastic variability associated with temporal trends was very high. We acquired 84,330 fixes from 11 GPS collars fitted on Alpine ibex females, representing an average acquisition rate of 0.927 with a range across all individuals from 0.859 to 0.980 (SD=0.031). The average proportion of 3D locations was 0.893 with a range across all individuals from 0.757 to 0.974 (SD=0.063). As expected (H2), PFix and P3D exhibited clear intra-annual and daily cycles. The full model with the spline effects of week and hour within season had unequivocal support (model weight=0.999). Both PFix and P3D were lowest (close to 85%) during the winter weeks, increased rapidly during spring to peak at the beginning of summer (<95%), and then declined in autumn (Fig. 1). Diel patterns of PFix and P3D differed between seasons (Fig. 2). During summer, PFix and P3D were lowest in the central hours of the day and highest at dawn and dusk, while in winter they were highest in the middle of the day, and lowest during the night. Diel patterns were more marked in winter, when minimum values were close to 85% and maximum values were 90–95% for both PFix and P3D, compared with summer, when values ranged between 90 and 95% for both variables.

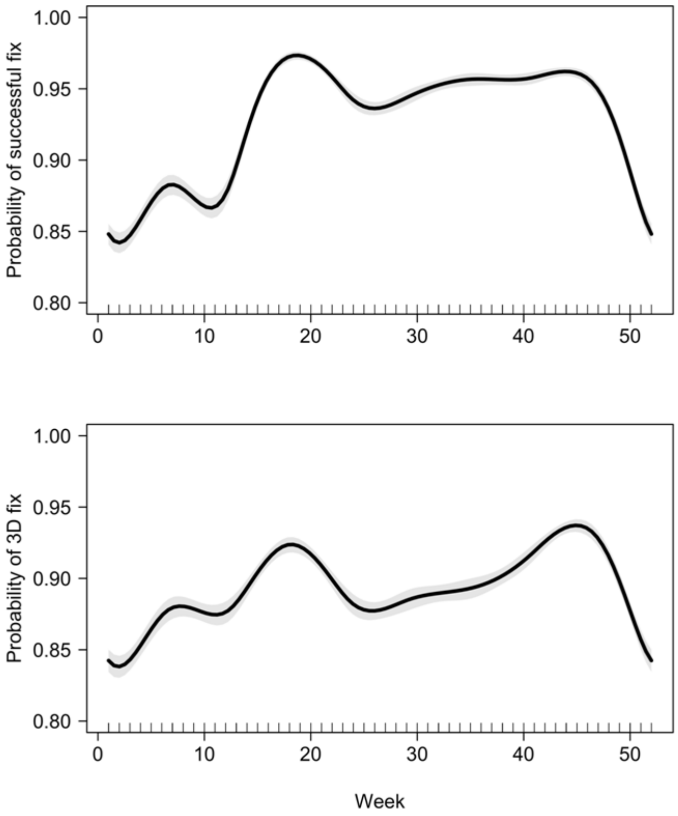

Figure 1 – Annual patterns (weeks 1–52, beginning December 21) of the probability of a scheduled fix being successful and of an acquired fix being classified as 3D in female Alpine ibex. Patterns were modeled with generalized additive mixed models and plotted in R with the package "visreg 2.2-0". Grey bands represent 95% confidence intervals.

In summer, PFix was best modeled by sky view, individual activity and precipitation, and P3D was best modeled by the same factors with the addition of temperature (Tab. 3). The sky view of the areas used daily by ibex had a positive effect on both variables (Tab. 4), and this,

Table 1 – Selected models for probability of acquiring a location (PFix, acquired vs. missed fixes), probability of an acquired location to be classified as 3D (P3D, 3D vs. 2D fixes) and location error (LE, m, transformed as log(1+x)) in stationary collar tests. All models included the collar location point as random factor. Models are ranked according to the Akaike information criterion (AIC) until their summed weights (ωi) were $\geqslant$0.90. We selected the model (in bold) with the lowest AIC if the nearest competing model had a delta AIC (ΔAIC) >2, otherwise we selected the most parsimonious model within the range of 2 ΔAIC.

Variable	Model	Sky view	Land cover	Fix interval	Navigation	AIC	ΔAIC	ωi
PFix	**5**	**X**				**2012.46**	**0.00**	**0.532**
	3	X		X		2014.44	1.98	0.198
	2	X	X			2014.45	1.99	0.197
P3D	**3**	**X**		**X**		**2734.07**	**0.00**	**0.722**
	1	X				2735.99	1.92	0.277
LE	**1**	**X**	**X**	**X**	**X**	**12785.39**	**0.00**	**0.742**
	4		X	X	X	12789.14	3.75	0.114
	5			X	X	12789.82	4.43	0.080

Table 2 – Estimates (log odds) and test statistics from the most parsimonious models analyzing probability of acquiring a location (PFix, acquired vs. missed fixes), probability of an acquired location to be classified as 3D (P3D, 3D vs. 2D fixes) and location error (LE, m, transformed as log(1+x)) in stationary collar tests.

	PFix			P3D			LE		
	Estimate	SE	*p*	Estimate	SE	*p*	Estimate	SE	*p*
Intercept	6.203	0.639	<0.001	5.184	0.564	<0.001	2.317	0.180	<0.001
Interval:									
30 vs. 5 min				-1.663	0.424	<0.001	0.392	0.117	<0.01
Sky view:									
80–89 vs. 90–100	-1.333	0.702	0.058	-0.289	0.546	0.596	0.331	0.161	<0.05
70–79 vs. 90–100	-0.424	0.686	0.537	-0.718	0.582	0.218	0.216	0.165	0.193
60–69 vs. 90–100	-3.086	0.892	<0.001	-1.316	0.664	<0.05	0.608	0.201	<0.01
50–69 vs. 90–100	-3.743	0.869	<0.001	-2.764	0.636	<0.001	0.778	0.199	<0.001
Land cover:									
open vs. forest							-0.475	0.147	<0.001
Navigation:									
3D vs. 2D							-0.480	0.042	<0.001

together with the lack of effects of land cover, confirmed the results of the stationary collar tests for these variables. PFix and P3D improved greatly with increasing activity (Tab. 4), in accordance with our expectation (H3). Temperature had a positive effect on P3D, which, together with the absence of an effect on PFix, was inconsistent with our expectation (H4) that higher temperatures would reduce GPS telemetry performance in summer. PFix and P3D were lower on days with precipitation than on days without (Tab. 4). In winter, PFix was best modeled by the full model including sky view, land cover, activity, precipitation, temperature, and snow depth, while P3D was best modeled by the same factors with the exception of land cover (Tab. 3). The effects (Tab. 5) were as predicted, i.e. positive for sky view, activity and temperature, and negative for forest and snow depth. Notably, the effect of precipitation was similar in both seasons, which contrasted with our expectation (H5) that it would be smaller in summer than in winter. Activity generally had a much larger effect than the other factors, but this was likely because we had hourly values for activity, while for the other factors we had only averaged daily values.

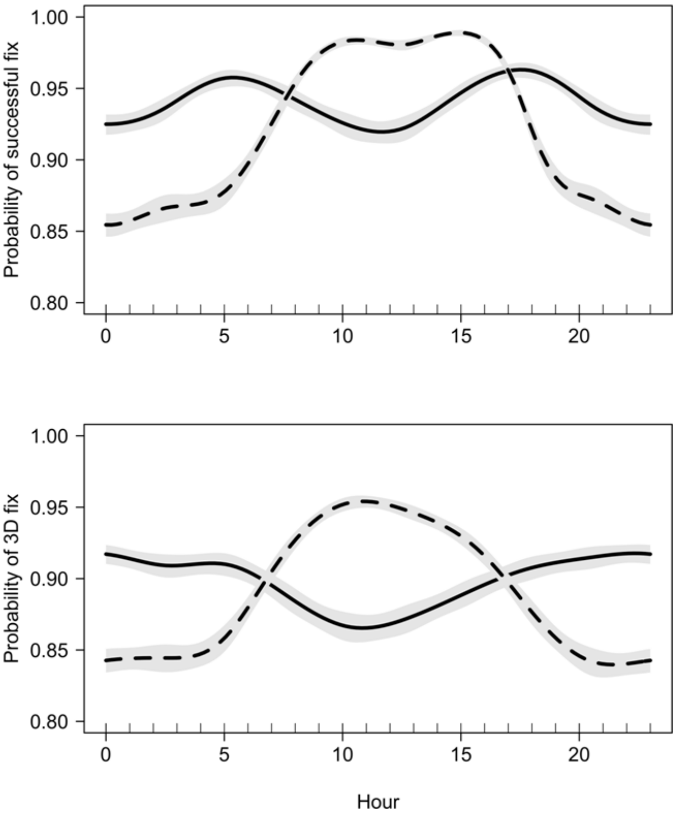

Figure 2 – Diel patterns (hours 0–23) by season (summer: weeks 23–42, continuous line; winter: weeks 43–22, dashed line) of the probability of a scheduled fix being successful and of an acquired fix being classified as 3D in female Alpine ibex. Patterns were modeled with generalized additive mixed models and plotted in R with the package "visreg 2.2-0". Grey bands represent 95% confidence intervals.

Discussion

The analyses of GPS location data from stationary test collars and free-ranging female Alpine ibexes concurred in indicating that GPS telemetry performs well at the high elevations, mostly open habitats, used by this species. In both tests, fix acquisition rate was close to 93%, and proportion of 3D locations acquired was close to 90%. Location error estimated from stationary collars was lower than 10 m for 50% of the locations, and lower than 20 m for 75%. These values are among the best reported in other studies (Moen et al., 2001; Cain et al., 2005; Janeau et al., 2004; Zweifel-Schielly and Suter, 2007; Forin-Wiart et al., 2015). In addition, and contrary to our expectations, we did not observe a notable reduction in PFixand P3D in free-ranging ibex compared with stationary test collars (Cagnacci et al., 2010). This suggests that the interactions between behavior and the mostly open, high-elevation habitats selected by free-ranging ibex had less influence on

Table 3 – Selected generalized additive mixed models for probability of acquiring a location (PFix, acquired vs. missed fixes) and probability of an acquired location to be classified as 3D (P3D, 3D vs. 2D fixes) for GPS collars on free-ranging ibex. In addition to the effects listed here, all models included the fixed effects of week and hour (estimated as splines) and the random effect of individual. Models are ranked according to the Akaike information criterion (AIC) until their summed weights (ωi) were ⩾0.90. We selected the model (in bold) with the lowest AIC if the nearest competing model had a delta AIC (ΔAIC) >2, otherwise we selected the most parsimonious model within the range of 2 ΔAIC.

	Model	Sky view	Land cover	Precipitation	Snow	Temperature	Activity	AIC	ΔAIC	ωi
Summer										
PFix	21	X		X		X	X	12359.69	0.00	0.377
	19	**X**		**X**			**X**	**12359.84**	**0.15**	**0.350**
	24	X	X	X		X	X	12361.67	1.98	0.140
	22	X	X	X			X	12361.78	2.09	0.133
P3D	24	X	X	X		X	X	20795.45	0.00	0.562
	21	**X**		**X**		**X**	**X**	**20795.97**	**0.52**	**0.434**
Winter										
PFix	**56**	**X**	**X**	**X**	**X**	**X**	**X**	**25452.79**	**0**	**0.950**
P3D	56	X	X	X	X	X	X	29781.08	0	0.659
	42	**X**		**X**	**X**	**X**	**X**	**29782.40**	**1.32**	**0.341**

Table 4 – Estimates (log odds) and test statistics from the most parsimonious generalized additive mixed models analyzing probability of acquiring a location (PFix, acquired vs. missed fixes) and probability of an acquired location to be classified as 3D (P3D, 3D vs. 2D fixes) for GPS collars on free-ranging ibex during summer (weeks 23–42).

		PFix			P3D	
	Estimate	SE	*p*	Estimate	SE	*p*
Intercept	3.384	0.187	<0.001	2.503	0.201	<0.001
Sky view:						
High vs. average	0.248	0.078	<0.01	0.133	0.054	<0.05
Low vs. average	-0.204	0.061	<0.001	-0.275	0.047	<0.001
Activity index						
High vs. average	1.807	0.120	<0.001	0.417	0.049	<0.001
Low vs. average	-0.773	0.054	<0.001	-0.307	0.045	<0.001
Precipitation: present vs. absent	-0.487	0.056	<0.001	-0.296	0.039	<0.001
Stochastic temperature						
High vs. average				0.101	0.050	<0.05
Low vs. average				-0.128	0.045	<0.01

Table 5 – Estimates (log odds) and test statistics from the most parsimonious generalized linear mixed models analyzing probability of acquiring a location (PFix, acquired vs. missed fixes) and probability of an acquired location to be classified as 3D (P3D, 3D vs. 2D fixes) for GPS collars on free-ranging ibex during winter (weeks 43–22).

		PFix			P3D	
	Estimate	SE	*p*	Estimate	SE	*p*
Intercept	3.241	0.403	<0.001	2.731	0.297	<0.001
Sky view:						
High vs. average	0.171	0.043	<0.001	0.309	0.041	<0.001
Low vs. average	-0.006	0.045	0.882	-0.176	0.042	<0.001
Land cover: open vs. forest	0.117	0.042	<0.01			
Precipitation: present vs. absent	-0.509	0.036	<0.001	-0.340	0.329	<0.001
Stochastic temperature						
High vs. average	0.601	0.053	<0.001	0.327	0.047	<0.001
Low vs. average	-0.471	0.040	<0.001	-0.386	0.039	<0.001
Stochastic snow						
High vs. average	-0.241	0.044	<0.001	-0.729	0.045	0.108
Low vs. average	0.458	0.061	<0.001	0.132	0.051	<0.001
Activity index						
High vs. average	1.712	0.109	<0.001	0.298	0.051	<0.001
Low vs. average	-0.643	0.038	<0.001	-0.510	0.036	<0.001

GPS telemetry performance than the behavior-habitat interactions of large herbivores (Zweifel-Schielly and Suter, 2007; Stache et al., 2012) or carnivores (Sager-Fradkin et al., 2007) in forested habitats at lower elevations. We know of no published results obtained in conditions similar to those of our study, which precludes further speculation.

Although GPS telemetry performance was on average good, we found appreciable variation in response to habitat features, individual activity and climatic variability. In both stationary and free-ranging ibex tests, the most important habitat feature affecting the performance of GPS telemetry was visible sky due to land topography, while forest had only minor effects, contrary to our expectation. Forest cover in the areas used by ibex females was sparse and the thin foliage of the dominant tree, European larch, likely created only a partial obstacle to the satellite signal. Other authors (Stache et al., 2012; Zweifel-Schielly and Suter, 2007) found that performance of GPS telemetry improved when canopy cover decreased. In ibex, individual activity increased PFix and P3D in both seasons, as expected. GPS performance can be impaired when animals are resting if the orientation of the antenna shifts from the vertical (D'Eon and Delparte, 2005; Jiang et al., 2008), or if it is screened by the animal's body, as found for grizzly bears (*Ursus arctos*) (Graves and Waller, 2006; Heard et al., 2008; Graves et al., 2013). However, these failures are more likely to occur with animals that have a round neck, facilitating collar rotation, and a large body that can easily shade the antenna, than with ibex females that have thin, oval shaped necks. We assume that the reason the ibex in our study had better PFix and P3D when they were more active was mainly because they were using habitats with high sky visibility, such as grasslands and screes, while they were using rocks or forest when they were inactive. In other species, activity either improved GPS performance (Mediterranean mouflon *Ovis gmelini musimon*: Bourgoin et al., 2009; wolverine *Gulo gulo* and Lynx *Lynx lynx*: Mattison et al., 2010) or decreased it (Moose *Alces alces*: Moen et al., 2001) depending on the obstruction of sky view in the habitats used during active and inactive periods. During winter, PFix and P3D improved when temperatures were higher than usual, in days without than with precipitations, and with decreasing snow depth. We had predicted these results, because winter conditions in our study area are harsh and with low temperatures, adverse weather, and deep snow animals reduce movement and seek cover in sheltered habitats (Beier and Cullough, 1990; Dussault et al., 2005; Signer et al., 2011; Apollonio et al., 2013; Richard et al., 2014). To our knowledge, however, no published studies have so far related GPS performance with precipitation and snow depth. During summer, higher temperatures had little effect on or tended to improve GPS performance. Instead, we had expected a negative effect, because other large herbivores react to high temperatures taking shelter in forest or shaded areas (Dussault et al., 2004; Bourgoin et al., 2011; van Beest et al., 2012). However, in response to excessive heat Alpine ibex move to higher altitudes (Grignolio et al., 2004; Aublet et al., 2009), even to the top of rocky cliffs, where the sky view is usually good. This might explain why high temperatures did not impair GPS performance. On the other hand, it is also possible that temperatures high enough to induce heat stress were reached only for a short period in the peak of summer. Daily average temperatures above 10 °C, which may correspond to daily maximum temperatures exceeding 15 °C, a threshold above which ibex reduce activity and foraging (Aublet et al., 2009), were frequent in July and August, but rare in June and September (Fig. S2). We expected precipitations to have little influence on PFix and P3D during summer, because we presumed that rainfalls should have little impact on the animals' behavior when temperatures are high. Instead, we found a negative effect as we had found in winter. In our Alpine study area, precipitation was less abundant in winter than in summer (Fig. S1), when events could often be in the form of thunderstorms, which can be particularly intense at high elevations. This might explain why summer rainfalls, as well as winter snowfalls, had a negative effect on GPS performance.

The behavioral responses of ibex to changing weather may explain the contrasting seasonal patterns that we observed. In winter, missed and 2D locations were more frequent than in summer. In winter ibexes are much less active, especially in the coldest months (Signer et al., 2011), and select habitats at lower elevations sheltered from snow (Grignolio et al., 2003; Scillitani et al., 2012), which are likely to have a narrower sky view. We also found that PFix and P3D had strong diel patterns in winter, being lowest at night and highest at midday, but weak diel patterns in summer, being slightly lower at midday and higher at dawn and dusk. In winter, ibex are mostly inactive during the night and more active at midday (Signer et al., 2011), while in summer they tend to rest during the hottest hours and feed at dawn and dusk (Aublet et al., 2009). Various studies with large herbivores found seasonal patterns of GPS telemetry performance, which either agreed with our results (Edenius, 1997; Wells et al., 2011; Stache et al., 2012), or contrasted with them (Biggs et al., 2001; Janeau et al., 2004) according to the morphology and forest cover and/or type of habitat used in the different seasons. Similarly, different diel patterns of the probability of acquiring a fix have been observed in different species, which could generally be explained by inactivity periods and related habitat selections (Graves and Waller, 2006; Zweifel-Schielly and Suter, 2007; Heard et al., 2008; Mattison et al., 2010).

In general, home range estimates can be biased when the probability of acquiring locations is highly variable (e.g. 0.5–1.0), or when areas with low fix acquisition rates concentrate within one portion of the home range (Horne et al., 2007). With our schedule of 24 locations attempted/day, individual days with a fix acquisition rate of 92–100% (22–24 locations acquired) were more than 70% of the total in winter, and 80% in summer. Individual days with fix acquisition lower than 50% (less than 12 locations received) were less than 2% in winter and less than 0.5% in summer. We assume that with high frequency of locations and low bias in probability of acquiring locations, such as those we observed here, appreciable bias in home range studies could be introduced only over very short temporal scales (e.g. 2-days home ranges). Fix acquisition rates lower than 90% are likely to introduce bias in resource selection studies (Frair et al., 2004, 2010). In these cases, researchers may apply sample weighting or iterative simulation to correct for biased fix acquisition rate (Frair et al., 2004; Bourgoin et al., 2009; Nielson et al., 2009; De Cesare et al., 2012). However, the decision whether to use corrected or uncorrected data remains somewhat subjective. For instance, recent studies focusing on resource selection often considered the threshold of 90% of fix acquisition rate as sufficient to justify assumption of unbiased results (Morehouse and Boyce, 2013; Ewald et al., 2014; Northrup et al., 2015; Dupke et al., 2016), while Lone et al. (2014), with an average fix acquisition rate of 96% during winter (range 87–99%) and 90% during summer (range 83–97%), applied sample weighting. We assume that during summer when PFix is 95–98% missed locations should have no appreciable impact on habitat selection estimates, but during winter when PFix is lower (85–90%) this possibility cannot be ruled out a priori. More generally, our results underline the need for complementing stationary collars tests with analysis of the patterns of PFix in animals' deployed collars. For this purpose, it is important that the temporal scale at which PFix is modelled match the scale of the spatial and habitat selection analyses. The high frequency of locations achievable with GPS telemetry allows to examine habitat selection patterns at short time scales, for instance at the diel scale, and we observed here that PFix had different diel patterns between seasons. In addition to indicating the risk of bias, the patterns of PFix can be related with animals' activity, climatic variables, and, indirectly but effectively as we found in this study, the habitat features of the areas used. This would provide essential information to understand not only whether but also how analysis and interpretation of the results might be biased.

In conclusion, in Alpine habitats GPS telemetry can perform as well as or better than in forested habitats at lower elevations, where it has been much more widely used. However, in Alpine habitats, and likely in all similar conditions where large mountain herbivores live in extreme climatic conditions, missed GPS locations underestimate periods of inactivity and use of habitats providing shelter, especially during winter and in adverse climatic and weather conditions. Since bias in GPS telemetry performance will vary according to the behavioral patterns of different species and the environmental features of the study area, we recommend that researchers examine their datasets to identify specific patterns in fix acquisition rates in relation to the animals' activity and climatic factors, in order to reduce the risk of biased interpretations and conclusions.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Distribution of the location errors obtained in stationary collar tests.

Table S2 Generalized linear mixed models and linear mixed models.

Table S3 Generalized additive mixed models (summer period).

Table S4 Generalized additive mixed models (winter period).

Figure S5 Proportion of acquired over attempted locations obtained from stationary collars.

Figure S6 Proportions of 3D locations acquired by stationary collars in different sky view classes.

Figure S7 Location errors acquired by stationary collars in different sky view classes.

Figure S8 Mean daily temperatures, precipitations, and snow depth recorded during the study period.