

Reciprocal modulation of internal and external factors determines individual movements

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Summary

1. Movement is fundamental to individual and population dynamics, as it allows individuals to meet their basic requirements. Although movement patterns reflect interactions between internal and external factors, only few studies have examined the effects of these factors on movement simultaneously, and they generally focused on particular biological contexts (e.g. dispersal, foraging).

2. However, the relative importance of these factors in driving individual routine movements might reflect a species' potential flexibility to cope with landscape changes and therefore buffer their potential impact on fitness.

3. We used data from GPS collars on Scandinavian brown bears to investigate the relative role of these factors, as well as an additional factor (period of the year) on routine movements at two spatial scales (hourly and daily relocations).

4. As expected, internal factors played a major role in driving movement, compared to external factors at both scales, but its relative importance was greater at a finer scale. In particular, the interaction between reproductive status and period of the year was one of the most influential variables, females being constrained by the movement capacity of their cubs in the first periods of the year. The effect of human disturbance on movement was also greater for females with cubs than for lone females.

5. This study showed how reciprocal modulation of internal and external factors is shaping space use of brown bears. We stress that these factors should be studied simultaneously to avoid the risk of obtaining context-dependent inferences. Moreover, the study of their relative contribution is also highly relevant in the context of multiple-use landscapes, as human activities generally affect the landscape more than they affect the internal states of an individual. Species or individuals with important internal constraints should be less responsive to changes in their environment as they have less freedom from internal constraints and should thus be more sensitive to human alteration of the landscape, as shown for females with cubs in this study.

Key-words: animal movements, movement ecology, spatial ecology, spatial scales, *Ursus arctos*

Introduction

Despite its importance in population ecology, our mechanistic understanding of individual space use is poor and still lacks a unified theory (Holyoak et al. 2008; Snider & Gilliam 2008). The recent movement ecology paradigm proposed by Nathan et al. (2008) states that the movement process results from interactions between components inherent to both individuals and their environment (internal and external factors, respectively; see Fig. 1; see also Martin et al. 2008). Internal factors that potentially affect movements include the following: reproductive status, which may lead individuals to actively search for reproductive partners or females to protect their cubs, motivation (hunger, satiation, resting requirements, etc.) and age (potential proxy for the knowledge of the environment). Also, environmental variables can potentially affect space use, including factors associated with forage availability, competition, predation risk, refuge areas, mates, breeding sites, or physical conditions, such as temperature or humidity. Observed movement patterns are a response of the interaction between environmental variables and internal states and additionally reflect expected survival and reproductive outcomes. Few studies have tried to investigate the role of internal and external factors on animal movements simultaneously (Holyoak et al. 2008; but see Delgado et al. 2010 on dispersal movements) and even fewer on the routine movements that give rise to an animal's space use patterns. In this paper, we investigate yearly variation in the role of internal and external factors on female brown bear routine movements, that is, movements occurring during an animal's daily activities.

Understanding how the interaction between internal and external factors affects routine movements under real conditions and over long time periods is a key issue for both fundamental and applied perspectives, because variation in these movement patterns mechanistically underlies variation in space use. The behavioural response of individuals to these interacting factors reflects their flexibility to cope with landscape changes and buffer their potential impact on fitness. This relative role of internal vs. external factors should differ with species' ecology (Nathan et al. 2008); when internal constraints on behaviour are strong, we expect individuals to have less freedom to respond to environmental changes by moving, and therefore, they will be more affected by such changes (e.g. during the critical period after birth for income breeders; Jonsson 1997). For example, a female with young cubs might be severely constrained in its movements, and the distribution of food resources and/or disturbance in the landscape might therefore be crucial for their survival. In contrast, when there are few internal constraints, we can expect an individual to cope with external factors through plasticity in their behavioural responses (e.g. spatiotemporal change of food distribution, human-induced alteration of the landscape). Such increased plasticity in response to environmental changes can result in a behavioural buffering of the fitness and population consequences of environmental change.

The brown bear, and especially the well-studied Scandinavian population, is a suitable model species for the investigation of the role of internal vs. external influences on movement patterns, because there is large variation in internal states and external factors. First, the bears'

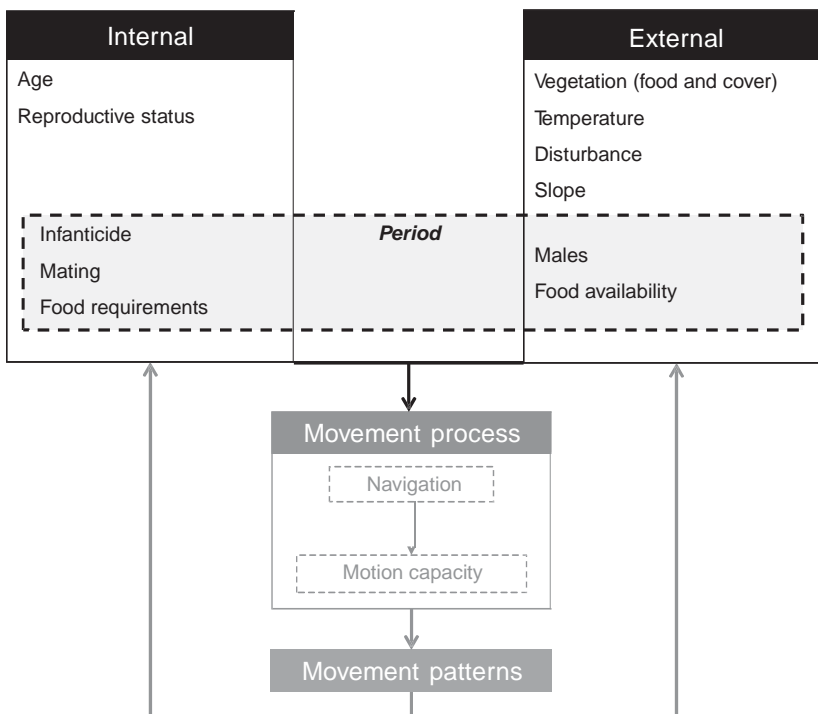


Fig. 1. Conceptual scheme of components potentially influencing movement patterns. Black frames: factors influencing movement processes (grey frames). Dashed frame: indirect influence of period of the year on movement through its influence on internal and external factors. For example, the mating season generally occurs only during a short period of the year and food availability may vary greatly throughout the year.

requirements vary greatly throughout the year (winter dormancy, period of hypo- and hyperphagia, short mating period). Secondly, the diet of bears also varies greatly through the seasons, following the distribution of food resources. Thirdly, cubs are very small at den emergence (Steyaert et al. 2012) and vulnerable to infanticide by males during the mating season (sexually selected infanticide; SSI), which is an important cause of cub mortality (Swenson et al. 1997). Moreover, the Scandinavian population inhabits landscapes with few vegetation types, which facilitates interpreting its influence on movement. The landscape also has a well-developed road network and anthropogenic structures that are potential causes of disturbance for bears (Nellemann et al. 2007; Martin et al. 2010). We expect that these temporal variations in internal state and external factors will induce variations in movement patterns. Most variables are clearly internal (i.e. individual variation) or external (i.e. spatial variation). Unfortunately, because both individual's environmental and internal factors may change with time (Fig 1), it is sometimes difficult to interpret some factors as purely internal or external, such as the period of the year. In this case, the interaction of this variable with external and with internal factors provides the ground for understanding their relative roles (e.g. Revilla & Palomares 2002).

Here, we investigated variations of main movement characteristics (velocity and linearity) of observed movement trajectories of female Scandinavian brown bears according to their internal components (reproductive status and age), external variables (weather, vegetation, human disturbance, etc.), a variable describing the relevant biological periods in which both internal and external determinants change, the period (Fig. 1) and their interactions. We investigated these variations at two temporal scales: hourly (two relocations per hour) and daily (one relocation per day). For each scale, we assessed the role of internal vs. external factors on the movement patterns independently.

As brown bears are large, omnivorous, opportunistic feeders, we expected (H1) relatively few external constraints compared to internal constraints, which are expected to be important at both scales, especially their interactions with temporal variables (hour and period). Rettie & Messier (2000) suggested that habitat selection should reflect limiting factors at a spatial and temporal scale (i.e. most limiting factors should be selected/avoided at higher spatiotemporal scales). Following Rettie & Messier's (2000) suggestion that the most limiting factors should be selected/avoided at larger scales, we expected (H2) habitats related to mortality risk (e.g. near anthropogenic structures) to have a greater effect on movement at the daily scale than on hourly scale, because adult female mortality is the most sensitive demographic parameter for bears (Wiegand et al. 1998). Habitats related to foraging should have a more prominent effect at a finer scale.

Materials and methods

study area and species

We conducted the study in the southernmost reproductive area of the Scandinavian brown bear population, in the counties of Dalarna and Gavleborg in southcentral Sweden (61°N, 15°E; Appendix S1). The terrain is hilly, and the elevation ranges from 200 to 700 m. The area consists of highly managed productive forest (80%), bogs and lakes (together 20%). The forest is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and consists of patches of differently aged stands ranging from clear-cuts to 90- to 100-year-old forests (Swenson et al. 1999). Human settlements and high-traffic roads are rare, but isolated houses and low-traffic roads are evenly distributed throughout the study area. The mean temperatures in January and July are -7° and 15° , respectively. Snow cover lasts approximately from late October until early May. Average precipitation is c. 600–1000 mm annually (Swenson et al. 1999). Bears are intensively hunted in the study area in the fall, from late August and until mid-October.

The brown bear is a solitary species that is active about 6–7 months annually, from April to October in our study area. It is omnivorous, and the diet varies among populations. In Scandinavia, bear diet varies greatly across seasons and is mainly composed of graminoids, forbs, berries, ants and ungulates (Dahle et al. 1998; Persson et al. 2001).

The year was divided into four biological periods, each corresponding to particular foraging behaviours (related to food availability) and reproductive status (Dahle et al. 1998; Dahle & Swenson 2003b; Zedrosser et al. 2007). The pre-mating period (15 April–8 May) corresponds to the emergence from winter hibernation. During this period, bear diet is mainly composed of herbaceous vegetation and ants, but also old berries (Dahle et al. 1998; Persson et al. 2001). The mating period (9 May–22 June) corresponds to the females' oestrous period (Dahle & Swenson 2003b). During this period, brown bears become more carnivorous, mainly hunting moose calves (Swenson et al. 2007) and both males and females roam to mate (Dahle & Swenson 2003a). Because the implantation of the embryo is delayed until November, females give birth during the following winter, generally in January. There is no paternal care in this species; the young follow their mother for 1.5 to 2.5 years. Females that separate from dependent cubs before or during the mating period become receptive within a few days after separation (Bellemain, Swenson & Taberlet 2006). Infanticide (the killing of dependent young by conspecific males) has been reported in this population and is considered the most important factor influencing cub survival (Swenson et al. 1997).

During the postmating period (23 June–31 July), bears mainly eat ants and forbs (Dahle et al. 1998; Swenson et al. 1999; Persson et al. 2001). The last biological period we defined (1 August – den entrance) corresponds to the period of hyperphagia, when bears consume mainly berries rich in carbohydrates (Dahle et al. 1998) to fatten before entering the winter den.

data collection

We analysed relocation data of female brown bears during 3 years (2005, 2006 and 2007). Twenty females were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark) and equipped with GPS-transmitter collars

(GPS-plus-3; VECTRONIC Aerospace GmbH, Berlin, Germany). Because of the high battery capacity of the collars, some females were followed 2 or 3 consecutive years (8 and 1 females, respectively), resulting in 30 bear-years of data. Females with cubs were not captured for ethical reasons. However, some lone females equipped with GPS collars gave birth the following winter, which allowed us to follow them the year of parturition. As a result, 6 of the 30 bear-years were from females accompanied by cubs of the year. GPS collars were programmed to record relocation every 30 min (i.e. 48 daily relocations). Given the amount of relocations data ($n = 114, 457$) for the hourly-scale approach, we used only 1 day every third days ($n = 37, 256$) for computational convenience. For the daily-scale approach, we subsampled the data set, using one relocation per day at midday. We eliminated large location errors by data screening based on two- and three-dimensional (2D and 3D) fixes in relation to the positional dilution of precision (PDOP; Lewis et al. 2007); 3D positions having a PDOP > 15 and 2D positions having a PDOP > 5 were removed. The remnant GPS error was small (± 10 m).

movement parameters

To estimate hourly movement patterns, we used speed between successive locations as a measure of movement rate. For each female, movements were characterized independently as discrete segments connecting successive relocations. Speed between relocations was estimated by dividing distances between each relocation with the time separating relocations (i.e. 30 min). For the daily scale, we took the distances between daily relocations. This frequency of relocation also corresponds to common sampling protocols found in literature when using VHF radiotracking.

To measure linearity, we used absolute values of relative angles (or turning angles, Turchin 1998), which are defined by the angle between the original direction of the trajectory (straight line between relocation at time $t-1$ and t) and the straight line connecting relocations at time t and $t+1$. The higher the value, the more sinuous was the movement.

To avoid any bias resulting from missing data at the hourly scale, we removed estimates of speed and relative angles that were obtained from 2 relocations separated by one or more missing data points. Analyses were carried out using R (R Development Core Team 2008) and the package 'adehabitat' (Calenge 2006; Calenge, Dray & Royer-Carenzi 2009).

habitat and environmental variables

The study area was divided into a grid of square pixels (200 \times 200 m) characterized for three variables: slope, vegetation and human disturbance. We derived slope from a Digital Elevation Model available for the whole study area (GSD-Hojdkurvor, 25 m ekvidistans Lantmateriet, Sweden). We used the CORINE Land Cover map (CLC00) to define 3 vegetation types: bogs, coniferous forests and regenerating forests (young-aged forests stands from clear-cut to young forest).

An index of human presence was computed, using 4 anthropogenic variables: distances to public and private roads, to isolated houses and to human settlements, each derived from digital data of Sweden (GSD-Oversiktskartan, Lantmateriet, Sweden). As the influence that distances to these structures might have on bears may not be linear, we assumed that the potential influence remained constant above a given threshold. Although bears

express a relative tolerance for human-caused disturbance, a review by Linnell et al. (2000) revealed an avoidance of human activity at 1–2 km. Moreover, Swenson & Sandegren (1996) found that brown bears preferred den sites > 3 km from villages. We therefore chose a maximum threshold value of 2000 m for distances to roads and houses and 3000 m for distances to settlements. Above these thresholds, distance values were equal, that is, the potential influence was the same. We added the 4 distance maps to create the human influence index. The resulting map provided an index ranging from 200 to 9000, with low values corresponding to high human influence. To facilitate interpretation, we standardized the index, dividing it by the maximum value and inverted it so that a low index corresponded to low disturbance. This index gives the same weight for each feature, although their effects might be different. Unfortunately, there is no quantitative assessment of their potential effects in the literature to allow differential weights to be assigned objectively and doing so fell outside the scope of this paper. Nevertheless, we assessed the sensitivity of our results to this metric by removing each of the four anthropogenic variable individually (see Results section). ArcView version 3.2a (ESRI Inc., Redlands, CA, USA) was used for preliminary preparation of spatial data and the package 'adehabitat' (Calenge 2006) for R for the computation of the index.

We used average daily temperature from weather data obtained from Sarna and Sveg weather stations. We averaged climatic data values from these stations, as the study area is located between them. Time of sunrise and sunset was available for Ostersund (63.18°N, 14.65°E) at <http://www.cactus2000.de/uk/sonne/esw.shtml>. We reported the range of values for each variable in Table A1 in Appendix S1.

statistical analyses

Hourly scale

We used multiple regressions to assess the influence of individual factors (reproductive status, biological period and age) and environmental factors (temperature, vegetation type, slope and human influence) on movement parameters: speed in km per hour and absolute values of relative angles (higher values correspond to sharp angles and therefore sinuous movement). Because of the strong effect of time of day on bear activity found in literature (Kaczensky et al. 2006; Moe et al. 2007; Martin et al. 2010) and in our unpublished preliminary analyses of mobility data, a null model without daytime would not make biological sense. Hence, we included daytime (in hours) in all our models for this scale.

We used Generalized Additive Models (GAM, Hastie & Tibshirani 1990) to account for both nonlinear effects of time of day on mobility (Kaczensky et al. 2006; Moe et al. 2007) and linear effects of internal and external factors. A GAM is a flexible semi-parametric method to model both linear and nonlinear relationships between a response variable and its explanatory variables. The nonlinear relationship is modelled by a smooth function of these explanatory variables. We used a cyclic cubic spline smoother to model the nonlinear and cyclic effect of time of day (this smoother is available in the R package 'mgcv', Wood 2006). In this cubic spline, the point at the end of the day is constrained to be the same as that at the beginning. The degree of smoothing is determined by generalized cross validation (Wood 2006). This approach results in a robust smoother that explains most of the variance while avoiding an over-fitting of the data.

Therefore, in GAMs, the shape of the function is not restricted by a parametric form; the function's shape is determined by the data. Because of potential temporal autocorrelation between successive relocations, we included a first-order autoregressive process (AR1) in our model structure to account for the dependence of the previous relocation. We log-transformed the speed to obtain a Gaussian distribution.

We measured the movement pattern repeatedly for each individual, causing dependence between observations, that is, pseudo-replication. We also expected that movement parameters may be more similar during a given day. Thus, we used GAMMs (R package 'mgcv', Wood 2006) to model movement patterns with day nested within year and individual as random effects and all other explanatory variables as fixed effects, using a cyclic cubic spline smoother for time of day only.

Daily scale

At the daily scale, we subsampled the data set to obtain one relocation at midday for each bear. As for the hourly scale, we investigated the influence of internal and external factors on daily distances and daily linearity using multiple regression analyses. Because we did not have the constraint of the nonlinear effect of time of day for this scale, we used Generalized Linear Mixed Models (GLMM) instead of GAMM. We included individual and year as random factors and kept the AR1 in the models to account for possible autocorrelation between days.

The distribution of daily distances (Fig. A2 in Appendix S1) revealed that females apparently adopted two tactics: remaining within the same area during consecutive days (distances < 200 m) or moving to another area (distances > 200 m). Therefore, we studied daily distances using two complementary approaches: first, using GLMM models with binomial distribution to study factors that may influence this tactic, with 0 for distances < 200 m and 1 for distances > 200 m. Secondly, for distances > 200 m, we used GLMM models with a Gaussian distribution to study factors influencing the distances between consecutive days. We log-transformed the distances in the models to obtain a Gaussian distribution. To investigate linearity of movement between consecutive days, we used GLMM with binomial distribution, with values 0 for $0^\circ \leq |\alpha| < 90^\circ$ and 1 for $90^\circ \leq |\alpha| < 180^\circ$. At this scale, differences of few degrees do not have a biological meaning, whereas using a binomial variable gave a stronger biological significance: the movement is globally linear (0: the bear kept the same direction from day to another) or globally sinuous (1: the bears preferentially came back or stayed in the same area from a day to another).

As this scale was higher than the hourly scale, we averaged the values of the variables for all the relocations (bi-hourly relocations) of females between 2 daily relocations to study the influence of environmental factors on daily distances > 200 m and linearity. Thus, we examined how the environment experienced by the individual affected the distance moved between 2 days. Because we had 3 vegetation types with bogs, which occurred only at low frequencies, we calculated and used the proportion of young forest used by the individual between 2 days.

Common procedure for the two scales

The influence of each model and variable was assessed using the Akaike Information Criterion (Johnson & Omland 2004; AIC, Burnham & Anderson 2002) approach. We divided each

procedures (i.e. 5 procedures: hourly velocity, hourly linearity, daily distances, daily distances > 200 m and daily linearity) into several stages. First, we assessed the influence of internal factors only (stage I for internal) but including period and selected the best-fitting model. Secondly, we did the same for external factors only (stage E for external), including period as well. Third, we assessed the combined effect of internal and external factors in the same model (stage I + E for external factors, taking into account internal factors or stage E + I for internal factors taking into account external factors), but considering additive effects only. To reduce the number of models, we used the best-fitting model (with the smaller AIC) of stage I or E to select the other category of factors (e.g. if the best-fitting model of individual factors had a smaller AIC than the best-fitting model of environmental factors, we used the best-fitting model of individual factors to select environmental factors, that is, I + E). Finally (stage I \ominus E), we investigated the role of interaction effects for the best-fitting model of stage I + E or E + I and iteratively included the interaction between internal and external factors that had biological meaning: status \ominus disturbance, status \ominus vegetation and age \ominus disturbance. We calculated Akaike weights for each model within each model selection procedure. The relative importance of each variable or interaction was estimated using the cumulative Akaike weights. To assess the relative importance of each factor or interaction in the final best-fitting model, we calculated the Δ AIC between the best-fitting model and each model for which we removed the factor or the interaction.

Results

Female Scandinavian brown bears showed a circadian movement (and activity) pattern with 2 peaks around dawn and dusk and a resting period during the day (Fig. 2). The bears' biological rhythm followed the time of sunrise and sunset: velocity and linearity of lone females' movement were greatest 1–2 h after sunrise and 1–2 h before sunset (Fig. 2). The same general pattern was found for females with cubs, although with a timing difference. During the pre-mating period, females with cubs tended to be most mobile during one period, 7 to 10 h after sunrise. During the mating period, they established a bimodal movement pattern, although they still were more active at midday, about 2 h later than lone females for the first activity peak and 1.5 h earlier for the second peak. Both categories of females tended to show comparable patterns during the hyperphagia period, with a greater peak of movement in evening (especially females with cubs) compared to other periods (Fig. 2). Overall, both categories of females were less active during the pre-mating period. Indeed, the frequency of short movements (< 15 m), which may result from GPS inaccuracy while resting, was higher during the pre-mating period, irrespective of reproductive status (Table A1 in Appendix S1).

Females had large movement capacities, with a maximum hourly velocity of 13.8 km h⁻¹ and maximum daily distance moved of 18 km (Table A1 in Appendix S1). However, their movements were generally slow (average hourly velocity of 0.33 km h⁻¹), especially for females with cubs during the first 2 periods (0.04 km h⁻¹ and

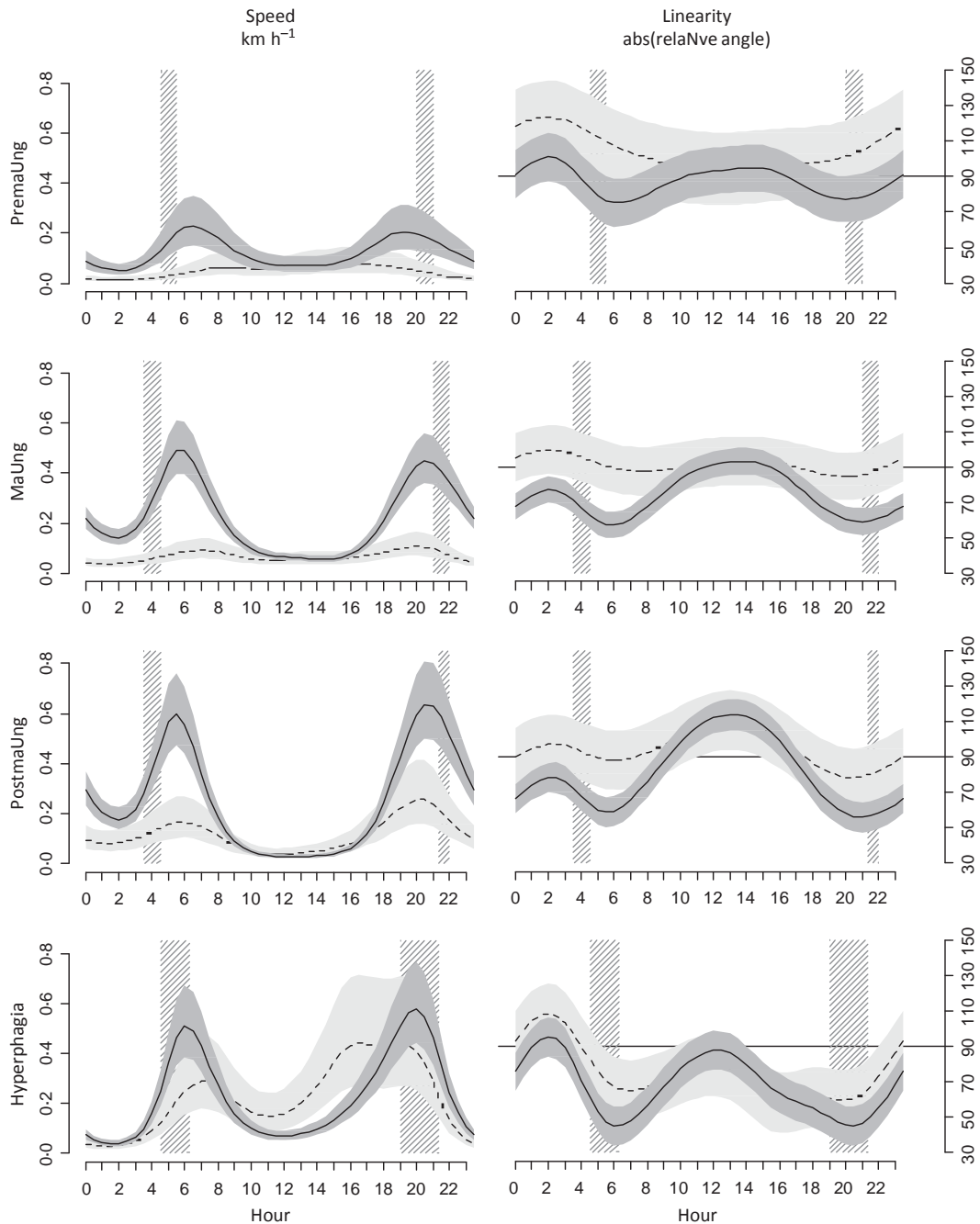


Fig 2. Influence of hour on speed (left panels) and linearity (absolute value of relative angles; right panels) of female brown bears in Sweden, predicted by generalized additive mixed models. Solid line and dark grey shade: prediction and confidence interval for lone females. Dashed line and light grey shade: prediction and confidence interval for females followed by cubs of the year. Dashed areas: timing for sunrise and sunset averaged on the period of the year considered (e.g. pre-mating period).

0.13 km h⁻¹ during pre-mating and mating periods, respectively). On average, females moved 4 km day⁻¹ (Table A1 in Appendix S1). Regarding linearity, females tended to keep the same direction when they moved fast, whereas their movements were more tortuous when travelling slowly (Table A1 in Appendix S1). For example, daily distance moved by females with cubs was less during the pre-mating period and trajectories were more sinuous (Table A1 in Appendix S1; Appendix S2).

role of internal and environmental factors on hourly velocity and daily distances

Internal factors, including age and interaction between reproductive status and biological period, affected hourly speed (see Table C1, stage I in Appendix S3; Table D1 in Appendix S4). Of environmental factors only (stage E), slope, temperature and vegetation and the interaction between human disturbance and period affected hourly

speed (Table C1 in Appendix S3). However, the best-fitting model for environmental factors poorly explained movement speed (ΔAIC between the 2 best models in stage I and E = 317, see Table C1 in Appendix S3). When taking internal factors into account first and only main effects (stage I + E), the same environmental variables were retained (see Table C1 in Appendix S3; Table D1 in Appendix S4). Including the interaction between internal and environmental factors improved the model slightly (Table C1, stage I \ominus E in Appendix S3; Table D1 in Appendix S4). The best model (see Table 1) revealed that older females moved more slowly (about 1 km h^{-1}) than younger females ($-0.03 \pm 8 \cdot 10^{-3}$, slope \pm SE). Globally, all females increased their movements through the periods of the year (Fig. 2), the most important variable for model fit (larger ΔAIC with the best model; Table 2) along with its interaction with hour of the day. Lone females stabilized their movement during the postmating period, whereas females with cubs increased their movements until the hyperphagia period, when their movement speed was higher than for lone females (Fig. 2). Status and status \ominus hour also had a great influence on model fit, much greater than external variables (Table 2). Daily temperature had a positive influence on movement speed ($0.03 \pm 4 \cdot 10^{-3}$, slope \pm SE). Females reduced their travelling speed in steep areas ($-0.02 \pm 4 \cdot 10^{-3}$, slope \pm SE) and in coniferous and young forests (Fig. 3a), especially during the 2 first periods. The effect of vegetation type was greater for lone females than female with cubs (Fig. 3b). Both types of females increased their movement speed close to anthropogenic structures (disturbance; 0.23 ± 0.1 , slope \pm SE), but females with cubs even more than lone females (increase in slope \pm SE for females with cubs: 0.54 ± 0.3). Note that we assessed the sensitivity of our results to the disturbance metric by removing one of the four anthropogenic variables at the time. We found no substantial differences and the AIC-values of the best model invariably increased with the removal of each variable.

The influence of internal and external factors on daily distances between day beds was different than for hourly velocity (Table 1). Considering females' tactics (remaining on-site or moving to another place between 2 days), status

and period had a strong interaction effect, but not the age (Table D1 in Appendix S4; Fig. 4). Although all females often moved more than 200 m between consecutive days (Fig. 4), lone females increased this tendency during the mating period, whereas females with cubs reduced it. Disturbance (-2.04 ± 1.01 , slope \pm SE), slope (0.15 ± 0.06 , slope \pm SE) and temperature (-0.04 ± 0.02 , slope \pm SE) influenced this tactic, but vegetation did not. Any interactions between internal and environmental variables were retained in the model selection procedure. Internal factors (interaction between period and status) explained the largest part of the model fit (Table 2).

Neither season nor age influenced movements >200 m at the daily scale (Table 1; Table C2 in Appendix S3; Table D1 in Appendix S4). Disturbance explained most of the model fit and no internal factors were retained (Table 2). Females increased their movement when daytime disturbance was high (0.49 ± 0.21 , slope \pm SE). They moved more when in rugged terrain (higher frequency of steep slopes: 0.02 ± 0.01 , slope \pm SE).

role of internal and environmental factors on hourly and daily movement linearity

Internal factors (only status and periods and their interaction) better explained hourly movement linearity than environmental factors only (ΔAIC between the selected models in stage I and E = 224; Table A1 in Appendix S1; Table 2). Only slope, temperature and the interaction between period \ominus vegetation were retained in stage I + E (Table D1 in Appendix S4; Fig. 3d). Only one interaction between internal and environmental variables was significant: status \ominus vegetation (Table D1 in Appendix S4; Fig. 3c; Table C1 in Appendix S3). As for hourly speed, hourly movement linearity also increased with biological periods, with a more pronounced tendency for females with cubs (Fig. 2). Females' movements were more sinusoidal in steep areas (0.49 ± 0.1 , slope \pm SE) and in closed, secure areas (coniferous and young forests), with stronger differences during the mating period (Fig. 3d). During days with higher temperature, females had more linear movements (-0.54 ± 0.1 , slope \pm SE). Internal factors had a greater influence on model fit than external variables

Table 1. Best models for the five analyses of female brown bear movement in Sweden. A model selection procedure using Akaike Information Criterion was performed for each of the five different movement metrics

Movement metric	Best models
Hourly speed ln(speed in km h^{-1})	Spline (Hour \ominus Period) + spline (Hour \ominus Status) + Period \ominus Status + Age + Period \ominus Vegetation + Temperature + Slope + Status \ominus Disturbance + Status \ominus Vegetation
Hourly linearity abs(relative angles)	Spline (Hour \ominus Period) + spline (Hour \ominus Status) + Status \ominus Period + Period \ominus Vegetation + Temperature + Slope + Status \ominus Vegetation
Daily distances binomial : ζ or > 200 m	Temperature + Disturbance + Slope + Status \ominus Period
Daily distances > 200 m ln(distance in m)	Disturbance + Slope + Status
Daily linearity binomial: $ a < \text{or } \zeta 90^\circ$	Age \ominus Disturbance

Table 2. Assessment of the importance of each variable (or interaction) separately in the model fit explaining movements of female brown bears in Sweden. ΔAIC was calculated between the best model and each model for which the targeted variable or interaction was removed. For example, for period, the ΔAIC corresponds to the difference between the best model and the same model after we removed the main effect of period. The higher the ΔAIC , the higher the importance of the variable in the model fit. A grey bloc appears when the variable (or interaction) was not included in the best model

Models	Hourly velocity ΔAIC	Hourly linearity ΔAIC	Daily distances (binomial) ΔAIC	Daily distances >200 m ΔAIC	Daily linearity ΔAIC
Best model	0	0	0	0	0
Period	949.5	554.3	1.6		
Hour \cap Period	787.7	386.5			
Status	428.3	268.5	1.6		
Hour \cap Status	332.5	165.7			
Period \cap Status	73.3	6.9	0.05		
Age	12.1				
Disturbance	8.3		2.4	12.3	
Vegetation	39.5	6.7			
Temperature	57.9	13.2	0.9		
Slope	27.2	10.9	3.7	7.4	
Period \cap Vegetation	13.2	2.2			
Period \cap Temperature					
Period \cap Disturbance					
Status \cap Disturbance	1				
Status \cap Vegetation	7.6	2.6			
Age \cap Disturbance					1.4

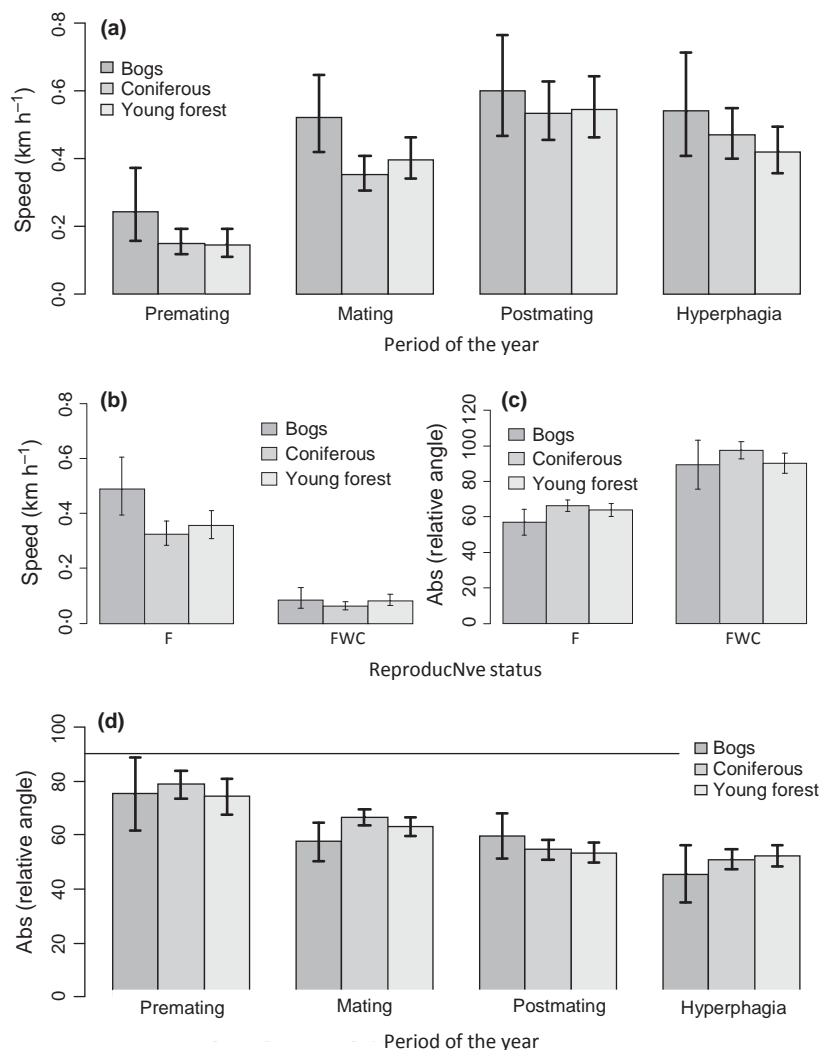


Fig. 3. (a) Influence of the interaction of period and vegetation and (b) status and vegetation, on hourly speed of female brown bears in Sweden, and influence of the interaction of (c) status and vegetation and (d) period and vegetation on hourly linearity of their movement. F denotes lone females, and FWC denotes females with cubs of the year.

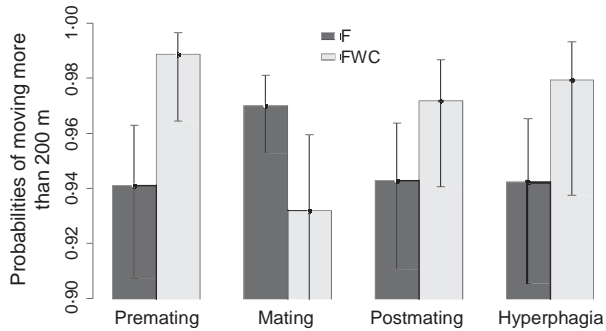


Fig. 4. Combined influence of reproductive status and periods on the probability of moving more than 200 m between days in female brown bears in Sweden. F denotes lone females, and FWC denotes females with cubs of the year.

(Table 2). The interaction between age and disturbance influenced daily linearity (-0.32 ± 0.13 , slope \pm SE), with younger females having less linear movement when disturbance is low compared to older females.

Discussion

Our study shows a strong relationship in movement responses measured by speed and linearity, as would be expected given their similar effect on the residence time in an area. As expected (H1), internal factors played a major role in driving bear movements compared to environmental factors, both in hourly and daily movement patterns. Reproductive status was one of the main drivers of these movements, especially in interaction with temporal variables (hour of the day and period), which partly reflected the bears' changes in physiological states during the day and throughout the year. We found that females with cubs were more constrained in their movements (moving less and in a more sinuous manner) than lone females, but that this changed progressively throughout the seasons, as the cubs grew and the risk of infanticide diminished (Swenson et al. 1997).

However, the relative importance of internal and external factors for bear movement varied with spatiotemporal scale. At the daily scale, their importance was relatively similar, and the importance of external factors was even higher for the daily movement tactic (staying in the same area between consecutive days or moving). Moreover, the relative importance of external factors differed by spatial scale, supporting H2, which was based on Rettie & Messier's (2000) prediction. At the hourly scale, vegetation and temperature had greater effects than those related to disturbance, although slope was also important. Few factors influenced distance moved at the daily scale. Disturbance was the major factor explaining the distances moved between consecutive days, before slope and status. Bears reacted to high disturbances areas by moving further, possibly as a tactic to avoid predation risk (Fahrig 2007).

We found a strong influence of temporal variables on routine movements of brown bears. Consistent with the lit-

erature on brown bear activity rhythms (Kaczensky et al. 2006; Moe et al. 2007), we observed a circadian rhythm with movement peaks around twilight and a main resting period during daylight. This may be partly explained as a response to human disturbance during daylight hours, as bears tend to shift to nocturnal activity in areas with high human density (Klinka & Reimchen 2002; Kaczensky et al. 2006) and tend to select less disturbed areas during this period (Martin et al. 2010), presumably to avoid human disturbance. Nevertheless, we found variability in this rhythm according to reproductive status. After den emergence and during the mating period, females with cubs were active during the daylight hours, contrary to lone females. Being more active during daylight and less active during dawn and dusk during the premating and mating periods may be a counterstrategy to infanticide, to avoid potentially infanticidal males when they are active. Although we did not have data on male movement patterns, we expect they synchronized their movements with those of lone females during the mating period to increase the encounter probability (Dahle & Swenson 2003b).

The second temporal variable, period of the year, was one of the most influential variables on routine movements, especially in interaction with both internal (the reproductive status) and external (vegetation type) variables. Generally, period is one of the most challenging variables to interpret, as it has an internal and an external component. For the bears, it represents changes in physiological state (hypo-, normal-, hyperphagia), change in reproductive status (cub growth, mating), but also in vegetation, disturbance, etc. However, our results suggested that period might be more related to internal factors, as its interaction with reproductive status and hour of the day explained movements much better than interactions with external factors.

Our results illustrate the complexity of mechanisms underlying bear space use. Understanding how internal, external and temporal factors jointly influence movement allows the identification of stressful periods, periods of high susceptibility to environmental influence or sensitive categories of animals. Our results showed that disturbance affected females with cubs and lone females in the same way, but with a higher impact for the first. Having cubs entails important constraints in females' movement capacity, which limits their abilities to buffer environmental heterogeneity through movement. During the first part of the year, they probably move less as a tactic against infanticide. However, if human disturbance increases within their home range at this time, our results show that they will increase their movements and therefore might increase the risk of infanticide, by increasing the probability of encountering a male.

These complex relationships between internal, external and temporal factors are likely to vary among species. For example, movement patterns of species that have marked biological periods during the year should show stronger effects of internal factors than environmental fac-

tors, as demonstrated in this study. Similarly, species that have large spatial requirements, such as large carnivores, may be more affected by internal constraints (e.g. restriction of movement by dependent cubs). On the contrary, prey species, which are often limited by predation, should be more sensitive to environment and should be less restricted by their young, which often are capable of moving soon after birth.

Important differences may also be expected between income vs. capital breeders, everything else being equal, because of their different tactics of resource use. Whereas capital breeders acquire and store resources before a reproductive event, income breeders use resources concurrently available with reproduction (Jonsson 1997). Therefore, an income breeder (e.g. roe deer *Capreolus capreolus*) should be very sensitive and responsive to the environment during the 2–4 weeks after giving birth (e.g. need to find quality/high quantity of food). A female roe deer will succeed or fail its yearly breeding event during this brief period (Andersen et al. 2000). For a capital breeder (e.g. red deer *Cervus elaphus*), the energy acquired during the whole year is much more important; hence, responsiveness through a longer period should be more important (Stephens et al. 2009), although the period just after birth may also be more important than those later in the summer. Interactions between internal and external factors would be stronger in income breeders than in capital breeders. For our model study, although bears can be considered as capital breeders, they also have a marked sensitive period in terms of reproductive success during the mating season, because of the high risk of infanticide.

To our knowledge, this is the first study to provide such detailed information on the source of movement variability in female bears. Our results showed that variability in internal states, requirements and motion capacity induce important variability in the movement patterns of the bears, and confirmed, from another angle, that mating season is a critical period for female brown bears that are followed by cubs of the year (Swenson et al. 1997). Our results suggest that female bears have to make trade-offs to ensure security of their cubs, by being more active during daylight to avoid encountering males although they may be disturbed by human activity. Moreover, urbanization of the landscape can also increase indirect effects on SSI by making females move more and by increasing the risk of being detected by infanticidal males. We also reported a higher activity of females with cubs during the hyperphagia season, and especially during daylight, which may increase the encounter probability with hunters and berry pickers. In the context of the growing and expanding bear and human populations, it is relevant to document factors that could increase the probability of bear–human encounters.

Our approach using statistical models provided a simple and straightforward way of investigating the relative role of internal and external factors, for a large data set. More complex modelling procedures, such as state-space models (see Patterson et al. 2008 for a review), have shown prom-

ise for studying animal movement, allowing the simultaneous modelling of steps and angles. However, these computationally challenging approaches are focused mainly on the identification of underlying states, which was not the aim of our study. Our study focuses instead on the respective role of internal vs. external constraints.

Conclusions

We investigated the combined effects of internal and external factors and their relative influence on routine movements. Our results showed that these factors must be integrated together to fully understand the ecology of movement. Consideration of only one of these components may lead to context-dependent inferences. Such integrative frameworks can address many questions in ecology and evolution (Holyoak et al. 2008) and have important implications from both fundamental and applied perspectives. Movement plays a key role in ecology through its effects on, for instance, spatial distribution of individuals, space use or population dynamics. From an applied perspective, the contribution of internal vs. external constraints is also highly relevant in the context of multiple-use landscapes. Human activities generally affect the landscape more (external factors) than they affect the internal states (internal factors) of an individual. Therefore, we can expect that for species with important internal constraints or during critical biological periods, individuals should be less responsive and thus more sensitive to human alteration of the landscape or disturbance, as shown for females with cubs in this study.

We encourage further work linking both internal and external factors to fine-scale movement processes in species with different physiological stages and constraints throughout the year (e.g. carnivore vs. herbivore species, income vs. capital breeders). Those studies will set the basis for a thorough understanding of movement mechanisms and the interrelationship of internal and external effects that should in turn be related to the expected behavioural responses in response to landscape variability.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed description of the study area, movement characteristics and variables influencing movement of the brown bear in Sweden.

Appendix S2. Movement mechanism of female brown bear in Sweden.

Appendix S3. Detailed results of model selection procedure on factors influencing brown bear movements in Sweden.

Appendix S4. Akaike weights for each explanatory variables, for each of the 5 categories of models.

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