

What determines global positioning system fix success when monitoring free-ranging mouflon?

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Abstract We have assessed behavioural and environmental factors influencing the success of global positioning system (GPS) fixes recorded from 15 collared free-ranging female Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp.). We have demonstrated that fix success was 8% lower in resting animals (0.81, 95% CI=0.79–0.84) than in active animals (0.89, 95% CI=0.86–0.91) at an average temperature (13.8°C), but was similar and relatively constant at lower temperatures. When

temperatures increased above the average temperature, fix success strongly decreased in resting animals (0.44, 95% CI=0.36–0.52 at 30°C) as compared to active animals (0.76, 95% CI=0.65–0.85). These results probably involved behavioural changes in habitat use of mouflon, as temperature and activity strongly influence the use of cover in ungulates. We also found that the success of GPS fixes was influenced by habitat types, increasing from 0.76 to 0.93 (under average sky openness of 33%) along a continuum going from forested to open areas. After controlling for differences in vegetation, sky openness had a positive effect on fix success (from 0.76 to 0.97 in evergreen oak forest). Our approach based on free-ranging animals and using a robust interpolation procedure should provide biologists with a more reliable method to account for bias in GPS studies.

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Introduction

The use of global positioning system (GPS) collars has increasingly allowed biologists to collect a large quantity of accurate location data on animals over short time intervals and at large spatial scales. However, two main sources of error have been associated with GPS location data (D'Eon et al. 2002; Frair et al. 2004; Lewis et al. 2007): location inaccuracy and failure to locate.

Location inaccuracy generally leads to ambiguous inference regarding habitat selection or to a misclassification (Nams 1989; Visscher 2006; White and Garrott 1986). The magnitude of such biases depends on the degree of location error and on the scale of the landscape

heterogeneity (Visscher 2006). However, since the intentional degradation of satellite signals by the US military ended in May 2000, the accuracy of GPS locations has predictably improved (Adrados et al. 2002; Hulbert and French 2001), typically exceeding the resolution of habitat maps (e.g. Dussault et al. 2005; Mahoney and Virgl 2003).

Our work focused on the second source of error, location failure, which occurs when a GPS collar fails to acquire a fix. This can markedly influence habitat selection studies because location failures are expected to be non-random. Several experimental studies have explored the factors influencing the probability of acquiring a fix (PAF), such as topography (e.g. Cain et al. 2005; D'Eon et al. 2002), animal activity and movements (e.g. Cargnelutti et al. 2007; Graves and Waller 2006; Moen et al. 2001) and vegetation characteristics (e.g. Di Orio et al. 2003; Frair et al. 2004; Hansen and Riggs 2008; Janeau et al. 2004; Rumble and Lindzey 1997).

Whilst such studies have undoubtedly improved our understanding of factors influencing location failure and have led to GPS-bias models that allow predicting PAF in order to correct habitat selection analysis, several problems still limit the optimal use of these models. First, the majority of the field trials have been performed using static GPS collars, although it has been shown that collar movements can reduce the proportion of successful fix attempts (Cargnelutti et al. 2007; Edenius 1997). Therefore, field trials are likely to underestimate the bias that results from failure to acquire a fix. Moreover, among recent studies using mobile collars, most of them only accounted for the role of vegetation and topography on the PAF (Cargnelutti et al. 2007; DeCesare et al. 2005; Zweifel-Schielly and Suter 2007). Second, short fix intervals (i.e. time interval between two fix attempts) often used for test trials are likely to result in higher PAF than those obtained when using longer fix intervals typical of the analysis of free-ranging animals (Cain et al. 2005; Janeau et al. 2004). Third, the fix success of GPS collars on free-ranging animals has been reported to be lower than that obtained during trials in the same study area (e.g. Sager-Fradkin et al. 2007; Zweifel-Schielly and Suter 2007). Thus, trial-based models of GPS bias failed to correct for the majority of missing data (D'Eon 2003; Sager-Fradkin et al. 2007), most likely because of the influence of animal behaviour on PAF (Hebblewhite et al. 2007). In field trials, reproducing and simultaneously testing all the associated components of animal behaviour (i.e. travelling speed, collar distance from the ground and position and microhabitat selection among other factors) is impractical.

Alternatively, we used GPS datasets collected from free-ranging animals (see also Graves and Waller 2006)

to account for the influence of behaviour and habitat on the PAF. We assessed the factors influencing the PAF of GPS 3300S collar (Lotek Engineering Inc. 2003) worn by Mediterranean mouflon (*Ovis gmelini musimon* x *Ovis* sp.) inhabiting a low mountainous area. In a first part, we used temperature and motion sensors on each collar to perform a fine-scale analysis of the influence of animal behaviour and ambient temperature on the PAF. We predicted a negative influence of temperatures on the PAF with lowest values when extreme temperatures occurred (Dussault et al. 1999) because ungulates often seek cover (where the PAF is lower) under stressing climatic conditions (Mysterud and Østbye 1999). We also predicted that animal inactivity would negatively affect PAF due to the proximity of the ground to the GPS collar (Bowman et al. 2000; Graves and Radandt 2004) and the tendency for sheep to seek shade during summer (Mysterud and Østbye 1999), as from forests and steep rocky areas (Auvray 1983). As no information was available on the used habitats by animals when GPS collars failed to locate, we tested in a second part an interpolation process based on animal activity to determine coordinates of missing locations and address bias in habitats used caused by missed fixes. Because changes in vegetation and topography can influence the communication with satellites, we predicted PAF when mouflon used habitats with low sky visibility (i.e. forested and hemmed areas) to be lower than when they used more open habitats (i.e. high sky visibility and open areas).

Materials and methods

Study area

We studied mouflon in the Caroux–Espinoise massif situated on the southern border of the Massif Central, France (43°38' N, 2°58' E, Fig. 1; Garel et al. 2005). Elevation ranged from 150 to 1,124 m above sea level. Climatic conditions consisted of dry summers (Garel et al. 2004), wet autumns and fairly cold winters (Thiebaut 1971). Wind was common throughout the year (139 and 133 days with wind speed >6 m/s in 2004 and 2006, respectively). The vegetation in open areas (especially the Caroux plateau top) mainly consisted of heather moorlands (*Calluna vulgaris*, *Erica cinerea*) and broom (*Cytisus purgans*, *Cytisus scoparius*), mixed with grasses (e.g. *Festuca panicula*, *Festuca ovina*, *Agrostis capillaris*). Part of the Caroux plateau had been replanted with coniferous woodland species (*Pinus* sp.), whereas beech (*Fagus sylvatica*), chestnut (*Castanea sativa*) and evergreen oak (*Quercus ilex*) forests occurred on the plateau slopes.

Fig. 1 Location of the study area in southern France



GPS collars

We caught eight, five and three females using traps on the Caroux plateau and fitted them with Lotek GPS collars 3300S (Lotek Engineering, Newmarket, ON, Canada) in spring 2003, 2004 and 2005, respectively. GPS collars were scheduled to record animal location at intervals of 20 min on 2-day periods (recording period), one to three times per month.

Location data were differentially corrected. Because location error may bias inference in GPS studies (Visscher 2006), we removed supposedly low-accuracy locations from the dataset: (1) 2D and 3D locations with a positional dilution of precision >10 (e.g. Adrados et al. 2002; Lewis et al. 2007) and (2) locations for which the three following criteria were supported: (a) the animal walked faster than 0.48 km/h between two successful recorded locations [equivalent to a displacement >160 m (i.e. two map pixels) from the first location]; (b) the animal walked faster than 0.48 km/h to the next successful location and (c) the geometrical angle created by the three recorded locations was $<40^\circ$.

Dual-axis motion sensors, from which animal activity was derived, recorded vertical and lateral animal head and neck movements (range from 0 to 255 for each motion sensor; Moen et al. 1996a) and the proportion of time the head was down at 5-min intervals.

GPS bias covariates

Temperature and mouflon activity

In the first part of our study, we tested the influence of the temperature and of the activity of the mouflon. For the temperature, we used data from thermal sensors internal to the canister of GPS collars, which recorded apparent ambient temperature every 5 min.

To estimate activity of mouflons based on dual-axis motion sensors data (see above), we used the discriminant model developed in a previous calibration procedure (Bourgoin et al. 2008). This model allowed classifying animals as either inactive (i.e. sleeping, ruminating or resting) or active (i.e. feeding, standing, travelling and other activities such as interactions or scratching) for each 5-min

period based on the data from motion sensors. Using the computed linear model for the motion sensor data, animals were correctly classified in 85.4% (95% CI=77.4–93.6) and 87.3% (95% CI=81.9–91.6) of cases as active and inactive, respectively. We applied this model to data collected from the 15 free-ranging females in our current study population after standardisation [i.e. centred (mean=0) and scaled (SD=1)] of their motion sensors.

Vegetation and topography

To assess terrain obstruction, we calculated the proportion of available sky (AS) using a 15×15-km point grid in the sky (250-m resolution), 100 m above the highest elevation (e.g. D'Eon et al. 2002) and a second point grid (81-m resolution) on the ground. For a point of the ground grid, we defined AS as the proportion of points of the sky grid visible. We derived a vegetation map (same resolution) from 2001 aerial photography. We distinguished eight vegetation classes: open area, conifer forest, leaf-on deciduous forest (1 April–31 October), leaf-off deciduous forest (1 November–31 March), mixed deciduous and conifer, evergreen oak forest, sparse evergreen oak and rock.

Interpolation procedure

Description

In the second part of our study, we tested the influence of vegetation and topography on the PAF. As we had no GPS coordinates and, hence, no environmental information when GPS collars on the field failed to locate, we needed to estimate the locations of animals at these occasions. We thus interpolated missing locations (i.e. failed and removed low-accuracy locations; see Cargnelutti et al. 2007 for a similar approach) to assess the used topography and vegetation and their influence on the PAF. To improve the interpolation accuracy, we accounted for locations of a resting animal that did not change by including animal activity in the computation. We placed the animal at the same location when it was inactive during the 20 min separating 2 GPS locations (i.e. resting period). During a resting period, we approximated the missing coordinates as the mean coordinates of successful 3D locations (or 2D locations when no 3D locations were available) during this resting sequence. We interpolated missing locations during an active sequence as the midpoint between previous and next successful locations.

Validation of the interpolation procedure

To test the accuracy of the interpolation process, we performed a sensitivity analysis by keeping a limit of one

to six successive missing locations during active sequences (above this limit, called “maximal number of successive missing locations”, missing locations were not interpolated). We selected the 22 longest trajectories (i.e. ≥ 60 successive locations, mean=71, SD=11.4). We randomly sampled one of the 22 location sequences and removed a proportion of locations (randomly selected in the range of observed proportion of missing locations per recording period in the whole dataset, i.e. 2.1–68.1%, median=20.1). We then interpolated the missing locations. This procedure was bootstrapped 1,000 times for each maximal number of successive missing locations. We computed the proportion of missing locations interpolated for each bootstrap and reported mean and confidence intervals (2.5% and 97.5% quantiles). The reliability of the interpolation was measured as the number of map pixels (resolution 81 m) between the true location and the interpolated location (based on all the interpolated locations from the 1,000 bootstraps).

Application to the whole dataset

We interpolated the missing locations of the whole dataset using the same one to six maximal number of successive missing locations (leading to six datasets called “sensitivity datasets”) to test the influence of the maximal number of successive missing locations on the model selection procedure.

Statistical analysis

To model PAF, we used generalised linear mixed models fit by the Laplace approximation with binomial error and logit link (for more details, see, e.g. Agresti 2002, chapter 12) because we had more than one observation within our sampling units (animal identity and recording period) and we expected these observations to be correlated within such a given sampling unit. As opposed to hierarchical models in which random effects are assumed to be nested, we used animal identity and recording period as crossed random effects because of each observation potentially belonging to any combination of levels of these two factors (Gelman and Hill 2007). We accounted for the effects on the PAF of: (1) animal activity (categorical variable, two levels) and temperature (continuous variable) and (2) AS (continuous variable) and vegetation class (categorical variable, eight levels) known to be relevant factors. To get independent predictors, we accounted for the effect of factors (animal activity/vegetation class) on covariates (temperature/AS, respectively) by performing the regression of the covariate on the corresponding factor (called corrected temperature/corrected AS hereafter). Increasing temperature, inactivity of animals and habitat with low visibility (i.e. forested and hemmed areas) were expected to decrease PAF (e.g. D'Eon

et al. 2002; Dussault et al. 1999; Graves and Waller 2006; Hansen and Riggs 2008). Candidate models ($n=9$ and 6, see Tables 1 and 3) also included quadratic effect of temperature and AS to account for potential nonlinear relationships between PAF and these covariates (e.g. Dussault et al. 1999). We also accounted for a two-way interaction between temperature and activity because temperature might also have different effects depending on animal activity. Some vegetation classes were poorly represented and/or used by female mouflon in our study area (i.e. mainly “conifer” and “leafy and conifer”). In addition, locations recorded did not necessarily span the entire range of AS within a given vegetation class. Fitted probabilities were then sometimes very close to 0 or 1. Whilst in such conditions deviance can still be used to compare models, the usual asymptotic normality of the parameter estimates breaks down and leads to improbable coefficient estimates (Venables and Ripley 2002). We thus did not account for interaction between the vegetation classes and AS.

We decided to fit models on data subsets of eight locations, randomly sampled out of 144 for each animal–recording period pair (i.e. for a given animal and a given recording period) to limit spatiotemporal autocorrelations among data (one record every 20 min). In addition, fitting models on the whole dataset ($n>48,000$) led to a very high statistical power, yielding significant effects for all factors and making interpretation difficult. This procedure was replicated 1,000 times. For each of the 1,000 subsamples, we computed the Akaike weights (AICc weight; Burnham and Anderson 2002) of each candidate model (see above). Weights can be interpreted as the likelihood that a model is the best among the set of candidate models, thus allowing a relative comparison of the performance of the models (Burnham and Anderson 2001). Using AICc weights from

the 1,000 subsamples, we computed mean AICc weights for each candidate model. We then used the 1,000 subsamples to get the distribution of parameter estimates (including differences between, for instance, vegetation-specific coefficients). We reported mean and confidence intervals (2.5% and 97.5% quantiles) and assessed the significance of a given estimate by comparing its distribution to 0.

For the candidate models with the AS and vegetation class covariates, these steps were replicated for each of the six sensitivity datasets (i.e. missing locations of the whole dataset were interpolated using the one to six maximal number of successive missing locations). To test the influence of the maximal number of successive missing locations in the interpolation procedure on the PAF predictions, we computed predictions for each of the six resulting average models. Predictions were obtained for a dataset combining each vegetation class and a range of 200 AS values ranging from 4.3% to 100%. We then computed the correlation between prediction sets.

We performed statistical analyses, interpolation procedures and computation of available sky map with R 2.8.0 (Ihaka and Gentleman 1996) using libraries *ade4* (Chessel et al. 2004) and *adehabitat* (Calenge 2006). We conducted generalized linear mixed models using the function *lmer* in library *lme4* (Bates and Sarkar 2007).

Results

Data from GPS collars

In 2003, collar movement sensors of one female failed. We removed this animal from the study and performed all of

Table 1 Set of logistic regression models fitted to predict the GPS PAF in relation to mouflon activity and corrected temperature (see text for details) in the Caroux–Espinoise, France, 2003–2006

| Model ^a | Mean AICc weights |
|--|-------------------|
| Corrected temperature + corrected temperature² + activity + corrected temperature × activity | 0.466 |
| Corrected temperature + corrected temperature ² + activity + corrected temperature × activity + corrected temperature ² × activity | 0.290 |
| Corrected temperature + activity + corrected temperature × activity | 0.193 |
| Corrected temperature + corrected temperature ² + activity | 0.036 |
| Corrected temperature + activity | 0.015 |
| Corrected temperature + corrected temperature ² | 0.000 |
| Corrected temperature | 0.000 |
| Activity | 0.000 |
| Null | 0.000 |

We computed mean AICc weights by averaging AIC weights of each model over the 1,000 subsamples

^a In model notation, “+” corresponds to additive effects, “×” to interaction and “²” to the quadratic effect of covariate. The selected model (highest mean AICc weights) occurs in bold type

the analyses on the 15 remaining females. Two of them were harvested in autumn 2003 and 2005 and were monitored during eight and 16 recording periods, respectively (i.e. 1,152 and 2,304 fix attempts), whilst the 13 remaining ewes were monitored during 20–37 recording periods (mean=26.7, SD=5.8) representing 2,880–5,328 fix attempts. An average of 19.0% of failed locations per animal was registered (SD=6.6), ranging from 9.7% to 31.8%. After removing low-accuracy locations, we had no coordinates for 24.3% (SD=6.5) of the total fix attempts (caused by both failure to locate and the loss of low accuracy locations), ranging from 14.5% to 37.7%.

Influences of animal activity and temperature on the PAF

The top model ($\bar{w}=0.466$) included an effect of the interaction between corrected temperature and animal activity and a quadratic effect of corrected temperature (see Table 1). The second most supported model ($\bar{w}=0.290$) also included an interaction between squared corrected temperature and animal activity, whilst the third most supported model ($\bar{w}=0.193$) only had an interaction between corrected temperature and animal activity, but no quadratic effect of corrected temperature.

According to the top model, the PAF was lower when females were resting (0.81, 95% CI=0.79–0.84) than when they were active (0.89, 95% CI=0.86–0.91) at the average ambient temperature of the study area (13.8°C, Fig. 2). However, the PAF was similar and roughly constant between active and resting females at lower temperatures. PAF at ambient temperatures above 13.8°C in resting females decreased (0.44, 95% CI=0.36–0.52 at 30°C, Fig. 2b) whilst remaining relatively high in active animals (0.76, 95% CI=0.65–0.85 at 30°C, Fig. 2a).

Validation of the interpolation procedure

The interpolation procedure allowed interpolating most of the missing locations (mean>75%) even if we did not interpolate missing locations when we had more than one missing location during an active period (i.e. maximal number of successive missing locations=1, Table 2). The percentage of interpolated missing locations increased with the maximal number of successive missing locations, reaching 95.6% for the maximal number of successive missing locations, six. The interpolated locations were more than 55.9% of the time in the same pixel of the map than the original locations (Table 2). The accuracy of the interpolation decreased as the maximal number of successive missing locations increased. However, whatever the maximal number of successive missing locations we chose (i.e. from one to six), the interpolated locations were in the same pixel or in the eight neighbouring pixels $\geq 95\%$ of the time (Table 2).

Influences of topography and vegetation on the PAF

Model selection to predict the PAF based on vegetation class and available sky was performed on each of the six sensitivity datasets (i.e. datasets computed by interpolating missing locations with a maximal number of successive missing locations of one to six). The top model ($\bar{w}=0.591$) was consistently the same for the six sensitivity datasets (Table 3). It included an effect of the vegetation class and a quadratic effect for corrected available sky. The second best model ($\bar{w}=0.380$) included the linear effect of the corrected available sky and an effect of the vegetation class, whilst the third most supported model ($\bar{w}=0.028$) included only the effect of the vegetation class.

Fig. 2 Effects of corrected temperature (see text for details) on the GPS probability of acquiring a fix (PAF) when the female mouflon was active (a) and inactive (b) in the Caroux–Espinouse, France, 2003–2006. Filled circles ($\pm 95\%$ CI) are observed values grouped by class of corrected temperature from GPS collars (1,000 resampling). Symbols are proportional to the sample size. Continuous line (mean) and dotted lines (2.5% and 97.5% quantiles) are selected model (Table 1, model in bold type) predicted values (1,000 resampling)

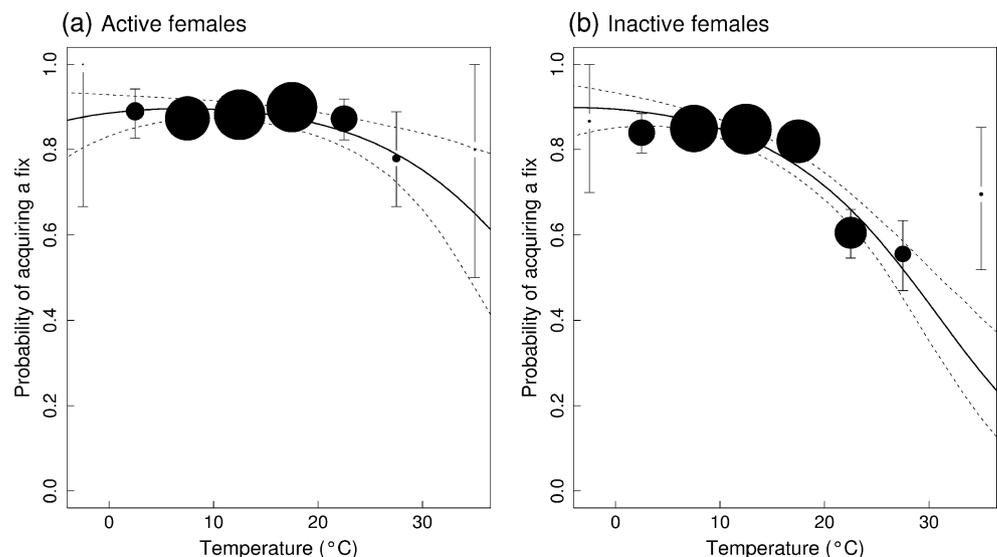


Table 2 Results of the validation of the interpolation procedure of the missing locations based on 22 complete trajectories (mean number of successive locations=71, SD=11.4) and 1,000 bootstraps

| Maximal number of successive missing locations | Mean percentage of missing locations (95% CI) | Mean percentage of interpolated missing locations (95% CI) | Percentage of the interpolated locations for each distance class (in pixels) from the true location | | | | | |
|--|---|--|---|------|-----|-----|-----|------|
| | | | 0 | 1 | 2 | 3 | ≥4 | ≤1 |
| 1 | 22.9 (4.8–54.7) | 78.9 (41.7–100.0) | 61.4 | 35.1 | 2.9 | 0.5 | 0.2 | 96.5 |
| 2 | 23.5 (4.8–54.8) | 89.5 (55.3–100.0) | 58.9 | 37.1 | 3.2 | 0.7 | 0.1 | 96.0 |
| 3 | 23.6 (4.8–55.7) | 93.4 (64.7–100.0) | 57.5 | 38.0 | 3.5 | 0.9 | 0.1 | 95.5 |
| 4 | 23.4 (4.8–54.8) | 94.7 (72.2–100.0) | 57.0 | 37.9 | 4.1 | 0.8 | 0.2 | 94.9 |
| 5 | 23.2 (4.8–54.8) | 95.5 (75.0–100.0) | 56.3 | 38.6 | 3.9 | 0.8 | 0.2 | 95.0 |
| 6 | 23.2 (4.9–56.3) | 95.6 (77.7–100.0) | 55.9 | 39.0 | 4.0 | 0.8 | 0.2 | 95.0 |

Percentage of missing locations randomly removed from a trajectory and percentage of these missing locations interpolated (mean and 95% CI based on 1,000 bootstraps) and percentage of the interpolated missing locations per distance class (in pixels) from the true location (based on all the simulated locations from the 1,000 bootstraps) for each maximal number of successive missing locations (above this value, missing locations during an active sequence were not interpolated) used in the interpolation procedure

Predictions between the six average models (from the six sensitivity datasets) were similar, as we had *r* values ≥0.98. As the choice of the maximal number of successive missing locations had no influence on the predicted values of the PAF, we performed the following analyses using only the average model developed from the sensitivity dataset with maximal number of successive missing locations, three. This value is a compromise between the proportion of interpolated locations and the accuracy of the interpolation.

According to the corresponding top model, vegetation class had a high influence on the PAF (Fig. 3a) that was highest in open areas and lowest in evergreen oak forest. All the tested habitats had a lower PAF than open areas (*P*< 0.05), with the exception of conifer forests and mixed deciduous and conifer forests. The conifer forest was not different from any other vegetation class, and mixed deciduous and conifer forests only had a higher PAF than evergreen oak forest (*P*=0.036) and deciduous forest during

leaf-on period (*P*=0.052). The infrequent use of conifer and mixed forests by females (mean=0.85 and 0.96% of the locations in the 1,000 datasets, respectively) compared to other vegetation classes may explain this lack of significance. Rocky areas had a lower PAF than open areas (*P*= 0.018), but higher than evergreen oak (*P*=0.018) and deciduous forests during leaf-on period (*P*=0.008). We also recorded a difference (*P*=0.008) when female mouflon used deciduous forest during the leaf-on season compared to the leaf-off season, with lower PAF when foliage was present. Furthermore, we detected differences in PAF between mouflon in evergreen oak and deciduous forest during the leaf-off season (*P*=0.024). The PAF was not different in sparse evergreen oak forest than in dense evergreen oak forest (*P*=0.114) and in deciduous forest during the leaf-on season (*P*=0.232).

The probability of a successful GPS fix was lower when female mouflon used areas with low sky availability and

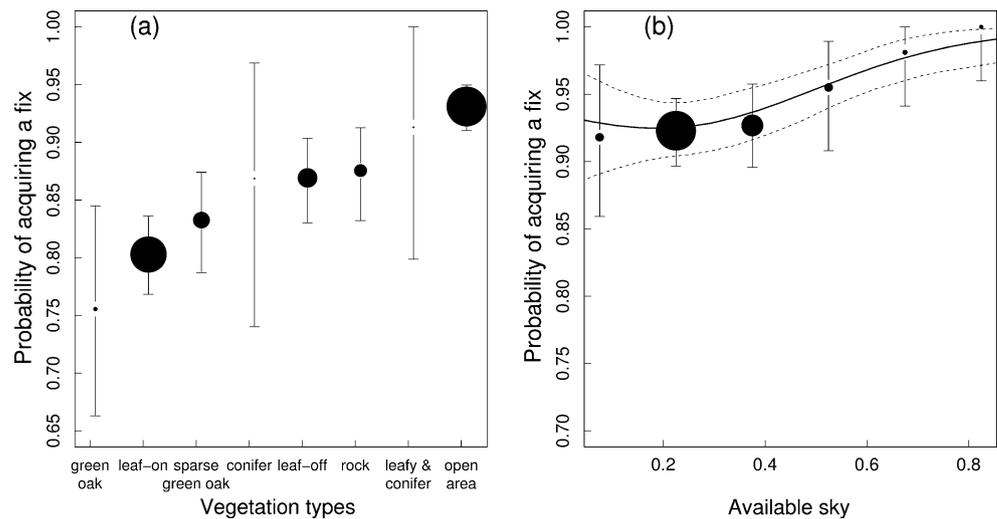
Table 3 Set of logistic regression models fitted to predict the GPS PAF in relation to vegetation class and corrected available sky (see text for details) in the Caroux–Espinouse, France, 2003–2006

| Model ^a | Mean AICc weights per sensitivity dataset | | | | | |
|---|---|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Corrected available sky + corrected available sky ² + vegetation | 0.607 | 0.600 | 0.585 | 0.583 | 0.586 | 0.587 |
| Corrected available sky + vegetation | 0.337 | 0.367 | 0.387 | 0.395 | 0.396 | 0.400 |
| Vegetation | 0.056 | 0.033 | 0.028 | 0.022 | 0.018 | 0.013 |
| Corrected available sky + corrected available sky ² | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Corrected available sky | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Null | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

We reported mean AICc weights for each of the six sensitivity datasets (i.e. each dataset was computed by interpolating missing locations with a maximal number of successive missing locations of one to six) and each model. Models were ranked according to their mean AICc weights

^a See Table 1 for model notation

Fig. 3 Effects on the GPS probability of acquiring a fix (*PAF*) in the Caroux–Espinouse, France, 2003–2006 of the vegetation class (predicted values) for the mean value of corrected available sky (33%, see text for details) (a) and of the corrected available sky in open habitats (b). Observed and predicted values were extracted from the sensitivity dataset and selected model (Table 3, model in *bold* type) with maximal number of successive missing locations, three. For further details, see Fig. 2



increased with sky availability (Fig. 3b). The mean predicted value of the PAF in our study area ranged from 0.93 (95% CI=0.88–0.97) to 0.99 (95% CI=0.97–1.00) and from 0.76 (95% CI=0.58–0.90) to 0.97 (95% CI=0.87–1.00) in open areas and evergreen oak forest, respectively.

Discussion

In a non-experimental context, we were able to assess the factors influencing the success of GPS fixes. We used fine spatial and temporal scale data recorded from GPS collars fitted on free-ranging female mouflon, which accounted for microhabitat selection and animal behaviour, in contrast with previous field experiments. The influence of animal behaviour on PAF was tested using motion sensors. By calibrating motion sensors to activity using direct observations of free-ranging female mouflon (Bourgoin et al. 2008), we were able to predict reliably their activity throughout the study. This information also provided the opportunity to derive an interpolation procedure to test for the influence of environmental conditions at a fine scale. Lastly, we performed analyses on independent predictors to test their independent influence. We were able to demonstrate that location failures did not occur randomly, but were influenced by high temperatures, animal behaviour, and habitat characteristics.

Dussault et al. (1999) reported a quadratic relationship between ambient temperature and fix success of moose *Alces alces* in the boreal forest (Québec, Canada), with the lowest values observed during hot and cold periods. During the summer in Alaska, Moen et al. (1996b) observed a similar decrease of fix success of moose during hot periods. Such variations in the fix success may mainly reflect changes in habitat use. In fact, to limit stress and energetic costs induced by extreme temperatures, ungulates preferentially use covered areas (Mysterud and Østbye 1999). For

example, moose spend more time in dense forest during hot periods, seeking shade (Dussault et al. 1999; Moen et al. 1996b). Climatic conditions during winter were less extreme in our study area (mean temperature=3.3°C, SD=3.8) than for moose in Canada, explaining the high and roughly constant value of the PAF at low temperatures. In addition, mouflon migrated to the valley to avoid adverse conditions (Auvray 1983), and females were mainly observed in open areas during winter (Bon et al. 1991) where the probability of getting a fix was high (Frair et al. 2004; Janeau et al. 2004; Rumble and Lindzey 1997). On the contrary, during hot periods, mouflon sheltered under dense cover (Auvray 1983; Santosa 1990), leading to the low PAF we observed. The high degradation of the PAF suggests that mouflon are strongly influenced by high summer temperatures that occur in the Caroux–Espinouse (see Garel et al. 2004; Bourgoin et al. 2008).

Lower fix success has been reported when animals were resting vs. active (Bowman et al. 2000; Graves and Waller 2006; Moen et al. 2001). The variable distance between collar and ground could influence such results (Graves and Radandt 2004). The collar of a bedded animal may be nearer the ground where it could be visually obstructed, leading to a poor connection between satellites and the GPS collar (Bowman et al. 2000). This effect might increase when the animal is lying because the antenna is not pointed to the sky but to the side or ground, leading to a lower PAF (D'Eon and Delparte 2005; Moen et al. 1996b). Also, the ground and the animal's neck may reflect or absorb part of the signal from satellites (Graves and Waller 2006). In the same way, when the animal is near a tree or a rock, the connection between the collar and the satellites is more likely reduced. Therefore, microhabitat selection should have a marked impact on fix success (Edenius 1997; Sager-Fradkin et al. 2007). However, fix success did not differ between active and resting female mouflon at low temperatures in our study area, suggesting that other factors were

producing decreased fix success during hot periods. Active mouflon are mostly feeding (Langbein et al. 1997), and as grazers (Hofmann 1989), their diet is mainly composed of grasses and shrubs year-round (Cransac et al. 1997; Faliu et al. 1990). Therefore, active mouflon are principally exploiting open habitats. In contrast, during summer, mouflon tend to rest in steep rock or closed habitats where they find shade (Auvray 1983; Santosa 1990), but also where the probability of getting a fix is low compared to open areas (Frair et al. 2004; Janeau et al. 2004; Rumble and Lindzey 1997). Hence, a switch in habitat use between seasons and animal activity might explain the differences in PAF between active and resting females during hot days.

Our sensitivity analysis highlighted that the maximal number of successive missing locations (between one and six) affected the proportion of interpolated locations and their accuracy [but a high proportion of interpolated locations ($\geq 95\%$) were in the same pixel or in the neighbouring pixels]. Nevertheless, the top model was the same. Predicted values of the PAF were highly correlated between average models whatever the maximal number of successive missing locations we chose for the interpolation procedure, supporting the robustness of our interpolation procedure and predictions on the PAF for our studied species and GPS collar schedule.

Some previous studies reported no influence of terrain obstruction (Frair et al. 2004; Graves and Waller 2006), whilst some others reported a lower fix success of GPS collars in low sky visibility areas (Cain et al. 2005; D'Eon et al. 2002; Hansen and Riggs 2008; Sager-Fradkin et al. 2007). In contrast with other studies, we corrected the sky availability for vegetation class and then tested the influence of sky availability independently of vegetation class effects. We detected a negative influence of terrain obstruction. With reduced visibility, GPS collars would predictably achieve lower fix success (Lewis et al. 2007). However, we found a high PAF (>0.90) even in very low visibility areas ($<10\%$) in open areas (Fig. 3b). This could be explained by the high performance of GPS collars and/or by the relatively low resolution (81 m) of the map used.

Vegetation characteristics also predictably influenced fix success, with the highest success occurring in open areas and the lowest one in forested areas. The decrease of the success of GPS fixes that occurred along a continuum from open areas to broad-leaved forest during the leaf-on season can easily be explained by the obstruction generated by trees (Rempel et al. 1995; Rumble and Lindzey 1997).

The foliage influence on the PAF has been a controversial question. The lower fix success in deciduous forests during the leaf-on season compared to winter suggests a foliage obstruction issue (Moen et al. 2001; Sigrist et al. 1999). However, in previous studies, the increase of fix success during the winter was not only observed in

deciduous forest but also in mixed and coniferous forests. It is possible that increased fix success in winter might have been caused by atmospheric changes between seasons, creating better conditions for GPS collar performance during winter (Dussault et al. 1999). In contrast to these studies, other field trials demonstrated higher fix success during leaf-on than leaf-off seasons (Cargnelutti et al. 2007) or to similar fix success (Hebblewhite et al. 2007; Janeau et al. 2004; Zweifel-Schielly and Suter 2007). In our work, we found improved fix success rates during the leaf-off season compared to the season with foliage, suggesting effects of leaf obstruction.

We report for the first time to our knowledge a test of the influence of rock formations on GPS fix success. Although no vegetative obstruction occurs in rock areas, we detected lower fix success in rock than in open areas. Perhaps multipathing (i.e. the signal from the satellite is reflected by some object before reaching the GPS collar) or obstruction generated by rocks occurred because these areas are steep, and when mouflon are lying against rock or in little rock caves (Bourgoin, G. and Garel, M., personal observations), the amount of visible sky is limited.

The method we developed (see also Graves and Waller 2006) allows biologists to compute a bias model specific to their GPS collars and study area without performing any costly and time-consuming field trial. With the help of this bias model, classical bias correction methods (e.g. sample weighting or iterative simulation, see Frair et al. 2004 for an application of these two methods) can be used to remove the habitat selection bias induced by GPS location failures. Although we demonstrated that the number of missing locations did not influence the accuracy of the interpolation procedure, we encourage biologists to perform a sensitivity analysis on their own dataset. Indeed, our procedure may be dependent on the habitat heterogeneity and the time interval between successive fixes (e.g. the precision of the interpolation may decrease with increasing time interval). The number of missing locations tolerated for interpolation should therefore be set as a compromise between the accuracy of the interpolation procedure and the proportion of interpolated locations (which will be used to compute the bias model).

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