

Effects of GPS relocation intervals on behavior metrics in brown bears

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ABSTRACT

Tracking wildlife with Global Positioning Systems (GPS) has become an invaluable tool in research, and allows the collection of very accurate relocation data with a very high temporal resolution. The longevity of the GPS devices is typically limited by the battery life or the number of positions that can be taken. Consequently, researchers experience a trade-off when designing a GPS tracking study, i.e. choosing a high temporal resolution relocation schedule or monitoring individuals for an extended period of time?

Within the Scandinavian Brown Bear Research Project, the 'base' relocation GPS schedule has been 1 relocation / 30 minutes since 2003. Reducing the temporal resolution may benefit the long-term demographic studies (i.e., more bears & longer tracking periods) of the SBBRP, as well as animal welfare (i.e., less captures per capita). However, it is not clear if a reduction in the relocation interval also affects research findings, and the compatibility of these findings with previous research. Here, I explore if we can reduce the base GPS relocation schedule of the SBBRP without losing biological information and compatibility with previous research finding.

Using a variety of techniques, I analyzed movement patterns, home range sizes, population wide resource selection, individual resource selection and, its repeatability (i.e., a personality measure), and spatiotemporal interactions between GPS marked bears in south-central Sweden (2003-2012) in relation to different GPS relocation schedules (30, 60, 120, and 180 minutes).

Prolonging the relocation interval inevitably implies a reduction in the level of detail and precision of the metrics. However, the biological effect sizes were not always large. For the movement parameters, home range sizes, and population-wide and individual-based resource

selection and personality measures, results were nearly identical for the 30-minute and 60-minute relocation intervals, but started to deviate at 120 and 180 minutes. The largest loss of detail due to an increasing GPS relocation interval is probably loss of a relatively large number of short-term interactions (< 50 m, no time lag) that remain undetected between individual brown bears (30 → 60 minutes: 14.5%, 30 → 120 minutes: 23.6% , 30 → 60 minutes: 28.2%). In all analyses (except the interaction analyses), 'reproductive status' was an important model term, irrespective of relocation schedule, suggesting that biological effects can still be detected using a temporally less detailed GPS relocation schedule. Based on these analyses and the near identical results at a 30-minute and 60-minute relocation schedule (except for the interaction analysis), I would suggest not increasing the relocation interval much above 60 minutes.

1. Introduction

Wildlife tracking using Global Positioning System (GPS) has become an extremely widespread and useful tool in wildlife research (Cagnacci et al. 2010). The great advantage of GPS tracking technologies is that animals can be monitored with an extremely high spatiotemporal resolution (< 5 m accuracy, > 1 position/minute), which can be especially valuable if the study species have secretive lifestyles. In addition, high-resolution GPS tracking also allows researchers to collect individual-based field data, such as prey remains, hair samples, feces, etc. Consequently, GPS tracking opened doors for posing new questions in behavioral ecology (e.g., social networks, species interactions, flight behavior, spatiotemporal segregation/niche differentiation, sexually selected infanticide, personality in elusive species, etc.) (Cagnacci et al. 2010), and the study of wildlife tracking using GPS became a science in itself (see for example the special issues in the *Philosophical Transactions of the Royal Society – Biology B* 2010 and the *Journal of Animal Ecology* 2013, and the establishment of specialist journals such as 'Movement Ecology') (Nathan and Giuggioli 2013). Besides the numerous advantages of GPS tracking, several drawbacks exist, for example, high costs, relatively few study units, data management and analytic challenges and difficulties, and an the risk of collecting too fine-scaled data with respect to the research questions (Hebblewhite and Haydon 2010).

The main research method of the Scandinavian Brown Bear Research Project (SBBRP) is capturing and marking individual brown bears (*Ursus arctos*), and monitoring them, preferably, from birth to death. Until around 2003, Ultra High Frequency (UHF) radio telemetry was the most common method of keeping track of the study animals. After 2003, GPS tracking became the standard tracking technique in the SBBRP. The GPS collars (the Vectronic GPS plus series, Vectronic Aerospace GmbH) are equipped with a GSM (Global System for Mobile communications) module, which sends location data (in batches of 7) to a central server per SMS (Short Message Service). The standard relocation schedule of the GPS marked bears in the SBBRP is 1 position per day during denning, and 1 position per 30 minutes during the 'active season' (i.e. from early may until late October), resulting in a vast (> 3 million valid positions between 2003-2013) and highly accurate relocation dataset, comprising about 370 bear years. Dependent on the battery capacity and type (2D, 3D - cell battery), and onboard sensory equipment, Vectronic GPS plus collars typically record and transmit around 15600 (2D) – 24800 (3D) GPS relocations (www.vectronic-aerospace.com). This implies that a tradeoff exists between the GPS relocation schedule and the longevity of a collar (Brown et al. 2012). Reducing the relocation schedule may elongate the period that individual bears can be monitored and can possibly benefit the long-term demographic studies within the SBBRP (i.e., following a larger number of individuals, especially yearlings and 2-year-old bears after family breakups), and can improve animal welfare (i.e., lower capture rate per capita) (Bischof et al. 2009). However, a reduced relocation schedule may also influence research findings and dilute fine-scaled behavioral mechanisms. This potential drawback is also the focus on this report: can we reduce the basic GPS relocation schedule without losing biological information and compatibility with previous research findings?

In this report, I investigate how a reduction in the relocation schedule (from 30 to 60, 120, and 180 minutes) affects metrics related to i) diurnal and daily movements, ii) home-range sizes, iii) population-wide resource selection, iv) individual-based resource selection and personality, and v) social interactions between individual bears.

2. Methods

All bear data originated from brown bears that were captured and marked with GPS collars in the southern study area of the SBBRP in south-central Sweden. For details on capture and handling procedures refer to Arnemo et al. (2011). For a detailed study area description, refer to Martin et al. (2010). We removed unvalidated relocations, relocations with DOP values > 5 , and relocations collected based on 2 satellites from the data to improve spatial accuracy relocations (Lewis et al. 2007).

2.1. Movement patterns

I used relocation data of GPS marked adult lone female brown bears (≥ 5 years, 34 females, 69 bear years) and females with cubs-of-the-year (females/cubs, 16 females, 16 bear years) during the peak of the mating season (15 May – 15 July) of 2004-2012. I calculated the movement speed between two consecutive 30, 60, 120, and 180 minute relocations for each individual, and used ‘movement speed’ (per relocation schedule) as the response variable in Generalized Additive Models. First, I tested if speed depended on ‘relocation schedule’. Here, I separately modeled speed as function of ‘relocation schedule’ for lone adult females and females with cubs. For both models, I included ‘time of day’ and ‘day of the year’ as regression splines per relocation schedule. I evaluated the importance of ‘relocation schedule’ as a fixed effect in each model with on AIC based model diagnostics (Burnham et al. 2011).

Secondly, and for each relocation schedule, I evaluated if I could detect differences in movement speed between lone adult females and females with cubs. Refer to Steyaert et al. (2014) for a theoretical motivation and methodological details. Here, I used regression splines (Generalized Additive Models, GAMs) on ‘time of the day’ and ‘day of the year’. As fixed effects, I only considered reproductive status (cubs present yes/no), and evaluated its importance using AIC based diagnostics. In all analyses, I ignored ‘bear ID’ and ‘year’ as random components because of computational constraints. I validated the models with fitted vs. residual plots (Zuur et al. 2009). I used the ‘adehabitatLT’ and ‘mgcv’ packages in R 2.15.0 (R Development Core

Team 2013) for calculating movement speed between relocations and constructing the GAMs, respectively.

2.2. Home ranges

I used the same dataset as in 2.1. to calculate 95% minimum convex polygon home ranges, but extended the period (15 April – 20 August). I excluded positions in the hunting season (> 20 August), because several outliers in terms of home range size appeared to be present in the dataset (probably due to extreme movements of hunter-chased bears, or the transport of hunter-killed bears outside the study area).

I used linear mixed-effect regression models to evaluate the effect of GPS relocation schedule on home range size. I log-transformed the response variable 'home range size' to improve model fit, and considered 'reproductive status' and 'GPS relocation schedule' as fixed factors and included 'year' and 'bear ID' as random factors. I used a backward stepwise model selection procedure based on likelihood ratio tests and a $\alpha = 0.05$ threshold level for statistical significance (Zuur et al. 2009). I calculated the interclass correlation coefficient (ICC) of 'bear ID' to assess the importance of the individual bear on home range size under various relocation schedules following Zuur et al. (2009). I used the 'adehabitatHR' and 'lme4' packages in R 2.15.0 (R Development Core Team 2013) for calculating home range sizes and constructing the mixed effect regression models, respectively. I validated the models with fitted vs. residual plots (Zuur et al. 2009).

2.3. Resource selection

I used an existing dataset (see page 10-11 in Zedrosser et al. 2013) to model resource selection of adult males (7; 18 bear years) and lone adult females (8; 16 bear years) during the mating season (15 May – 15 July) (Steyaert et al. 2012a) of 2008-2012. I evaluated how resource selection was affected by changing the relocation schedule from 30 to 60, 120, and 180 minutes. I used resource selection functions (RSFs) to model resource selection. This approach links resource 'use' (i.e. wildlife relocations) and resource 'availability' (i.e. random points) with a set of landscape variables, and contrasts 'use' and 'availability' with statistical models

(typically logistic regression) (Manly et al. 2002, Aarts et al. 2012). I evaluated resource selection on two scales, i.e. on the population level, and on the individual level. I sampled availability within the home range of each individual bear and according to a 1:1 use vs. availability ratio.

I considered the following landscape variables in the RSFs: 'Normalized Difference Vegetation Index' (NDVI), terrain ruggedness (local and landscape scale, TRI and TRI1000), land cover type (old forest, young dense forest, young open forest, bog), and distance (m) to settlements, buildings, forest roads, and supplementary feeding sites. For a detailed description and justification of the landscape variables, refer to Zedrosser et al. (2013) and Steyaert et al. (2012b). We used Erdas Imagine 9.1 and Arcgis 9.2 for all spatial analyses.

On the population level, I used generalized linear mixed effect regression models with a binomial error structure (use vs. availability) and a logit link function. As fixed terms, I considered all above mentioned landscape variables, except 'distance to supplementary feeding sites', and included 'year' and 'bear ID' as a nested random factor. I modeled resource selection separately for males and for females, and for the active (nighttime, 18:00 – 8:00) and passive (daytime, 8:30 – 17:30) hours (Moe et al. 2007). I used a backward stepwise model selection procedure based on likelihood ratio tests and a $\alpha = 0.05$ threshold level for statistical significance (Zuur et al. 2009). I repeated the analysis for each relocation schedule, and visually inspected the stability of the parameter estimates and standard errors.

I modeled individual based RSF using generalized linear regression models with a binomial error structure (use vs. availability) and a logit link function, and with 'distance to supplementary feeding sites' as the only fixed effect. I repeated this analysis for the four GPS relocation schedules, and evaluated the stability of the parameter estimates using repeated paired sample t-tests. In a second step, I summarized the parameter estimates for supplementary feeding site selection per relocation schedule and individual bear (for all the bears that had > 1 'bear year'), and added bear specific reproductive status data (male/female, adult/subadult). I included 'bear ID' nested per 'year' as a random effect on the intercept, and evaluated the ICC as a measure of repeatability or personality for each relocation schedule (Zuur et al. 2009, Nakagawa and

Schielzeth 2010). I used 'lme4' and the 'stats' package in R 2.15.0 (R Development Core Team 2013) for all statistical analyses.

2.4. Bear encounters

I identified all encounters between adult males (21 adult males, 58 bear years) and all other GPS marked bears during the mating season 2008-2012 using R 2.15.0 (code developed by M. Leclerc). I defined an encounter as any occasion in which an adult male was less than 50 m from another GPS-marked bear without time lag. I simply calculated the total number of interactions and the number of unique bear-pairs for each GPS relocation schedule to evaluate whether or not the relocation schedule influenced bear encounter detection probability.

3. Results

3.1. Movement metrics

The number of movement records declined with a decreased GPS relocation schedule: 144363, 67782, 33936, and 20871 relocations for lone adult females, and 35230, 15572, 7744, and 4846 relocations for females/cubs for a 30-, 60-, 120- and 180-minute GPS schedule, respectively. After correcting for interval duration, however, 'data loss' was relatively little. An increased relocation interval reduced data volume with approximately 13 – 20 % from a 30- to 120-minute relocation schedule for lone adult females and females/cubs, respectively.

Results from the GAMs showed that relocation schedule has a significant and negative effect on movement speed; excluding relocation data from the models increased AIC scores by 216.7 and 127.2, for lone adult females and females with cubs, respectively. For lone adult females, movement speed decreased from an average of 473 m/h at a 30-minute relocation schedule by 54.1 ($t = -7.5$, $p < 0.001$), 102.0 ($t = -10.96$, $p < 0.001$), and 128.1 ($t = -11.21$, $p < 0.001$) m/h for a 60-, 120-, and 180-minute relocation schedule. For females/cubs, movement speed decreased from an average of 136.5 m/h at a 30-minute relocation schedule by 28.9 ($t = -6.66$, $p < 0.001$), 48.4 ($t = -8.61$, $p < 0.001$), and 55.6 ($t = -7.94$, $p < 0.001$) m/h for a 60-, 120-, and 180-minute relocation schedule.

Reproductive status was an important model term, irrespective of relocation schedule.

Removing reproductive status as a model term increased the AIC scores by 1935.9, 1023.6, and 598.6 for 30-, 60-, and 120-minute relocation schedules (note that AIC differences $> 2-6$ are considered as strongly significant). Females/cubs always had significantly ($p < 0.001$) lower movement speed than lone adult females (table 1). Note, however, that the model based on a 180-minute schedule did not converge. The GAMs always detected diurnal bimodal movement patterns for lone adult females, whereas these patterns faded out for females/cubs at a relocation schedule of 120-minutes (Table 1, Figure 1). Trends in seasonal movement patterns were always detected for lone adult females (p values were systematically < 0.001), albeit in decreasing strength (see the decreasing E.DF values in Table I, and Figure 1).

Table 1. Results of generalized additive regression models to evaluate movement speed by lone adult female brown bears and females with cubs-of-the-year (females/cubs) during the peak of the mating season (15 May – 15 July) in south-central Sweden, between 2004 and 2012. We compared 4 GPS relocation schedules (30, 60, 120 and 180 minutes). The 180-minute schedule model did not converge and is not presented. β 's and σ 's represent parameter estimates and standard errors of the fixed effects, respectively. E.DF and RDF represent the effective and reference degrees of freedom of the smooth terms (diurnal and seasonal). E.DF and Ref.DF indicate the level of nonlinearity in the data, with values > 1 indicating nonlinear patterns.

<i>30-minute schedule</i>	Fixed terms	β	σ	t value	p value
	Intercept	474.694	3.951	120.1	< 0.001
	Status: Female/cubs vs. Lone adult females	-339.627	7.615	-44.6	< 0.001
	Smooth terms	E. DF	Ref. DF	F value	p value
	Diurnal: Lone adult female	7.861	7.994	344.989	< 0.001
	Diurnal: Female/cubs	5.363	6.483	5.445	< 0.001
	Seasonal: Lone adult female	4.292	5.282	66.644	< 0.001
	Seasonal: Female/cubs	1.373	1.655	27.206	< 0.001
<i>60-minute schedule</i>	Fixed terms	β	σ	t value	p value
	Intercept	419.983	4.936	85.08	< 0.001
	Status: Female/cubs vs. Lone adult females	-313.214	9.640	-32.49	< 0.001
	Smooth terms	E. DF	Ref. DF	F value	p value
	Diurnal: Lone adult female	7.812	7.990	188.289	< 0.001
	Diurnal: Female/cubs	4.347	5.450	2.342	0.0342
	Seasonal: Lone adult female	3.469	4.302	38.513	< 0.001
	Seasonal: Female/cubs	1.000	1.000	18.323	< 0.001
<i>120-minute schedule</i>	Fixed terms	β	σ	t value	p value
	Intercept	371.574	5.803	64.03	< 0.001
	Status: Female/cubs vs. Lone adult females	-282.857	11.346	-24.93	< 0.001
	Smooth terms	E. DF	Ref. DF	F value	p value
	Diurnal: Lone adult female	7.516	7.933	109.96	< 0.001
	Diurnal: Female/cubs	0.000	0.000	0	NA
	Seasonal: Lone adult female	2.894	3.597	28.27	< 0.001
	Seasonal: Female/cubs	1.000	1.000	13.45	< 0.001

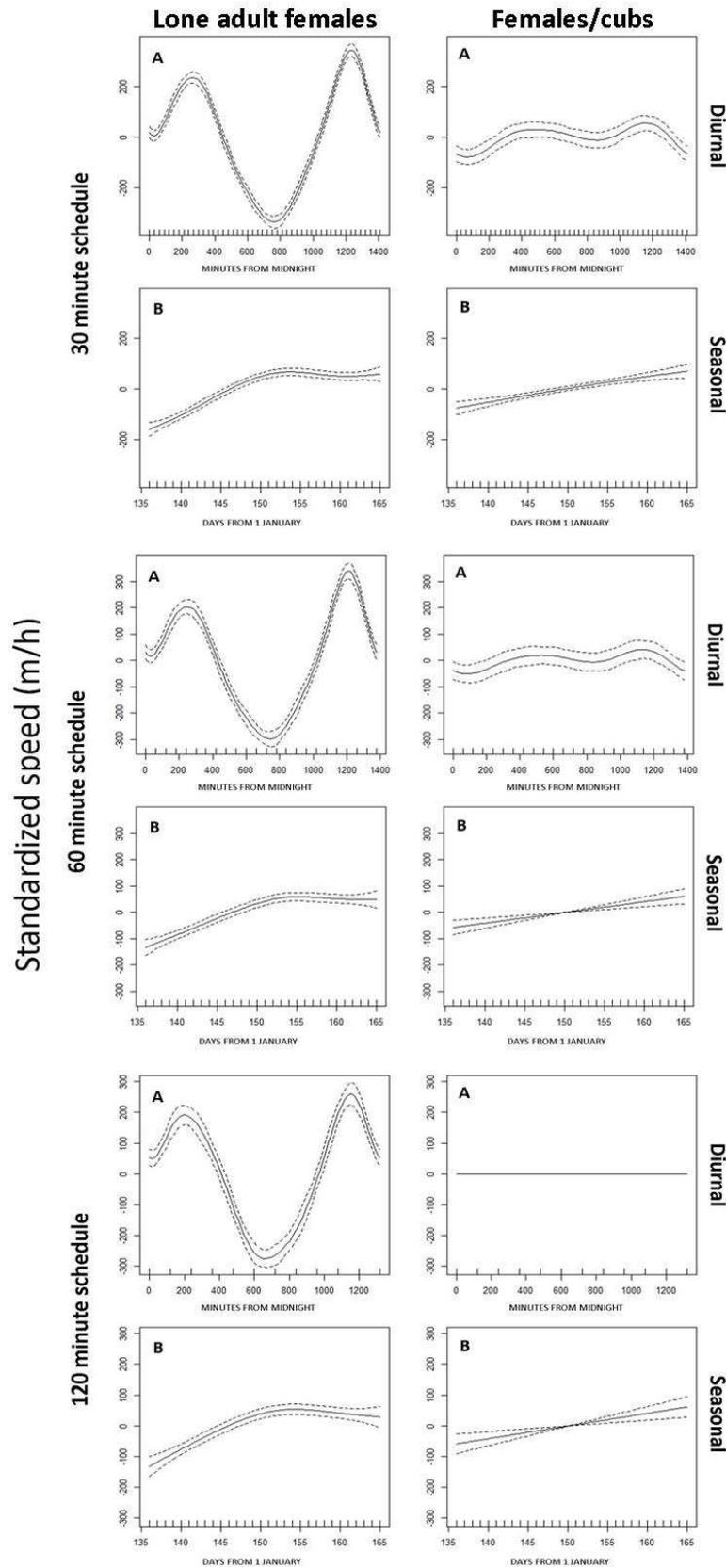


Figure 1. Predicted diurnal (A, minutes after midnight) and seasonal (B, days from 1 January) movement patterns (m/h, standardized around 0) of GPS marked adult lone female brown bears (34 females, 69 bear years) and females with cubs-of-the-year (females/cubs, 16 females, 16 bear years) during the peak of the mating season (15 May – 15 July) 2004-2012. We used Generalized Additive Models to evaluate movement patterns according to three GPS relocation schedules (30, 60, 120), with regression splines on 'time of the day and day of the year'. The '180' model did not converge.

3.2. Home range analysis

Home range size was negatively affected by a decreasing GPS relocation schedule (from 30 to 60 minutes: $\beta = -0.029$, $\sigma = 0.016$, $t = -1.83$, 30 to 120 minutes: $\beta = -0.034$, $\sigma = 0.016$, $t = -2.11$, and 30 to 180 minutes: $\beta = -0.1$, $\sigma = 0.016$, $t = -6.27$) (Table 2, Figure 2). Lone adult females had larger home ranges compared to females with cubs-of-the-year $p < 0.001$, irrespective of GPS relocation schedule (Table 2, Figure 2). The intraclass correlation was very high (ICC = 0.72, bear variance 0.2843, residual variance 0.109, year variance = 0).

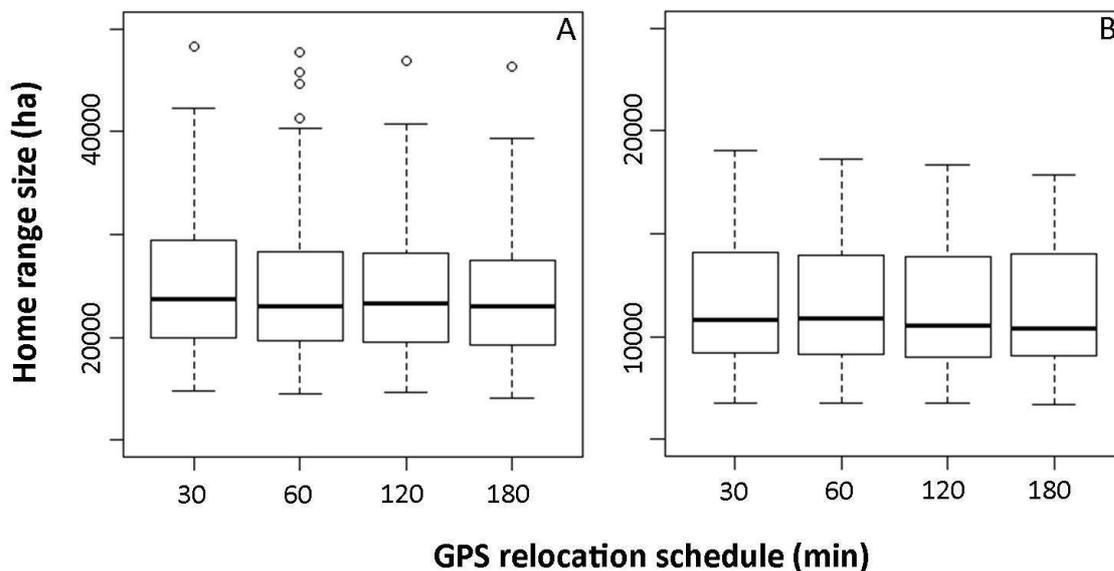


Figure 2. Home range (15 April – 20 August) sizes (95% minimum convex polygons, hectares) of lone adult females (A, 34 females, 69 bear years) and females with cubs-of-the-year (B, females/cubs, 16 females, 16 bear years) according to different GPS relocation schedules (30, 60, 120, and 180 minutes).

Table 2. Results of a linear mixed effect regression model to evaluate the effect of GPS relocation schedule (30, 60, 120, and 180 minutes) and reproductive status (lone adult females, females with cubs-of-the-year – females/cubs) on home range size (95% minimum convex polygons) of brown bears monitored in south-central Sweden between 2004 and 2012. MCPs were calculated for the period 15 April – 20 August. We log-transformed the response variable to improve model fit.

Model term	β	σ	t value	p value
Intercept	4.10207	0.127	32.37	n.s.
Reproductive status:				
Lone adult females vs. Females/cubs	0.87211	0.141	6.21	< 0.001
Interval: 60 vs. 30	-0.02927	0.01595	-1.83	< 0.001
Interval: 120 vs. 30	-0.03374	0.01595	-2.11	
Interval: 180 vs. 30	-0.10006	0.01595	-6.27	

3.3. Resource selection

The model selection procedure of the RSF revealed an identical model composition for the 30 and the 60 GPS relocation schedule. For females, the following fixed effects were always included in the top ranked models at a 30- and 60-minute relocation schedule: 'NDVI', 'TRI1000', 'old forest', 'young dense forest', 'young open forest', 'bog', and distance to 'settlements' and 'buildings'. 'TRI' and distance to 'forest roads' were never included in the top-ranked models of a 30- and 60-minute relocation schedule. For females during daytime, the land cover type 'bog' was removed from the top model for the 120- and 180-minute relocation schedule. For females during nighttime, 'bog' and 'NDVI' were removed from the top model at a 120-minute schedule. At a 180-minute relocation schedule, NDVI was the only excluded model term, and distance to 'forest roads' was -uniquely- included (Table 3).

The male models appeared to be more stable: during daytime and irrespective of relocation schedule, 'NDVI', 'TRI1000', 'old forest', 'young dense forest', 'bog', and distance to 'settlements' and 'buildings' were always included, whereas distance to 'forest roads' and 'TRI' were always excluded. During nighttime, all models always included 'TRI', 'TRI1000', 'old forest', 'young dense forest', 'young open forests', 'bog', and distance to 'settlements' and 'buildings' and 'forest roads', except for the 180-minute relocation schedule model, when 'bog' was excluded from the top-ranked model (Table 3). A visual inspection of the parameter estimates and their standard errors showed that parameter estimates and standard errors of the RSFs were relatively stable (except for the intercept), irrespective of GPS relocation schedule, sex, and period of the day (Figure 3).

For the individual-based RSFs, parameter estimates for 'supplementary feeding site selection' were stable irrespective of the GPS relocation schedule ($0.051 < p < 0.563$ for all pairwise comparisons per GPS relocation schedule). However, it seemed that the GPS relocation schedule did matter for few individuals during certain a year (e.g., W0703-2010, W0825-2011, Figure 4). The ICC's increased with a decreasing relocation schedule (30 minutes: 0.122, 60: 0.142, 120: 0.149, 180: 0.186).

Table 3. Model selection results of brown bear resource selection functions. Brown bears (8 adult females, 16 bear years, upper part; 7 adult males, 18 bear years, lower part) were monitored in south-central Sweden between 15 May and 15 July, 2008-2012. '✓' indicates whether or not a model term was included in the final model for a certain GPS relocation schedule (30, 60, 120 or 180 minutes between consecutive relocations). We used a backward stepwise selection procedure with an $\alpha = 0.05$ cutoff value for statistical significance.

Model term	Females, daytime				Females, nighttime			
	30	60	120	180	30	60	120	180
<i>NDVI</i>	✓	✓	✓	✓	✓	✓		
<i>TRI</i>								
<i>TRI1000</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Old forest</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Young dense forest</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Young open forest</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Bog</i>	✓	✓						
<i>Settlement</i>	✓	✓	✓	✓	✓	✓		✓
<i>Building</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Forest road</i>								✓

Model term	Males, daytime				Males, nighttime			
	30	60	120	180	30	60	120	180
<i>NDVI</i>	✓	✓	✓	✓				
<i>TRI</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>TRI1000</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Old forest</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Young dense forest</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Young open forest</i>					✓	✓	✓	✓
<i>Bog</i>	✓	✓	✓	✓	✓	✓	✓	
<i>Settlement</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Building</i>	✓	✓	✓	✓	✓	✓	✓	✓
<i>Forest road</i>					✓	✓	✓	✓

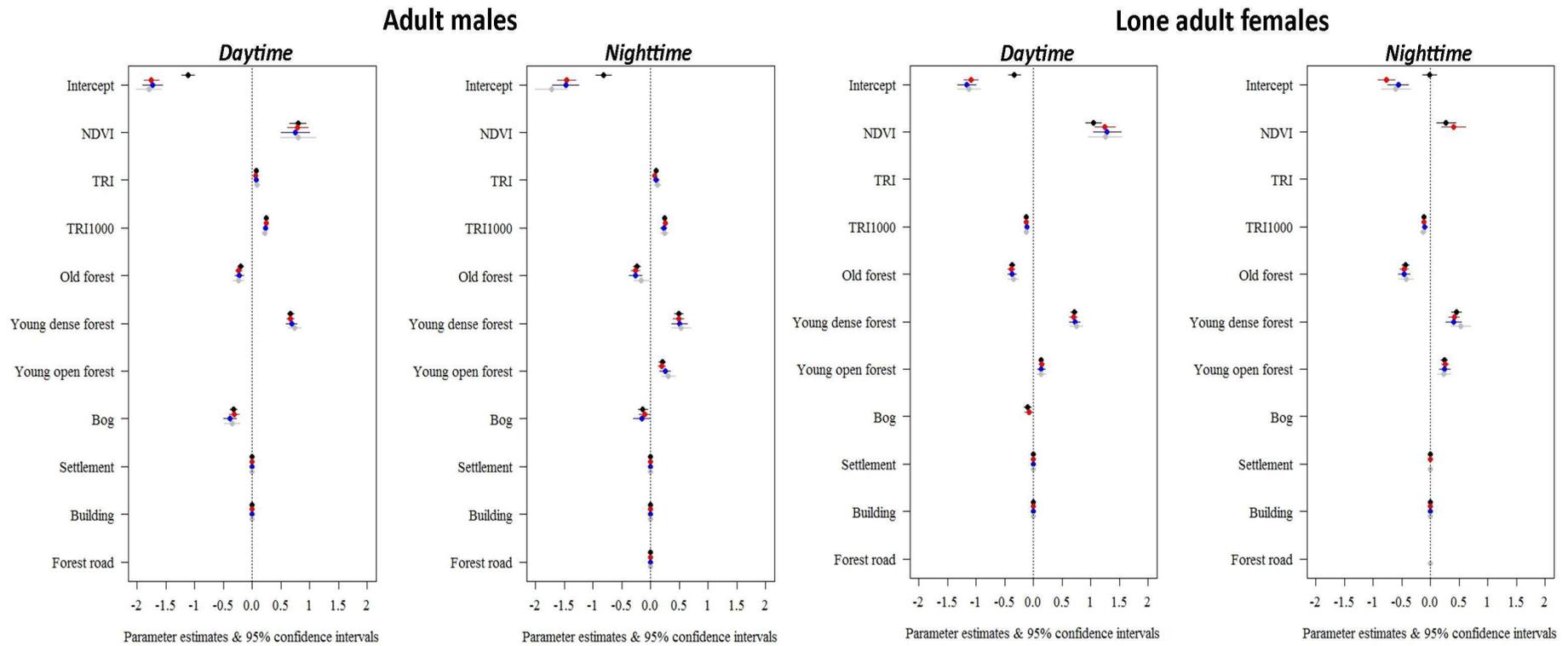


Figure 3. Resource selection modeling results (parameter estimates and their 95% confidence intervals) for 8 adult females (16 bear years) and 7 adult male brown bears (18 bear years) during the mating season in south-central Sweden. We generated separate models for males and females, and day and nighttime, and according to 4 GPS relocation schedules (30 minutes, **black**; 60 minutes, **red**; 120 minutes, **blue**; and 180 minutes, **grey**). Note that negative values for the distance related variables 'settlement', 'building', and 'forest roads' would imply selection for, and *vice versa*.

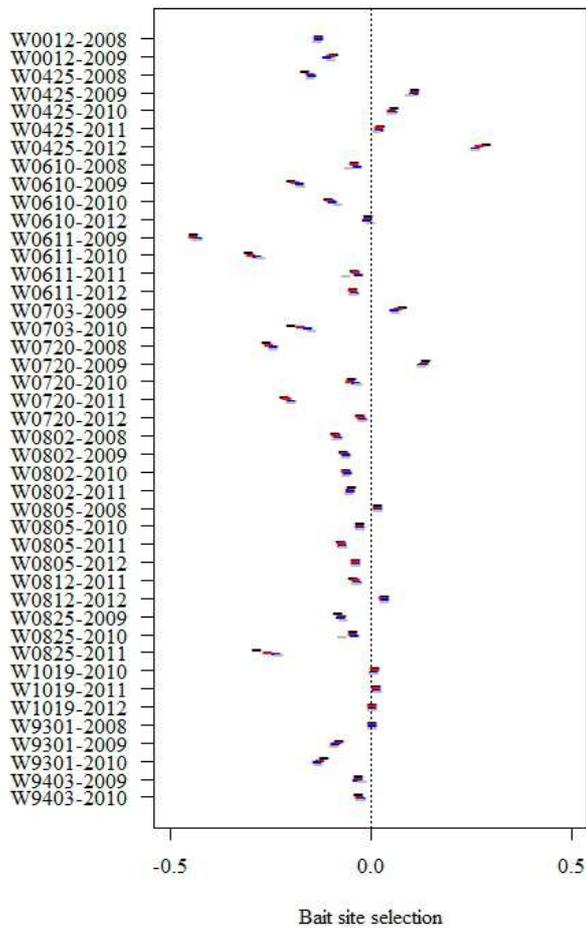


Figure 4. Individual-based resource selection modeling results (parameter estimates) for 8 adult females (16 bear years) and 7 adult male brown bears (18 bear years) during the mating season in south-central Sweden. We generated separate models according to 4 GPS relocation schedules (30 minutes, **black**; 60 minutes, **red**; 120 minutes, **blue**; and 180 minutes, **grey**). Note that negative values imply selection for.

3.4. Encounter rates

The number of interactions between bears decreased progressively when the relocation schedule was decreased from 30 (N = 7389) to 60 (N = 3692), 120 (N = 1865), or 180 (N = 1417) minutes (Figure 4). Also, decreasing the relocation schedule reduced the number of unique bear-pairs (30 min: 110 unique interactions; 60 minutes: 94 pairs; 120 min: 84 pairs; 180 min: 79 pairs). Especially short-term interactions (i.e., only detected with a 30-minute relocation schedule) remain undetected with longer relocation intervals (Figure 4).

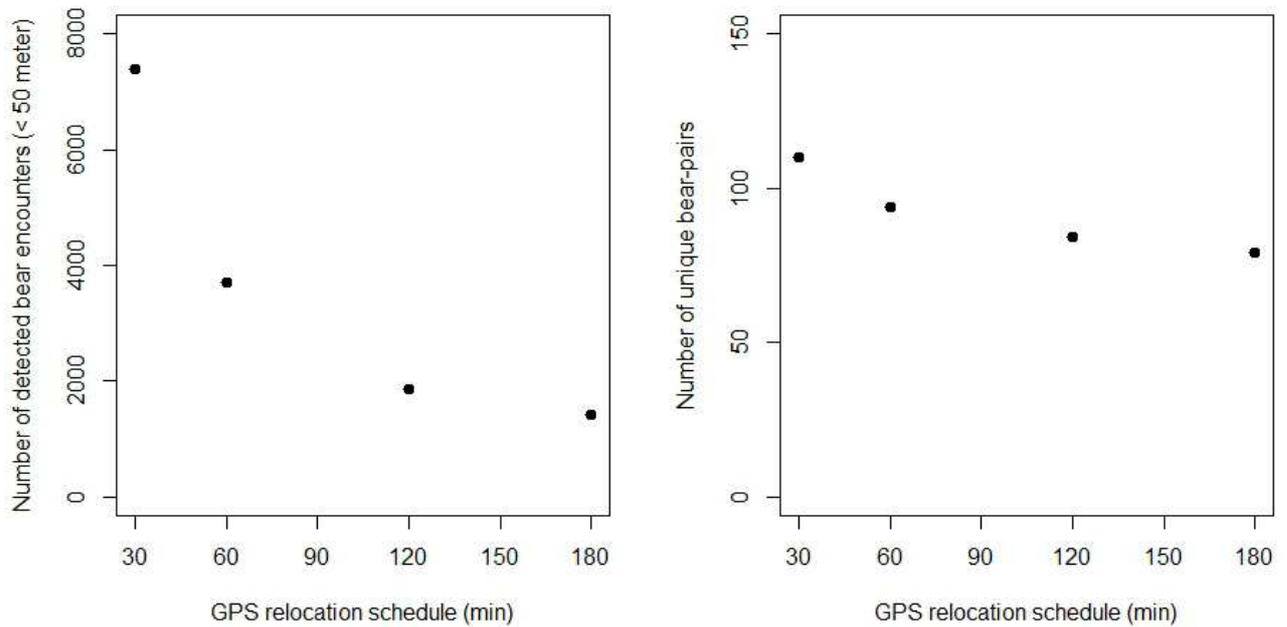


Figure 4. Number of detected interactions (left panel) and unique bear-pairs (right panel) between adult male brown bears (21 individuals, 58 bear years) and all other GPS marked bears (242 bear years) that were monitored between 2008 and 2012 in the SBBRP.

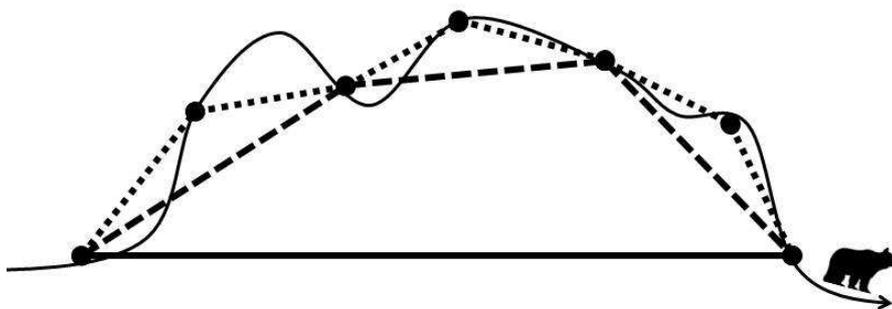


Figure 5. Simplification of an animal track using different GPS relocation schedules. The animal track is represented by the thin black line, which is simplified using a relatively high (e.g., 30 min, dotted line), medium (e.g., 60 minutes, dashed line), or low (e.g., 180 minutes, full thick black line) temporal relocation resolution. Total distance per time unit (i.e. movement speed) covered during the entire interval is best represented by the highest temporal resolution schedule, and becomes increasingly underestimated with lower temporal GPS relocation resolutions.

4. Discussion

As expected, the GPS relocation schedule affected movement speed; the longer the relocation interval, the lower the registered speed. This is obviously the result of simplifying the real animal track into a number of Euclidean segments, in which longer intervals imply a decrease in the level of detail (including speed) (Figure 5). Seasonal and diurnal nonlinear patterns in movement were clearly detectable at a 30- and 60- minute relocation interval, whereas these patterns faded out at a 120-minute relocation schedule. The 180-minute schedule model did not converge, but should show –by definition– even less clear movement patterns than under the 120-minute schedule. Reproductive status was an important determinant of movement speed, and differences between lone adult females and females/cubs were detected, irrespective of relocation schedule.

Home range sizes were negatively affected by GPS relocation interval duration. However, the effect sizes were relatively small (with the exception of the 180-minute relocation schedule); compared with the 30-minute relocation schedule, home ranges reduced in size on average by 2.2, 3.2 and 11.4 % at a 60-, 120- and 180-minute relocation schedules for lone adult females and by 2, 3, and 5.8% for females/cubs, respectively. We could clearly differentiate between females/cubs and lone adult females, irrespective of relocation schedule. The intra-class correlation of individual bear ID was very high ($ICC = 0.72$), which implies that the results were similar for each individual under varying schedules; i.e. individuals with a large home range will have a relatively large home range, irrespective of the relocation schedule.

At the population level, RSFs appeared to be robust to a reduction in the GPS relocation schedule from 30 to 60 minutes. Further lengthening the interval resulted in different model selection results. However, irrespective of the relocation schedule, parameter estimates appeared to be stable. On the individual level, parameter estimates were stable under different relocation regimes, and the ICC (a measure of personality) did not appear to be negatively affected by prolonging the relocation interval.

The number of detected interactions between bears decreased progressively from a 30- to 60-, 120-, and 180-minute relocation schedule, as did the detected number of unique bear-pairs. Logically, short-term interactions between bears (< 30 minutes) had lower probabilities of being detected with longer relocation intervals (e.g., 60, 120 or 180 minutes); the number of unique bear pairs was reduced by 14.5, 23.6, and 28.2% from a 30- to a 60-, 120-, and 180-minute relocation schedule, respectively.

Overall, prolonging the relocation interval has a cost in terms of detail. However, this loss does not necessarily have serious consequences for the research findings; the 30- and 60-minute relocation schedules yielded nearly identical results for movement patterns and for resource selection on the population level. On the individual level, increasing the relocation interval had only minor effects on the parameter estimates and no negative effects on ICC values. Home range sizes differed according to relocation schedules, albeit with a small effect size for the comparison between 30, 60, and 120 minutes. Irrespective of the schedule, significant differences in home range sizes between reproductive classes could be detected. Detecting Interactions between individual bears was, however, sensitive to GPS relocation schedule. Especially short-term interactions will not be detected when increasing the relocation interval.

5. Literature

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