Does moonlight affect movement patterns of a non-obligate carnivore? Brown bears do not mind that the moon exists

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Abstract

Moonlight plays a significant role in prey–predator relationships. At full moon, predators' hunting success and activity rates generally increase. Even though the analysis of facultative carnivore movement patterns can improve our knowledge of how moonlight can change the behaviour of such a group of species with diverse ecological needs, few studies have been conducted with facultative carnivores and none with telemetric data. Here, we studied whether moonlight influences brown bear, Ursus arctos, movement behaviours. By analysing data collected from 2002 to 2014 for 71 collared individuals inhabiting Finland and Russian Karelia, we found that some internal and external factors are influencing brown bear movement patterns. In particular, this facultative carnivore moves more slowly and over shorter distances during hyperphagia periods than during the mating season. However, moonlight does not affect brown bear movements. Although brown bears are large carnivores, they are opportunistic omnivores with a high fruit diet and, therefore, the prey–predator relationships that are behind the dependence of carnivores on moonlight seem to be weaker than in obligate carnivores.

Introduction

The moon orbits the earth and, in this way, the positions of the sun, moon and earth reflect different illuminations of the moon called lunar phases. The lunar cycle (from new moon to new moon) has an average duration of 29.5 days. It can lead to several environmental modifications, such as changes in the nocturnal atmosphere, for example, on full moon nights, the amount of light is 250 times greater than on moonless nights (Foster & Roenneberg, 2008). These changes are used as benchmarks by some animals to synchronize the reproduction period (e.g. breeding, spawning) (Kronfeld-Schor et al., 2013), adjust the activity rate of finding food (Grant et al., 2012), and for communication (Penteriani et al., 2011). It is therefore not surprising that there is growing evidence that moon phases influence the behaviour of many animal species, including humans (Sjödin et al., 2015).

Night light plays a notable role in nocturnal vision of some mammals and thus prey–predator relationships (Dacke et al., 2003; Penteriani et al., 2013; San-Jose et al., 2019). Species that depend primarily on vision may be more successful at finding food with moonlight, and they may also face a lower risk of predation, as their capacity to detect predators should increase. Visual sensitivity and acuity vary considerably among nocturnal species and may explain why not all predators respond or respond in the same way at the time of the full moon (Heurich et al., 2014; Prugh & Golden, 2014). When the moon is close to full, cheetahs, Acinonyx jubatus and wild dogs, Lycaon pictus, are more active in order to maximize hunting success as their chase patterns require high visible conditions (Cozzi et al., 2012; Rasmussen & MacDonald, 2012). Therefore, their prey is more likely to remain in refuges, limiting their activity and becoming more vigilant (Brown & Kotler, 2004a; Daly et al., 1992; Griffin et al., 2005; Lima & Dill, 1990), feeding back on the activity rhythms of their predators. Similar behavioural patterns have also been observed in some omnivores like badgers, which synchronize their breeding behaviour on dark nights to avoid predators (Dixon et al., 2006). The activity patterns of Iberian lynx, Lynx pardinus, mirror the activity of their main prey, the rabbit, Oryctolagus cuniculus. In particular, rabbits move furthest from their dens and are more active around the new

moon, and consequently, lynxes reduce their travelling distances and concentrate their movements in the core areas of their home ranges, which generally match those areas with a high density of rabbits (Penteriani et al., 2013). In addition, as behavioural decisions made at one step can have an impact on the behavioural choices at the next step, it has been demonstrated that some carnivores that increase their hunting success on clear nights generally decrease their activity the following day (Cozzi et al., 2012; Rasmussen & MacDonald, 2012). Therefore, bright, moonlit nights may create a fitness trade-off by increasing carnivores' hunting success probability (Clarke, 1983; Kotler et al., 1988, 2002), but reducing their energy reserve through increased activity to search for hidden prey (but see Sàbato et al., 2006). These behavioural changes can be costly because they take time and energy away from others activities linked to fitness, such as parental cares or mating (Lima & Dill, 1990).

The animal's navigation and mobility capabilities determine how an individual will move in response to external factors and internal states (Nathan et al., 2008). Animals continuously make decisions on how, when and where to move to find suitable areas to meet their vital requirements (Estes et al., 1982; Nathan et al., 2008; Van Moorter et al., 2013). However, animal movements can also be affected by other factors, such as the availability of food and shelter, landscape structure, weather conditions and anthropogenic activities (Martin et al., 2008, 2013; Nathan et al., 2008). In this context, the analysis of the movement patterns of carnivores can improve our current knowledge on how moonlight may alter the behaviours of a group of well-differentiated species with diverse ecological needs such as carnivores (Wilson & Mittermeier, 2009). The ecological and evolutionary consequences that the moon may have at the individual, population and community levels are numerous; however, there is still a lack of information available on the effect of the different moon phases and the associated moonlight on carnivore movement patterns (but see, e.g., Cozzi et al., 2012; Di Bitetti et al., 2006; Grassman et al., 2005; Mukherjee et al., 2009; Penteriani et al., 2014).

Of the group of large carnivores, the potential effects of moonlight on movement patterns of brown bears, *Ursus arctos*, have not yet been studied. The brown bear is an intriguing large carnivore for two reasons. First, even though brown bears have the typical morphological features of carnivores (defined canine teeth, claws and a carnivore digestive tract), they are facultative, or non-obligate, carnivores. That is, they do not exclusively depend on the movements and rhythms of activities of given prey. Second, brown bears can be extremely flexible in their primary diel activity pattern, from diurnal to crepuscular to nocturnal (Rode & Robbins, 2000; Gende & Quinn, 2004; Swenson et al., 2007; Robbins et al., 2007), and their diel activity can be affected by human encroachment, hunting, bear population density and latitude (Hertel et al., 2017; Ordiz et al., 2012, 2013; Theuerkauf et al., 2003). Thus, even if moonlight has some effect on brown bear movement patterns, omnivory and flexibility in rhythms of activity may weaken moon-dependence, as earlier suggested by Richardson (2017) in a camera trap study.

The distinctive brown bear dietary preferences compared with other large carnivores may provide a different perspective on the potential influence of the moon on the movement strategies of facultative carnivores. To determine whether the lunar phases influence brown bear movements, we studied the daily movement behaviours of 71 brown bears (42 males and 29 females) in Finland and Russian Karelia from 2002 to 2014. On the basis of the main characteristics of brown bears, we hypothesize that movement patterns will not show dependence of bears on moonlight, even though they might have some preference for darker nights as a response to human avoidance and occasional predation events.

Materials and methods

Study area

The movements of our radio-collared brown bears covered most of southern and central Finland (220 000 km^2) and also involved a part of Russian Karelia (160 000 km^2), and ranged from 61.69°N to 66.56°N (Fig. 1). At these latitudes, the length of the night varies significantly between seasons. The topography is relatively smooth with elevation ranging from 100 to 576 m a.s.l. Both regions are largely dominated by highly managed productive boreal forest (Ahti et al., 1968; Hagen et al., 2015). About 86% of the land area is covered by forests, where the main tree species are the Scots pine *Pinus sylvestris*, the Norway spruce *Picea abies* and various birches, *Betula spp.* The terrain is also characterized by the presence of lakes and peat bogs. Isolated houses and low-traffic roads are widespread in the study area.

Data collection

From 2002 to 2013, 71 brown bears were captured in spring (*n* = 115 captures, as some individuals were captured several times; Table S1), after they left their winter dens. Brown bears were tagged until October shortly before entering dens. They were darted from blinds at temporary baits. Immobilization drugs and dosages followed the protocol by Jalanka and Roeken, (1990). The injected doses used to immobilize bears contained medetomidine (50 µg/kg) and ketamine (2.0 mg/kg) (Jalanka & Roeken, 1990). To dart bears in late summer or autumn, the spring dose was increased 25–50%, and longer needles were used because of body fat (Arnemo et al., 2007). Bears were sexed, weighed and aged (on the basis of cementum annuli counts of a first premolar removed at time of capture; Craighead et al., 1970). Yet, as the cementum annuli method did not allow determining the exact age of all tracked individuals, we categorized age as adult/subadult in order to avoid excluding these individuals from our analyses. Permission to capture and manipulate bears was issued by the County Veterinarian of Oulu and by the Regional State Administrative Agency of Lahti (Finland). Individuals were fitted with a collar that carried 1.5 kg global positioning system (GPS) transmitters (Televilt, Lindesberg, Sweden; Vectronic Airspace, Berlin, Germany). The weight of the collars was less than 1.0–2.0% of the bodyweight of adult females (mean
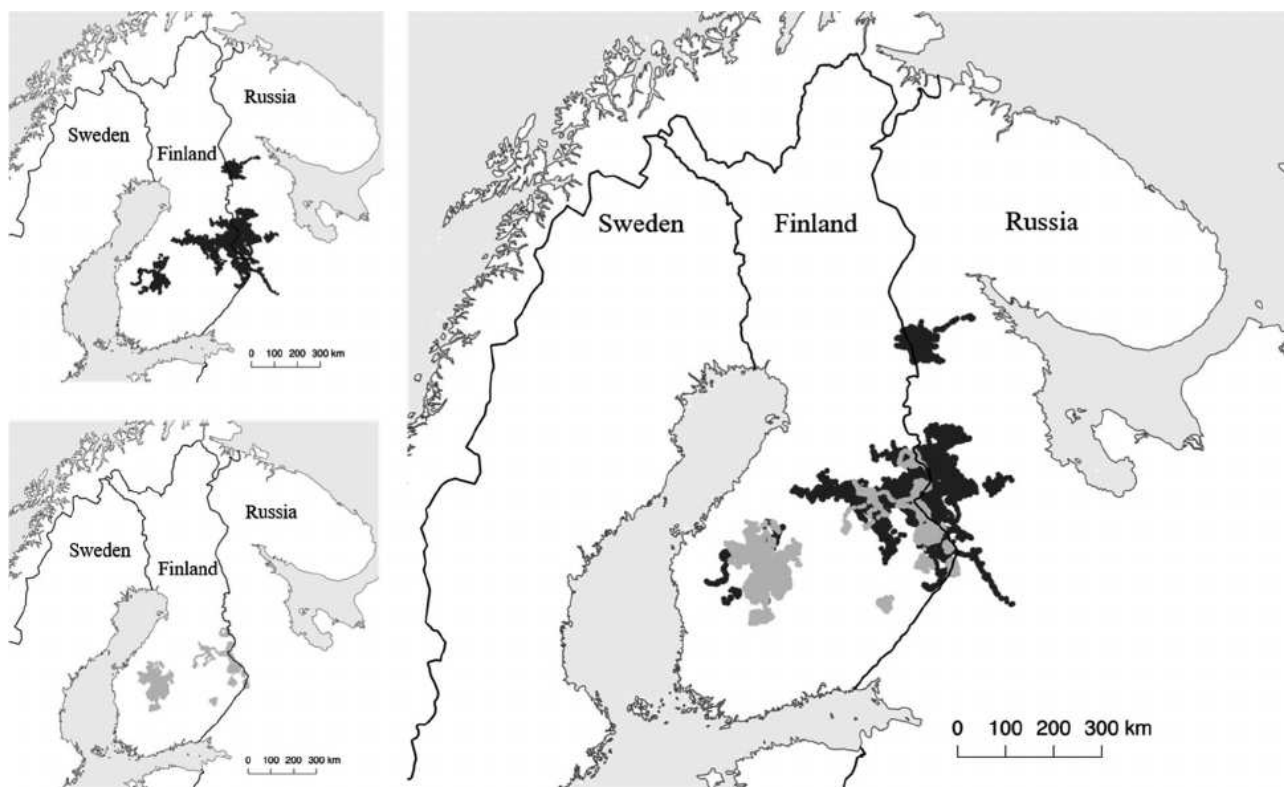
Figure 1 Distribution of GPS locations of 42 brown bear males (*n* = 15 subadults, black movement paths) and 29 females (*n* = 12 subadults, grey movement paths) spread across south-eastern Finland and Russian Karelia (2002—2014).

(kg) ± SD = 124.6 ± 27.5) and 0.5–1.0% of adult males (mean (kg) ± SD = 212 ± 61.4). Out of the 71 collared brown bears, 27 were subadults. As they might still grow, collars were adjusted so that they could expand and allow for increased body size. Brown bears were categorized as subadults when they were 4 years old and younger. Collars had a pre-programmed drop off mechanism with an average battery life of 1 year. Whenever the drop off did not work by the scheduled time owing to technical flaws, the bear was recaptured and the collar was removed. All collars were removed before the end of the project in 2014.

The GPS collars were calibrated to collect one brown bear location every four hours (*n* = 173 301 number of total locations; mean number of locations per individual ± SD = 2440.9 ± 2396.6). Radiotracking sessions (*n* = 4158 days) started at 2:00 and ended at 22:00. Therefore, data comprised locations collected during the day and the night (hereafter, daily scale). Signals from the satellite transmitters were recorded by the ARGOS satellite system (www.cls.fr). The data provided sufficient days (number of collared individuals per day ± SD = 5.97 ± 4.01, range: 1–20) among the different moon phases (Table S1). We recorded the positional dilution of precision (PDOP) value for all 3-D fixes and the horizontal dilution of precision for 2-D fixes. Following the method developed by D'Eon et al., (2002), we excluded all 2-D fixes. Although this data screening method reduces the

dataset, it allows a high percentage of detection of large location errors (Bjørneraas et al., 2010).

Movement patterns

Daily brown bear trajectories were obtained by using the *adehabitat* package version 0.4.15 for R software (Calenge, 2006).

We estimated the following movement parameters at a daily scale (i.e. we considered both day and night locations): (1) total distance, which is the cumulative sum of the distance between successive relocations on the same daily trajectory; (2) net distance, that is, distance travelled between the initial position and the final position on a daily scale; (3) average daily speed, which is the mean of the step distance (distance between two relocations) divided by the time interval between consecutive locations; and (4) mean turning angle, where angles between 0 to 90° correspond to directional persistence and angles above 90° indicate that the individual returns towards the previous location. Even though the resolution of the data might seem coarse to estimate the real tortuosity and total daily distance, the fact that all individuals were followed at the same resolution makes the comparison between parameter estimation feasible and reliable. Finally, we estimated (5) the size of the home range at a daily scale per individual (*n* = 11 424 daily home ranges) using the minimum convex polygon (MCP) method (Dahle & Swenson, 2003a; Mohr,

1947). MCP was chosen over the kernel estimator because it is applicable with fewer than 30 locations (Seaman et al., 1999). To set the limits of the home range, we used isopleth values of 95% density. We removed every day with less than five locations to get a better estimate of daily movements.

Moon phases

(6) Daily moon phases for the study area were obtained from the Naval Oceanography Portal (https://aa.usno.navy.mil/data/docs/MoonFraction.php) and expressed in terms of the fraction of the moon disc illuminated and whether the moon was waxing or waning. The different phases of the moon were calculated as in Penteriani et al., 2011. The fraction of the moon disc illuminated was transformed into radians to give each day an angular equivalent (θ), based on the periodic regression method (DeBruyn & Meeuwig, 2001). As a result, the moon cycle is represented by a continuous transition from 0 to 2π radians, that is, 0 and 2π radians correspond to the full moon and π radians is the new moon. In order to represent the entire lunar cycle, the fraction of the moon disc illuminated expressed in radians was introduced as an explanatory variable in the statistical model in the form of $\cos(\theta)$, $\sin(\theta)$, $\cos(2\theta)$ and $\sin(2\theta)$ (DeBruyn & Meeuwig, 2001). A semi-lunar cycle (two peaks in a lunar month) can be studied using the terms $\cos(2\theta)$ and $\sin(2\theta)$. Peaks are not necessarily of equal amplitude, so all terms are useful for analysing the lunar effect. A significant $\cos(\theta)$ regression coefficient reflects a peak emerging at the full moon or new moon, for example, a positive regression coefficient corresponds to a greater distance travelled at the time of the full moon and a shorter distance at the time of the new moon. A significant $\sin(\theta)$ regression included in the model reflects a peak emerging at first or last quarter, for example, a positive regression coefficient corresponds to a greater distance travelled at the time of the last quarter and a shorter distance at the time of the first quarter. A significant $\cos(2\theta)$ regression coefficient reflects two peaks one appearing between the first and last quarter and one between the full and new moon; for example, a positive regression coefficient corresponds to a greater distance travelled at the time of the new and full moon and a smaller distance at the time of the first and last quarter. A significant $\sin(2\theta)$ regression coefficient reflects two peaks appearing between the new moon and the first quarter and between the full moon and the last quarter, or between the last quarter and the new moon and between the last quarter and the full moon; for example, a positive regression coefficient corresponds to a greater distance travelled between full moon and the last quarter or between the new moon and the first quarter. The combination of significant coefficients for both θ and 2θ makes it possible to precisely determine when peaks occur and at what level.

Internal and external factors

In order to take into account other factors that may affect movement patterns, we also considered: (1) age class (i.e. subadults *vs.* adults); (2) sex; (3) period (i.e. mating *vs.*

hyperphagia season); and (4) vegetation types. The mating season lasts for about three months from den exit to the 31st of July (Dahle & Swenson, 2003b; Spady et al., 2007), and the period of hyperphagia begins the 1st of August and ends at the end of October when bears enter the den (Ordiz et al., 2017). Due to the extreme homogeneous landscape of Karelian landscape (essentially pine forests and lakes), the landscape GIS layer extracted from Earth Data – ORNL DAAC (https://webmap.ornl.gov/ogcdown/dataset.jsp?dg_id=10004_31), resolution 500 m, was reclassified into five vegetation types: (1) forest (i.e. hardwood and mixed forests); (2) softwood forest (i.e. conifer forests); (3) grasslands; (4) wetland areas; and (5) human settlements. The *Intersect tool* was used to extract information from each bear's daily home range, and then, it was transformed into a percentage of land use. Finally, we obtained the length of the night for the study area from the Naval Oceanography Portal (https://aa.usno.navy.mil/data/docs/MoonFraction.php).

Statistical analyses

Statistical analyses only covered vegetation parameters that were well represented in the area, that is, those with less than 20% of zeros in all the daily home range under consideration. The variables 'softwood forest' and 'forest' were highly correlated ($r = 0.88$), and we consequently excluded the variable 'forest', which is less characteristic of Finnish landscapes (Ahti et al., 1968).

For each movement parameter estimated at a daily scale (see Data collection for more details), we first built models including all explanatory variables except the moon phase variable, that is, age class, sex, period and vegetation types. While the residuals of the total and net distances were normally distributed, the ones for speed did not follow a normal distribution. Therefore, we built linear mixed models for total and net distances, and generalized linear mixed models for speed and turning angle (with Gamma distribution as a link function and Poisson distribution, respectively). Finally, as the duration of the night (which might influence the effect of the moon) varies significantly in our study area, we included night length as an offset. We created a set of competing models that included all potential combinations of predictors and selected the most parsimonious model according to Akaike's information criterion (AICc) (Burnham & Anderson, 2002). Parameter coefficients and the relative importance value (RIV) for the respective explanatory variables were calculated using model averaging approach on the 95% confidence set (Burnham & Anderson, 2002). Parameter estimates produced by model averaging derive from weighted averages of these values across all models in the set considered (Symonds & Moussalli, 2011). In particular, the relative importance value (RIV) of each explanatory variable was calculated by summing Akaike weights across all models which contain the variable (Burnham & Anderson, 2002). We considered this to be our *null model*. On the top of the effects of the factors included in the *null model*, the effect of the moon on each of the considered response variables was estimated at the daily scale. The moon (see section *Moon*

phases) was introduced in the form of cos(θ), sin(θ), cos(2θ) and sin(2θ) as continuous explanatory variables. We compared our *null model* with the one containing the moon phase using maximum likelihood (Myung, 2003). We assumed that the moon had an effect on movement parameters when the p-value between the two models was less than 0.03 (Zuur et al., 2009). As each brown bear was followed for several days (hereafter, sessions) and years, we considered the individual, the session (a session corresponds to one day, i.e., the first location until the last location of the day) and the year as nested random effects. We used the statistical software R v. 3.5.1 (R Development Core Team, 2018) with the *lme4* package (Bates et al., 2015) and *MuMIn* package (Bartoń, 2013) for model generation and model averaging.

Results

We found that internal and external factors influenced brown bear movements, which otherwise were not influenced by lunar brightness (Table 1 and Tables S2 and S3). That is, models containing the moon phases never performed better than our *null models* (Tables 1 and 2, Fig 2).

Our *null models* always included the variable period, with brown bears moving slowly, over short distances with more tortuous trajectories during the hyperphagia period than the mating period. (Table 1). Furthermore, brown bears generally moved long distances and showed extensive home ranges when moving in habitats dominated by conifers (Table 1). Finally, adult brown bears moved faster and demonstrated more tortuous trajectories within larger home range areas than did subadult individuals, especially during the mating period (Table 1). No differences were found between male and female movement patterns (Table 1), independent of age class.

Discussion

Changes in movement patterns between the different periods may be related to different biological needs across the breeding season. During the hyperphagic period, brown bears generally moved less and demonstrated torturous trajectories, probably restricting their activity around abundant local food resources (McLoughlin et al., 2000; Selva et al., 2017). In contrast, during the mating period, brown bears moved longer distances, most likely with the aim of increasing the probability of finding a potential partner (Graham & Stenhouse, 2014; Steyaert et al., 2012). These results are in line with previous studies showing that, during the mating season, oestrus females might increase their movements to maximize reproductive success and the survival of future cubs (Ebensperger, 1998; Hrdy, 1979; Soltis et al., 2000). Also, brown bears typically travelled long distances and showed extensive home ranges when moving in habitats dominated by conifers. Habitat quality and characteristics may engender diverse costs and benefits and consequently noticeable differences in movement behaviours (Delgado et al., 2010). In our study area, conifer forest may represent a vegetation type where the costs of movements are low, for example, increased visibility resulting in less need for vigilance, food source types and availability and/or fewer

landscape obstacles. Lastly, adult brown bears moved faster and demonstrated more tortuous trajectories within larger home ranges than subadult individuals, especially during the mating season (Table 1), which might suggest a behaviour mainly related to mating needs.

Although our data do not indicate any differences in movement patterns between males and females, this might be an area of focus for future studies. While we did not consider the reproductive status of females, previous evidence shows that females with cubs of the year may move less and in a more constricted area than other individuals during the mating season (Ordiz et al., 2017), when females with COYs restrict their movements to reduce probability of an infanticide.

Further, it is important to highlight here that in our study area, the hyperphagia period extensively overlaps with the hunting period. According to the Finnish Wildlife Agency, the hunting season indeed starts on the 20th of August and closes on the 31st of October. Even though it would have been interesting to include the effect of hunting in our models and separate for the ones due to the intrinsic and different biological needs across the breeding season, we neither had accurate data on hunting pressure variation over the entire hunting season and over the 12 years of this telemetry study, nor any kind of hunting data in Russia. Due to this lack of data, we cannot therefore discard the possibility that the recorded patterns of movement during the hyperphagia are also partially determined by the confounding effect of hunting. Actually, when human pressure is high, factors such as fear drive animals to adjust their behaviour to reduce risk. That is, bears can allocate part of their time to vigilance at the expense of other vital needs, such as searching for food, to avoid threatening encounters with humans (Gosselin et al., 2015; Loveridge et al., 2007; Ordiz et al., 2011, 2012, 2013). Thus, hunting pressure might also help explaining why brown bears moved slowly, over short distances and follow more tortuous paths when the hunting season was opened.

Contrary to many other carnivores that have been shown to follow the rhythm of moonlight patterns, brown bear movement patterns were not influenced by the moon phases (see also Richardson, 2017). Models containing the moon phases never performed better than our null models. Notably, even though brown bears have the typical morphological features of carnivores, they are opportunistic omnivores with a diversified diet (Bojarska & Selva, 2012). Although brown bears may show carnivore habits and feed on small mammals as well as large ungulates (Bojarska & Selva, 2012; Niedziałkowska et al., 2019), the brown bear diet is composed of more than 50% vegetal materials (e.g. grass, leaves and roots) and also rich fleshy fruits (e.g. bilberry *Vaccinium myrtillus*; Cronin, 2005; Persson et al., 2001; Rode & Robbins, 2000; Rode et al., 2001; Stenset et al., 2016). As a result, the prey–predator relationships that are behind the dependence of carnivores on lunar light (Berger-Tal et al., 2010; Bhatt et al., 2018; Brown & Kotler, 2004b; Penteriani et al., 2013) are weaker in brown bears than in other obligate carnivores. It is important to consider here that it would have been easier to detect a potential effect of the moon on movement patterns when linking bear displacements to habitat categories where the

Table 1 Values of AICc, ΔAICc and Weighted AICc of the best (ΔAICc < 2) linear mixed or generalized linear models (see text for more details), summary of the *null model* considered for each movement parameter and the analysis of variance (ANOVA with R2c (i.e. conditional *R* squared)) showing that the moon did not affect brown bear movement patterns

	Competing models		AICc	ΔAICc	Weighted AICc
Total distance	Conifer + period		39 897	0.00	0.50
		β[a]	SE[a]	P[a]	RIV[b]
	Intercept	6.54	0.14	<0.001	
	Period	−1.75	0.08	<0.001	1.00
	Conifer	0.08	0.06	0.16	0.67
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Conifer + period	7	39 886		0.88
	Conifer + period + *Moon phases*	11	39 245	0.02	0.88

	Competing models		AICc	ΔAICc	Weighted AICc
Net distance	Conifer + period		47 850	0.00	0.64
		β[a]	SE[a]	P[a]	RIV[b]
	Intercept	4.26	0.13	<0.001	
	Period	−1.98	0.07	<0.001	1.00
	Conifer	0.13	0.04	<0.001	1.00
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Conifer + period	7	47 839		0.90
	Conifer + period + *Moon phases*	11	47 913	0.02	0.90

	Competing models		AICc	ΔAICc	Weighted AICc
Home range	Period + conifer		29 557	0.00	0.65
		β[a]	SE[a]	P[a]	RIV[b]
	Intercept	1.52	0.10	<0.001	
	Period	−1.58	0.03	<0.001	1.00
	Conifer	0.04	0.02	0.07	0.59
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Period + conifer	7	29 592		0.89
	Period + conifer + *Moon phases*	11	29 624	0.41	0.89

	Competing models		AICc	ΔAICc	Weighted AICc
Speed	Period + conifer		39 897	0.00	0.50
		β[a]	SE[a]	P[a]	RIV[b]
	Intercept	−2.19	0.70	0.002	
	Period	0.04	0.01	<0.001	1.00
	Conifer	0.09	0.03	0.002	1.00
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**Deviance**
	Period + conifer	7	−225 590		−225 606
	Period + conifer + *Moon phases*	11	−225 325	1.00	−225 349

	Competing models		AICc	ΔAICc	Weighted AICc
Turning angle	Period + age		19 169	0.00	0.27
		β[a]	SE[a]	P[a]	RIV[b]
	Intercept	−0.22	0.08	0.006	
	Period	−1.69	0.03	<0.001	1.00
	Age	0.05	0.07	0.44	0.58
	ANOVA	**d.f.**	**AIC**	**Pr (>Chisq)**	**R2c**
	Period + age +	5	19 206		0.39
	Moon phases	9	19 239	0.52	0.39

[a]Model-averaged coefficients.
[b]Relative Importance Value.

Table 2 Values (mean ± SD, range) of movement parameters across moon phases (● Full moon; ● Last Quarter; ● New Moon; ● First Quarter)

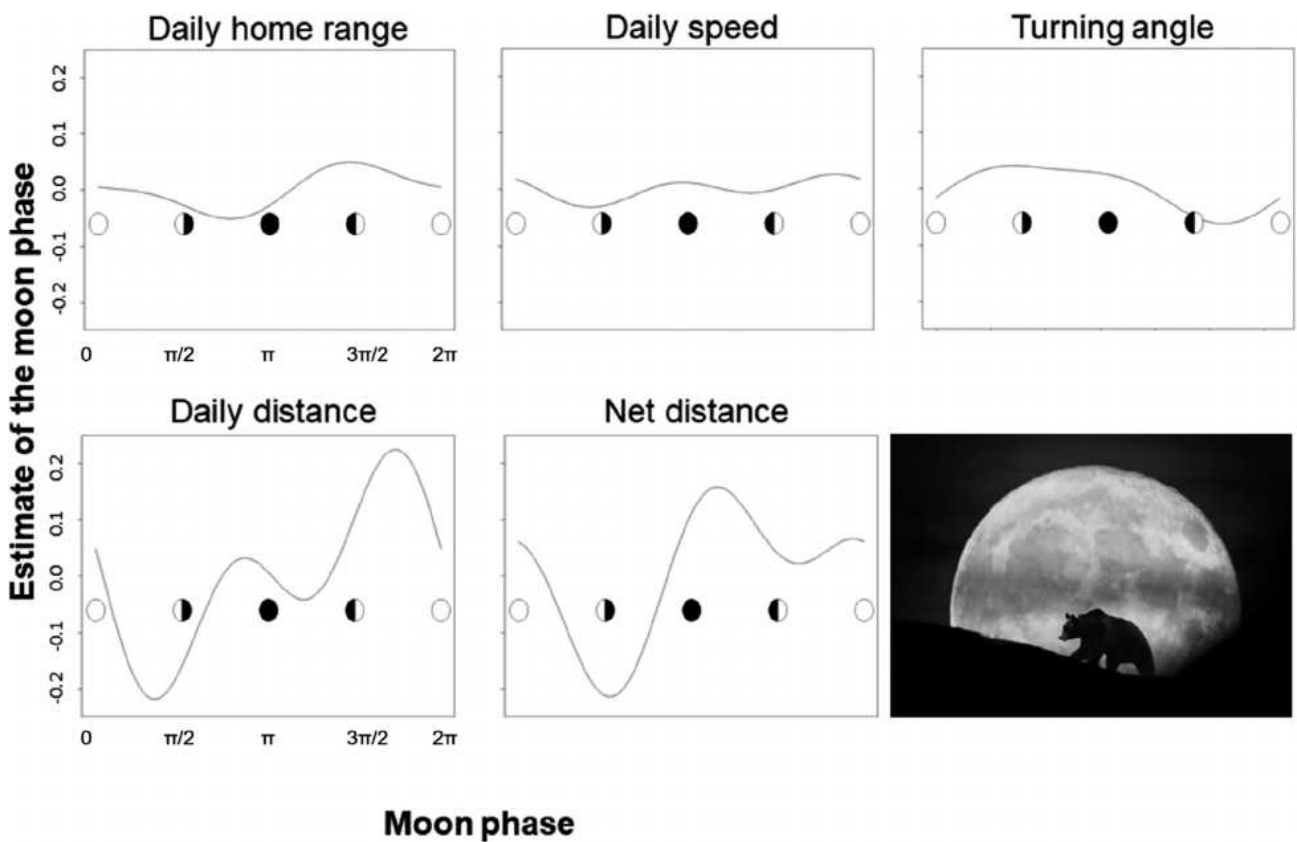|	Total distance (km)	Net distance (km)	Home range (km²)	Speed (km/h)
●	7.7 ± 6.6, 0–66.2	4.0 ± 4.6, 0–37.8	2.7 ± 7.0, 0–136	0.4 ± 0.7, 0–16.0
●	7.5 ± 7.0, 0–50.2	3.7 ± 4.8, 0–47.1	2.8 ± 8.1, 0–131.4	0.4 ± 0.8, 0–15.8
●	7.9 ± 7.1, 0–54.5	4.1 ± 4.7, 0–34.6	2.9 ± 7.4, 0–109.7	0.4 ± 0.9, 0–16.0
●	8.0 ± 7.1, 0–66.0	4.0 ± 4.7, 0–40.9	3.1 ± 8.8, 0–168	0.4 ± 0.9, 0–15.3

Figure 2 Moon phase estimated effect (smoothed grey lines) on daily home range, daily speed, turning angle, daily distance and net distance as estimated by linear mixed models for total and net distances, and generalized linear mixed models for speed and turning angle (with Gamma distribution as a link function and Poisson distribution, respectively) (Table 1). The moon cycle is represented by a continuous transition from 0 to 2π radians; that is, 0 and 2π radians correspond to the full moon and π radians are the new moon. In order to represent the entire lunar cycle, the fraction of the moon disc illuminated expressed in radians was introduced as an explanatory variable in the statistical model in the form of $\cos(\theta)$, $\sin(\theta)$, $\cos(2\theta)$ and $\sin(2\theta)$, which corresponds to 1 to 6 in the x-labels. (Brown bear picture: V. Penteriani).

brightness of the moon is really diverse (e.g. dense forest—presence of canopy cover—vs. open fields), as we did, rather than using many different habitat types very similar among them, for example dense stand, young stand and old-growth stand of forest, or clearcut, field and bog. In addition, some other factors may have further played a role in reducing the potential effect of the moon on brown bears in our study area. First, bear feeding patterns on natural food might be disrupted by the continuous supply of anthropogenic foods at artificial feeding points established for hunting and bear viewing

purposes (Penteriani et al., 2010; Penteriani et al., 2017, 2021; Kojola & Heikkinen, 2012). In fact, this practice can further modify the bears' non-dependence on prey (Steyaert et al., 2014) and, therefore, the potential influence of moonlight. Second, as stated above, we should also take into account that this Finnish-Russian bear population is managed through hunting and, as it has been previously demonstrated (Ordiz et al., 2011), bears under hunting pressure may alter their normal activity rhythms and movements. Further limiting factors that may have reduced the potential effect of the moon in our study area are cloud cover and the fact that the sun reflects less into the moon in summer at high latitudes. However, we could not consider the potential effects of real and local cloud coverage in a species that is performing large displacements like brown bears because such data simply do not exist. This is because the spatial resolution of the meteorological stations recording weather data is not as spatially fine-grained as bear displacements require. In addition, cloud coverage may change considerably at a short temporal scale. Thus, during their long displacements within their large home ranges, brown bears may be faced to different cloud coverage conditions even during the same night. Yet, we consider that if it would have been a lunar effect on bear movement behaviours, the duration of our telemetry study should have allowed us to it even if during some nights or during some portions of the nights that clouds could have partially covered moon brightness. In this regard, we should not forget that even in cloudy skies, the night brightness of full moon nights is higher than during new moon nights.

The lunar cycle is a major factor in activity changes, and many nocturnal and diurnal animals can alter their activity in response to moonlight variations. Thus, it is essential to study the effect of the moon on carnivores as increased hunting success may influence their behaviour in the following days. In the case of the brown bear, however, it seems that the lunar cycle does not influence their movement patterns. The results of this study suggest that predator–prey interactions and carnivore behaviour still merit further investigation that takes into account (1) the intrinsic characteristics of carnivores (e.g. facultative *vs.* obligate carnivores), (2) the physical environment in which they move (e.g. vegetation types and nocturnal light), and (3) the potential interference of human activities. In fact, the effects of some of the external pressures acting on predators, such as moonlight, might be hidden and/or greatly reduced by stronger forces like the needs of carnivores during specific periods of the year (e.g. mating), individual age, human avoidance and/or interference with feeding activity. A more global approach to the study of carnivore behaviours, which takes into account both obligate and facultative carnivores, might change the way we think about their interactions with the environment and humans, and bring to light more complex behavioural patterns than previously thought.

Acknowledgements

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their actions in North Western Europe. *Annales Botanici Fennici*, **5**, 169–211.

Arnemo, J. M., Fahlman, A., Ahlqvist, P., Brunberg, S., Segerström, P. & Swenson, J. E. (2007). *Biomedical protocol for free-ranging brown bears (Ursus arctos) in Scandinavia.*

Barton, K. (2013). Model selection and model averaging based on information criteria (AICc and alike). *The Comprehensive R Archive Network*, **1**, 13.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software* **67**, 1–48.

Berger-Tal, O., Mukherjee, S., Kotler, B. P. & Brown, J. S. (2010). Complex state-dependent games between owls and gerbils. *Ecology Letters* **13**, 302–310.

Bhatt, U. M., Habib, B., Sarma, H. K. & Lyngdoh, S. L. (2018). Catch me if you can: Species interactions and moon illumination effect on mammals of tropical semi-evergreen forest of Manas National Park, Assam, India. *bioRxiv.* https://doi.org/10.1101/449918

Bjørneraas, K., Van Moorter, B., Rolandsen, C. M. & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *Journal of Wildlife Management* **74**, 1361–1366.

Bojarska, K. & Selva, N. (2012). Spatial patterns in brown bear *Ursus arctos* diet: The role of geographical and environmental factors. *Mammal Review*, **42**, 120–143.

Brown, J. S. & Kotler, B. P. (2004a). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, **7**, 999–1014.

Brown, J. S. & Kotler, B. P. (2004b). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999–1014.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach.* Springer.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Clarke, J. A. (1983). Moonlight's influence on predator/prey interactions between short-eared owls (*Asio tlammeus*) and deermice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology*, **13**, 205–209.

Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W. & Schmid, B. (2012). Fear of the dark or

dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, 93, 2590–2599.

Craighead, J. J., Craighead, F. C. & McCutchen, H. E. (1970). Age determination of grizzly bears from fourth premolar tooth sections. *Journal of Wildlife Management*, 34, 353.

Cronin, T. W. (2005). The visual ecology of predator-prey interactions. In *Ecology of Predator-prey Interactions*, 105–138. Barbosa P. & Castellaris I. (Eds). New York: Oxford University Press.

D'Eon, R. G., Serrouya, R., Smith, G. & Kochanny, C. O. (2002). GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30, 430–439.

Dacke, M., Nilsson, D.-E., Scholtz, C. H., Byrne, M. & Warrant, E. J. (2003). Insect orientation to polarized moonlight. *Nature* 424, 33.

Dahle, B. & Swenson, J. E. (2003a). Home ranges in adult Scandinavian brown bears (Ursus arctos): Effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260, 329–335.

Dahle, B. & Swenson, J. E. (2003b). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos. Journal of Animal Ecology* 72, 660–667.

Daly, M., Behrends, P. R., Wilson, M. I. & Jacobs, L. F. (1992). Behavioural modulation of predation risk: Moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami. Animal Behavior* 44, 1–9.

DeBruyn, A. M. H. & Meeuwig, J. J. (2001). Detecting lunar cycles in marine ecology: Periodic regression versus categorical ANOVA. *Marine Ecology Progress Series*, 214, 307–310.

Delgado, M. D. M., Penteriani, V., Revilla, E. & Nams, V. O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology* 79, 620–632.

Di Bitetti, M. S., Paviolo, A. & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, 270, 153–163.

Dixon, D. R., Dixon, L. R. J., Bishop, J. D. & Pettifor, R. A. (2006). Lunar-related reproductive behaviour in the badger (*Meles meles*). *Acta Ethologica*, 9, 59–63.

Ebensperger, L. A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* 73, 321–346.

Estes, J. A., Jameson, R. J. & Rhode, E. B. (1982). Activity and prey election in the Sea Otter: Influence of population status on community structure. *American Naturalist* 120, 242–258.

Foster, R. G. & Roenneberg, T. (2008). Human responses to the geophysical daily, annual and lunar cycles. *Current Biology* 18, R784–R794.

Gende, S. M. & Quinn, T. P. (2004). The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82, 75–85.

Gosselin, J., Zedrosser, A., Swenson, J. E. & Pelletier, F. (2015). The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proceedings of the Royal Society B: Biological Sciences* 282, 20141840. https://doi.org/10.1098/rspb.2014.1840

Graham, K. & Stenhouse, G. B. (2014). Home range, movements, and denning chronology of the Grizzly Bear (*Ursus arctos*) in West-Central Alberta. *The Canadian Field-Naturalist*, 128, 223.

Grant, R., Halliday, T. & Chadwick, E. (2012). Amphibians' response to the lunar synodic cycle-a review of current knowledge, recommendations, and implications for conservation. *Behavioral Ecology* 24, 53–62.

Grassman, L., Tewes, M. & Silvy, N. (2005). Ranging, habitat use and activity patterns of binturong *Arctictis binturongand* yellow-throated marten *Martes flavigulain* north-central Thailand. *Wildlife Biology*, 11, 49–57.

Griffin, P. C., Griffin, S. C., Waroquiers, C. & Mills, L. S. (2005). Mortality by moonlight: Predation risk and the snowshoe hare. *Behavioral Ecology* 16, 938–944.

Hagen, S. B., Kopatz, A., Aspi, J., Kojola, I. & Geir Eiken, H. (2015). Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. *Proceedings of the Royal Society B-Biological Sciences* 282, 13–16.

Hertel, A. G., Swenson, J. E. & Bischof, R. (2017). A case for considering individual variation in diel activity patterns. *Behavioral Ecology* 28, 1524–1531.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G. R., Schmidt, K. & Linnell, J. D. C. (2014). Activity patterns of Eurasian Lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS One* 9, e114143.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, 13–40.

Jalanka, H. H. & Roeken, B. O. (1990). The use of medetomidine, medetomidine-ketamine combinations, and atipamezole in nondomestic mammals: A review. *The Journal of Zoo and Wildlife Medicine*, 21, 259–282.

Kojola, I. & Heikkinen, S. (2012). Problem brown bears Ursus arctos in Finland in relation to bear feeding for tourism purposes and the density of bears and humans. *Wildlife Biology*, 18, 258–263.

Kotler, B. P., Brown, J. S., Dall, S. R. X., Gresser, S., Ganey, D. & Bouskila, A. (2002). Foraging games between gerbils and their predators: Temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research* 4, 495–518.

Kotler, B. P., Brown, J. S., Smith, R. J. & Wirtz, W. O. (1988). The effects of morphology and body size on rates of owl predation on Desert rodents. *Oikos* 53, 145.

Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E. D., Dayan, T. & Helfrich-Forster, C. (2013).

Chronobiology by moonlight. *Proceedings of the Royal Society B-Biological Sciences* **280**, 1765.

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* **68**, 619–640.

Loveridge, A. J., Searle, A. W., Murindagomo, F. & Macdonalda, D. W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* **134**, 548–558. https://doi.org/10.1016/j.biocon.2006.09.010

Martin, J., Calenge, C., Quenette, P. Y. & Allainé, D. (2008). Importance of movement constraints in habitat selection studies. *Ecological Modelling*, **213**, 257–262.

Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P.-Y., Allainé, D. & Swenson, J. E. (2013). Reciprocal modulation of internal and external factors determines individual movements. *Journal of Animal Ecology* **82**, 290–300.

McLoughlin, P. D., Ferguson, S. H. & Messier, F. (2000). Intraspecic variation in home range overlap with habitat quality: A comparison among brown bear populations. *Entomologia Experimentalis Et Applicata* **14**, 39–60.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist* **37**, 223–249.

Mukherjee, S., Zelcer, M. & Kotler, B. P. (2009). Patch use in time and space for a meso-predator in a risky world. *Oecologia* **159**, 661–668.

Myung, I. J. (2003). Tutorial on maximum likelihood estimation. *Journal of Mathematical Psychology* **47**, 90–100.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052–19059.

Niedziałkowska, M., Hayward, M. W., Borowik, T., Jędrzejewski, W. & Jędrzejewska, B. (2019). A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in Eurasia. *Mammal Research*, **64**, 1–9.

Ordiz, A., Saebø, S., Kindberg, J., Swenson, J. E. & Støen, O.-G. (2017). Seasonality and human disturbance alter brown bear activity patterns: Implications for circumpolar carnivore conservation? *Animal Conservation*, **20**, 51–60.

Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59–67.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M. & Swenson, J. E. (2012). Do bears know they are being hunted? *Biological Conservation*, **152**, 21–28.

Ordiz, A., Støen, O.-G., Saebø, S., Sahlén, V., Pedersen, B. E., Kindberg, J. & Swenson, J. E. (2013). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*, **50**, 306–314.

Penteriani, V., del Delgado, M. D. M. & Melletti, M. (2010). Don't feed the bears! *Oryx*, **44**, 169–170.

Penteriani, V., del Mar Delgado, M., Kuparinen, A., Saurola, P., Valkama, J., Salo, E., Toivola, J., Aebischer, A. & Arlettaz, R. (2014). Bright moonlight triggers natal dispersal departures. *Behavioral Ecology and Sociobiology*, **68**, 743–747.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J. V., Fedriani, J. M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L. & Lourenço, R. (2013). Responses of a top and a meso predator and their prey to moon phases. *Oecologia*, **173**, 753–766.

Penteriani, V., Kuparinen, A., Delgado, M. D. M., Lourenço, R. & Campioni, L. (2011). Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. *Animal Behavior*, **82**, 413–420.

Penteriani, V., Lamamy, C., Kojola, I., Heikkinen, S., Bombieri, G. & Delgado, M. (2021). Does artificial feeding affect large carnivore behaviours ? The case study of brown bears in a hunted and tourist exploited subpopulation. *Biological Conservation*, **254**, 108949.

Penteriani, V., López-Bao, J. V., Bettega, C., Dalerum, F., Delgado, M. D. M., Jerina, K., Kojola, I., Krofel, M. & Ordiz, A. (2017). Consequences of brown bear viewing tourism: A review. *Biological Conservation*, **206**, 169–180.

Persson, I.-L., Wikan, S., Swenson, J. E. & Mysterud, I. (2001). The diet of the brown bear Ursus arctos in the Pasvik Valley, northeastern Norway. *Wildlife Biology*, **7**, 27–37.

Prugh, L. R. & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, **83**, 504–514.

R Development Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna: Austria.

Rasmussen, G. S. A. & MacDonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, **286**, 232–242.

Richardson, M. L. (2017). Daily and monthly activity of Brown Bears (Ursus arctos) near a proposed industrial project in coastal British Columbia. *Western North American Naturalist*, **77**, 118–123.

Robbins, C. T., Fortin, J. K., Rode, K. D., Farley, S. D., Shipley, L. A. & Felicetti, L. A. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos*, **116**, 1675–1682.

Rode, K. D. & Robbins, C. T. (2000). Why bears consume mixed diets during fruit abundance. *Canadian Journal of Zoology*, **78**, 1640–1645.

Rode, K. D., Robbins, C. T. & Shipley, L. A. (2001). Constraints on herbivory by grizzly bears. *Oecologia*, **128**, 62–71.

Sábato, M. A. L., de Melo, L. F. B., Magni, E. M. V., Young, R. J. & Coelho, C. M. (2006). A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. *Behavioural Processes*, **73**, 228–230.

San-Jose, L. M., Séchaud, R., Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., Gémard, C., Almasi, B.,

Béziers, P., Kelber, A., Amar, A. & Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nature Ecology & Evolution*, **3**, 1331–1340.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, **63**, 739–747.

Selva, N., Teitelbaum, C. S., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Bojarska, K. & Mueller, T. (2017). Supplementary ungulate feeding affects movement behavior of brown bears. *Basic and Applied Ecology*, **24**, 68–76.

Sjödin, A., Hjorth, M. F., Damsgaard, C. T., Ritz, C., Astrup, A. & Michaelsen, K. F. (2015). Physical activity, sleep duration and metabolic health in children fluctuate with the lunar cycle: Science behind the myth. *Clinical Obesity*, **5**, 60–66.

Soltis, J., Thomsen, R., Matsubayashi, K. & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology*, **48**, 195–202.

Spady, T. J., Lindburg, D. G. & Durrant, B. S. (2007). Evolution of reproductive seasonality in bears. *Mammal Review*, **37**, 21–53.

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S. M. J. G., Zedrosser, A., Brunberg, S. & Swenson, J. E. (2016). Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. *Wildlife Biology*, **22**, 107–116.

Steyaert, S. M. J. G., Endrestøl, A., Hackländer, K., Swenson, J. E. & Zedrosser, A. (2012). The mating system of the brown bear Ursus arctos. *Mammal Review*, **42**, 12–34.

Steyaert, S. M. J. G., Kindberg, J., Jerina, K., Krofel, M., Stergar, M., Swenson, J. E. & Zedrosser, A. (2014). Behavioral correlates of supplementary feeding of wildlife: Can general conclusions be drawn? *Basic and Applied Ecology*, **15**, 669–676.

Swenson, J. E., Adamic, M., Huber, D. & Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. *Oecologia* **153**, 37–47.

Symonds, M. R. E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, **65**, 13–21.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S. & Gula, R. (2003). Daily patterns and duration of wolf activity in the Białowieza Forest, Poland. *Journal of Mammalogy*, **84**, 243–253.

Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J. & Sæther, B. E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, **82**, 770–780.

Wilson, D. E. & Mittermeier, R. A. (Eds.). (2009). *Handbook of the mammals of the world – Volume 1, Carnivores*. Lynx Edicions in Association with Conservation International and IUCN.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

Supporting Information

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

Table S1. Distribution of days over the period and the lunar cycle (: Full moon;   : Last Quarter;   : New Moon;   : First Quarter) according to the sex and age of brown bears and the distribution of the number of individuals radio-tagged by year.

Table S2. Values of AICc, ΔAICc and Weighted AICc of all the models built for the five movement parameters where internal and external factors were analysed.

Table S3. Values of the variance and standard deviation of all the models built for the five movement parameters where internal and external factors were analysed.