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Reduced movement of wildlife in Mediterranean landscapes: a case study of brown bears in Greece

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Abstract

The survival of large carnivores in a rapidly changing, human-modified world depends largely on their movements; therefore, understanding how movement patterns change within space and time and which factors affect them most is of paramount importance for their conservation. In a case study in Greece using brown bears *Ursus arctos*, we evaluated the movement ecology of a recovering population in a Mediterranean landscape, where human activity is high. We found that during daytime bears moved less when ambient temperatures were high and when they were far away from forests and close to settlements, where human activity is expected to be high. During night-time, when human activity and mortality risk are expected to be low, bear movement was higher farther from forested areas, close to roads, and in less rough terrain. Although bear movement patterns in Greece were generally similar to those of other bear populations in Europe, home ranges were smaller than in northern populations. These findings indicate that increased human activity and high ambient temperatures reduce bear movement and ultimately contribute to the smaller home ranges in the warmer and human-dominated Mediterranean landscapes. We suggest that management and conservation actions in Mediterranean landscapes should aim on separating humans and bears in space or time, so that bear movements are not constrained and, in turn, minimum home ranges that cover their essential requirements are guaranteed.

Introduction

The ability of animals to survive in a changing environment or areas impacted by humans is determined to a large extent by the characteristics of their movements (Battin, 2004), which, in turn, influence their demographics and population dynamics (Allen & Singh, 2016). Movements are subject to inter-individual variation and are influenced by various intrinsic and extrinsic factors, such as age and gender (Minta, 1993; Gehrt & Frttzell, 1997), mortality risk (Fortin *et al.*, 2005), habitat (Bélisle, Desrichers & Fortin, 2001), climate (McLoughlin & Ferguson, 2000) and anthropogenic influences (Tucker *et al.*, 2018). These factors influence the decisions animals take in order to satisfy their essential requirements and adapt to spatio-temporal changes in the environment (Van Moorter *et al.*, 2016). In turn, these individual movements define how animals use space throughout time, which affects the size and characteristics of their home range (Burt, 1943).

Animal movements in human-dominated landscapes may be highly affected by human activities and density (Cramer & Portier, 2001; Moreira-Arce, Vergara & Boutin, 2015). Furthermore, fragmentation and degradation of habitats may result in increases in home ranges, as animals strive to find the necessary resources to survive in a patchy and impoverished environment (Šálek, Drahníková & Tkadlec, 2015). However, human activity can also artificially concentrate food resources at specific areas [(e.g. near human settlements (Prange, Gehrt & Wiggers, 2004)], change the timing of animal movements (Gaynor *et al.*, 2018), or create movement barriers (e.g. road networks) that may result in the reduction of home range size (Fahrig, 2007; Tucker *et al.*, 2018).

Brown bear (*Ursus arctos*) movements vary throughout time (Ordiz *et al.*, 2014) and are influenced by numerous factors, including reproductive maturity, sex (Dahle & Swenson, 2003a) and daylight (Klinka & Reimchen, 2002; Klinka & Reimchen, 2009). Bears are also sensitive to changes in environmental conditions (Molnár *et al.*, 2010; Zarzo-Arias et al., 2018) and human activity (Martin *et al.*, 2010; Ordiz *et al.*, 2017), often seeking refuge in areas with rough terrain, far from human settlements [(Nellemann *et al.*, 2007), but see also

Elfström *et al.,* (2014)] and roads [(Reynolds-Hogland & Mitchell, 2007; Skuban *et al.*, 2017; Find'o *et al.*, 2018), but see also Roever, Boyce & Stenhouse, (2010)] and close to forests and forest edges (May *et al.*, 2008; Stewart *et al.*, 2013). The combined effects of all these factors often result in differences in basic movement parameters (e.g. daily speed, core area size, seasonal home range) according to age, sex and season.

At the same time, movement parameters are highly interrelated (Van Moorter *et al.*, 2016), and thus, the parameters affecting bear movement (e.g. daylight, human activity, environmental conditions) at a proximate level could ultimately affect how bears use space in their attempt to make the utmost of the available resources, while avoiding human disturbance (Ordiz *et al.*, 2014) and adapting to environmental changes (Zarzo-Arias *et al.*, 2018). Studying the causal relationship between these movement parameters is therefore integral in understanding the strategies pursued by bears to survive in human-dominated (or human-modified) landscapes (Amstrup *et al.*, 2001; Tuomainen & Candolin, 2011; Ordiz *et al.*, 2014).

Brown bears in Greece reach their southernmost European distribution, are considered endangered (Mertzanis, Giannakopoulos & Pylidis, 2009) and occur in a largely human-dominated Mediterranean landscape with relatively high population density (30–40 persons/km^2). Thus, they provide an interesting case for studying the movement ecology of the species. Bear habitat in Greece has been undergoing during the last decades a progressive rewilding as a consequence of rural abandonment. In addition, since the early 2000s encouraging signs of bear recovery have been recorded in the country, including an increase in population size (Karamanlidis *et al.*, 2015b), a range expansion (Bonnet Lebrun et al., 2019) and a genetic recovery (Karamanlidis *et al.*, 2018). At the same time, human–bear conflicts have also been increasing (Karamanlidis *et al.*, 2011), creating an urgent need for understanding this recovery and developing new, effective management and conservation measures that will safeguard the future of this bear population.

Bear movement in human-dominated Mediterranean landscapes is still poorly understood. However, this knowledge is essential for effective animal conservation (Doherty & Driscoll, 2018). In order to understand the movement patterns of brown bears in Greece during their recovery, we carried out a study using GPS telemetry. The aims of the study were twofold: (1) Calculate various movement parameters (e.g. Brownian motion variance; daily activity rate, speed, tortuosity and core area; and seasonal and annual home range) and use them to describe the movement ecology. The description of brown bear movement ecology in Greece was based on the circannual and circadian assessment of movement patterns, the identification of the factors affecting bear movement and the identification of age-, sex- and season-specific differences in movement parameters. We hypothesized that, in an attempt to avoid high levels of human activity and high ambient temperatures, bears in Greece would be mainly nocturnal, showing movement peaks during the mating and hyperphagia season. We also expected age-, sex- and season-related movement parameters of bears in Greece to be similar to those of other bear populations in southern Europe and smaller than those of bear populations in northern Europe with lower levels of human activity and lower ambient temperatures. (2) Study the causal relationship between the movement parameters of bears in Greece by testing the hypothesis that daily activity rates influence daily speed, tortuosity, and core area size which, in turn, influence the size of seasonal home ranges.

Materials and methods

Study area and telemetry procedures

The study was carried out in the western part of the brown bear range in Greece in 2003–2013. Intensity of human activity in the study area ranges from areas with low human presence (i.e. 16 persons/km^2) to major cities with populations >50 000; there is a relatively high density of small villages (i.e. 6 human settlements/100 km^2), connected through an extensive road network (i.e. 1.24 km/km^2). This intensity of human activity has resulted in a mosaic landscape, where natural habitats are disrupted by agricultural patches (for details, see Supporting Information Appendix S1, Figure S1.1).

We fitted 3-D GPS (global positioning system) collars (Simplex, Televilt, Stockholm, Sweden; GPS Plus, Vectronic Aerospace GmbH, Berlin, Germany) to 12 adult (6F, 6M) and 6 sub-adult bears (1F, 5M) using a leather spacer destined to disintegrate and release the collar in 1–2 years. Animal capture and handling followed standard procedures for the species (Kreeger & Arnemo, 2007; Karamanlidis *et al.*, 2015a). We considered bears <4 years old to be sub-adults and older bears to be adults, pooling all individuals in three bear categories (i.e. adult females, adult males and sub-adult males). The collared sub-adult female bear was still accompanying her mother that was not collared and was therefore included in the adult female group for all the analyses. The GPS fix rate varied from 1 to 3 h (8–24 fixes/day). Seven bears (4 adult females, 2 adult males and one sub-adult male) were fitted also with a dual-axis motion sensor (Ziółkowska *et al.*, 2016). Thus, the final dataset consisted of 7 adult female, 6 adult male and 5 sub-adult male bears, for which a total of 37 499 GPS fixes over 3072 tracking days were collected (for details, see Supporting Information, Appendix S1, Table S1.1).

Patterns of movement

We calculated Brownian motion variances (hereafter, simply 'motion variance') for each time step (i.e. the spatio-temporal change between consecutive GPS locations) by fitting dynamic Brownian bridge movement models (dBBMMs) to the complete movement path of each bear, using the package 'move' (Kranstauber & Smolla, 2016) in the R statistical computing environment (R Core Team, 2013) (for details, see Supporting Information, Appendix S2). Motion variance provides a measure of an animal's movements, with lower values associated with more regular paths and/or shorter movements and higher values associated with irregular paths and/or longer movements (Kranstauber *et al.*, 2012).

To assess the circannual and circadian movement patterns of adult female and male and sub-adult male brown bears in Greece, we investigated motion variances through generalized additive mixed models (GAMMs), applying a cyclic cubic spline smoother to the two explanatory variables (i.e. date of year and hour of day), and including the individual bear ID and the year as random effects. We selected the number of knots used for each explanatory variable based on generalized cross-validation using the R package 'mgcv' (Wood, 2006). Based on the beginning and end of the motion variance peaks as predicted by the GAMMs, while considering seasonal cut-off dates and the species' ecology (e.g. average dates of reproductive events and of the production of major food resources, den entrance, etc.), we defined six ecologically sound seasons (Basille *et al.*, 2013) across the year: ['Emergence' (EM; 1 March–21 April), 'Mating' (MA; 22 April–21 June), 'Post-Mating' (PM; 22 June–7 August), 'Early hyperphagia' (eHY; 8 August–7 October), 'Late hyperphagia' (lHY; 8 October–15 December), 'Denning' (DN; 16 December–29 February)]. Collar performance with respect to the GPS schedule was considerably lower (43%) during the denning season compared to the rest of the year (80%), so these data were excluded from the rest of the analyses to avoid sampling bias.

To identify the factors influencing movement patterns, we converted motion variance into a binary variable and classified each time step as passive or active (Gervasi, Brunberg & Swenson, 2006) based on a previously defined separation point (for details, see Supporting Information, Appendix S2). Then, we fitted generalized linear mixed models (GLMMs) with a binary response and a logistic link (using the R package 'lme4') during each season, including the individual bear ID and the year as random factors. As potential explanatory variables, we considered sex (i.e. female = 0, male = 1) and age of the individual (i.e. reclassified as '1' for bears ≤ 3 years old, '2' for bears 4 - 6 years old, '3' for bears 7–10 years old, and '4' for bears ≥ 11 years old), daylight (i.e. night = 0, day = 1), local average temperature, local accumulated rainfall, terrain roughness, proximity to forested areas (i.e. mature forest and transitional shrublands), proximity to human settlements and proximity to paved roads (for details, see Supporting Information, Appendix S2, Table S2.1).

We expected that sex, age and daylight would be the variables conditioning the response of the other variables the most, and therefore, in order to identify which interacting variable predicts bear movements best for each season, we built three different candidate model sets. Each candidate model set included the 2-way interactions of all variables with sex, age and daylight, respectively. Within each candidate model set, we tested all possible combinations of variables and interactions. We selected the model with the lowest Akaike information criterion (AIC) value for each season as the best-fitting model for each candidate set (Burnham & Anderson, 2002; Hinton, van Manen & Chamberlain, 2015). The best-fitting final model was obtained following the same procedure, but testing all possible combinations of variables and their 2-way interactions with age, sex and daylight.

To identify age-, sex- and season-specific differences in the basic movement parameters, we calculated the daily activity rate, speed, tortuosity and core area, and the seasonal and annual home range. We calculated activity rate as the percentage of time steps classified as active for each day (i.e. 24-h period) and averaged the results for each bear and season. We calculated speed by measuring the straight line travelled between consecutive fixes along the day. Tortuosity (i.e. the opposite of linearity) was measured as the mean absolute value of the turning angles obtained in consecutive time steps along the day. These calculations were performed with the 'R' package 'adehabitatLT' (Calenge, 2006) using a standardized number of valid fixes per day; for bears with GPS fix frequency <3 h, we removed alternate records in order to retain 8 valid fixes, evenly distributed along the day. We also excluded from the dataset all days with less than 8 valid fixes or more than 4 h between any pair of consecutive fixes. To obtain daily core areas, we merged the dBBMM 50% UD time step contours at daily intervals (for details, see Supporting Information, Appendix S2, Figure S2.1). We estimated seasonal and annual home ranges by calculating the 95% minimum convex polygon (MCP 95%) using the package 'adehabitatHR' (Calenge, 2006) (for details, see Supporting Information, Appendix S2, Figure S2.2). We compared movement parameters between bear categories and across seasons through one-way analysis of variance and post hoc Tukey tests.

Relationship between movement parameters

To study the relationship between the daily movement parameters and seasonal home ranges, we used several of the basic movement parameters calculated in the previous analyses (i.e. daily activity rate, speed, tortuosity and core areas, and seasonal home range). To investigate the causal effects of activity rates on the seasonal home range, we followed a piecewise structural equation modelling (SEM) approach using the R package 'piecewiseSEM' (Lefcheck, 2015). We fitted the component models of the piecewise SEMs under the assumption that: (1) seasonal home range is influenced by the size of daily core areas of each respective season; (2) daily core areas are influenced by speed and tortuosity; (3) speed and tortuosity are influenced by activity rate. In all component models, we used linear mixed-effects models (LMMs) with a Gaussian distribution. For the first component model (i.e. effects of daily core areas on seasonal home ranges), we included the number of tracking days as a random term. For the other component models, we included as random terms the individual bear ID and the year. Standardized path coefficients were then calculated, and overall fits of the piecewise SEMs were evaluated using Shipley's test of direct separation (Shipley, 2000).

Results

Circannual and circadian movement patterns

Date of year and hour of day had a significant effect on the motion variances of all bear categories (all $P < 0.001$). Circannual movement was characterized by two peaks: one during the mating season, which was especially pronounced in adult males, and one during early hyperphagia, which in the case of sub-adult males was delayed until late hyperphagia (Fig. 1a). Movement was higher during night-time throughout all seasons. Diurnal movement increased in adult bears in Greece during mating and early hyperphagia and in sub-adult bears during late hyperphagia (Fig. 1b).

Factors influencing bear movement

Models including daylight interactions performed better than the ones including age or sex interactions, with the exception of late hyperphagia, when models including sex showed lower AIC values (Table 1). Models including age as the main interacting variable performed better than the ones including sex during emergence, mating and post-mating (Table 1; for details, see Supporting Information, Appendix S3, Table S3.1 and S3.2).

Overall, bear movement was higher during night-time, especially when bears were in less rough terrain, far from forests and close to roads (Fig. 2). During daytime, bear movement increased close to forests except during emergence, while terrain roughness and proximity to roads had less influence on bear movement during most of the seasons. Proximity to human settlements had generally a negative effect on bear movement during both day and night. Bear movement generally decreased with increasing average temperatures, with the exception of late hyperphagia to mating, when bear movement increased during night-time (Fig. 2).

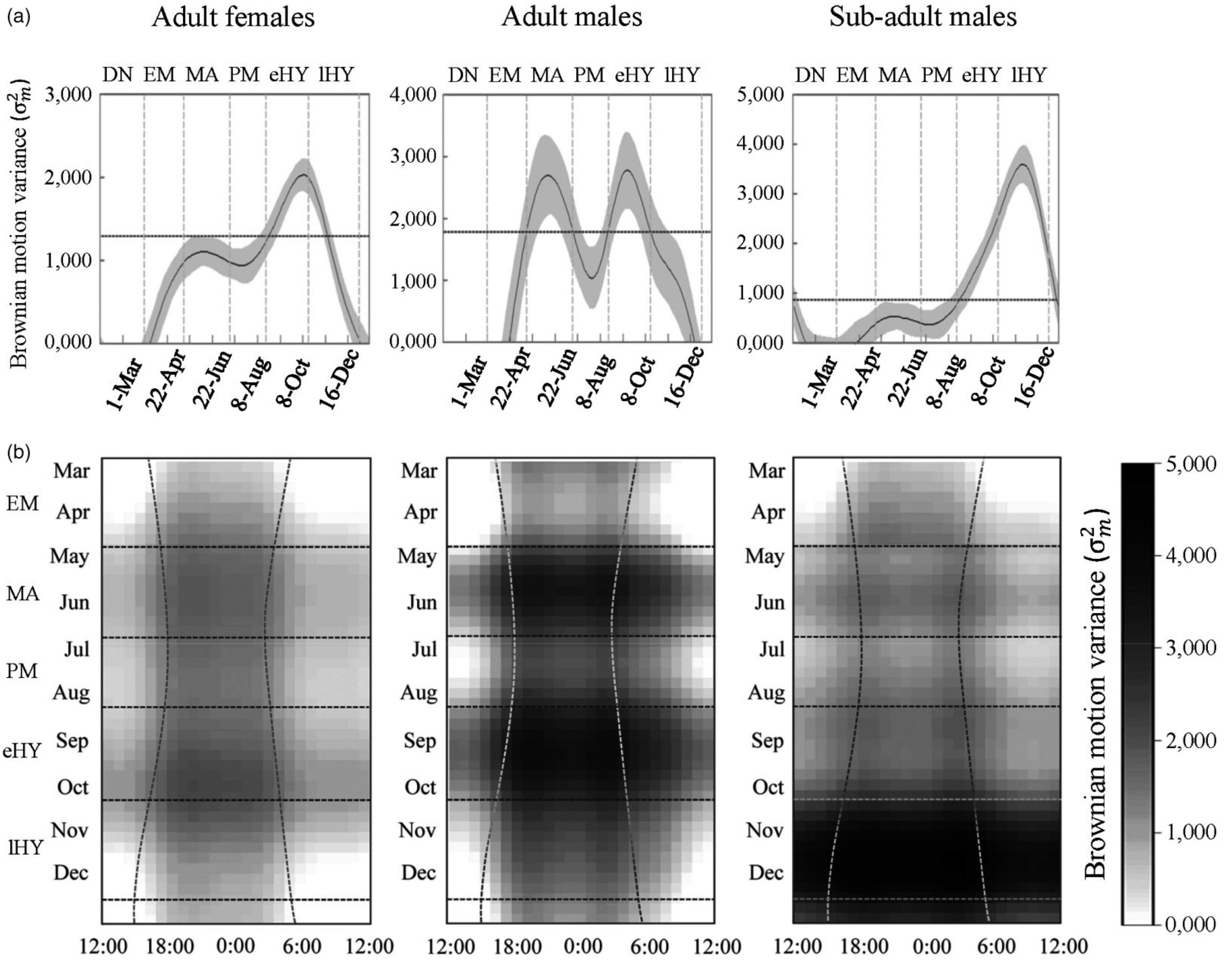

Figure 1 Average Brownian motion variance (σ_m^2) predicted by GAMMs for adult female and male and sub-adult male brown bears in Greece across the year (a) and across the day (x-axis) and year (y-axis) (b). Grey-shaded areas in (a) indicate the 95% confidence intervals, and the horizontal dashed grey lines indicate the average (σ_m^2) throughout the year. Dashed light lines in (b) indicate times of sunset and sunrise throughout the year. The cut-off dates for each biological season [i.e. denning (DN), emergence (EM), mating (MA), post-mating (PM), early hyperphagia (eHY) and late hyperphagia (lHY)] are indicated by vertical dashed lines in (a) and by horizontal dashed lines in (b).

Table 1 AIC and ΔAIC values for the best models within each candidate model set and for the final model (i.e. best-fitting model) predicting bear activity during each ecologically sound season in Greece

	Emergence			Mating			Post-mating			Early hyperphagia			Late hyperphagia		
Model set	d.f.	AIC	ΔAIC	d.f.	AIC	ΔAIC	d.f.	AIC	ΔAIC	d.f.	AIC	ΔAIC	d.f.	AIC	ΔAIC
Final model	20	3559	0	19	11 277	0	20	5479	0	21	5620	0	22	4917	0
Light ×	15	3606	47	15	11 346	68	16	5608	129	16	5731	111	14	5411	494
Age ×	11	3858	299	10	11 930	653	15	5612	133	16	5937	317	14	5572	655
Sex ×	14	3932	373	9	11 953	676	15	5659	180	15	5854	234	14	5277	360

Age-, sex- and season-specific differences in movement parameters

Activity rates were higher for adult than for sub-adult males, while sub-adults had higher activity rates than adult females ($F_{2,\ 1517} = 40.9$, $P < 0.001$; Table 2). Adult females had lower speed ($F_{2,\ 1517} = 289.5$, $P < 0.001$), more linear movements (i.e. less tortuous; $F_{2,\ 1517} = 141.5$, $P < 0.001$), smaller core areas ($F_{2,\ 1517} = 125.8$, $P < 0.001$) and smaller home ranges ($F_{2,\ 16} = 7.5$, $P < 0.01$) than male adults and sub-adults; adult males had the largest daily core areas, moved fastest, and their movements were more linear than that of sub-adults (Table 2; for details, see Supporting Information, Appendix S3, Table S3.3).

Relationship between movement parameters

Piecewise SEMs fitted the dataset well (Fisher's $C = 0.97$, $P = 0.615$), and all component models were significant (for details, see Supporting Information, Appendix S3, Table S3.4). Standardized path coefficients indicated a positive effect of the activity rate on speed ($T = 0.49$) and tortuosity ($T = 0.15$). Speed had in turn a strong positive effect on the daily core area ($T = 0.88$), which in turn had also a positive effect on the seasonal home range ($T = 0.28$) (Fig. 3). Thus, through daily speed and core area size, the activity rate had an overall positive effect on seasonal home range ($T = 0.12$).

Discussion

In the present study, we used telemetry data from brown bears in Greece to study their movement patterns. We found that bears moved less during daytime when ambient temperatures were high and when they were far away from forests and close to settlements, where human activity is expected to be high. During night-time, when human activity and mortality risk are expected to be low, bear movement was higher farther from forested areas, close to roads and in less rough terrain.

Circannual and circadian movement patterns

Circannual bear movement in Greece showed similar patterns to other populations in Europe (Kaczensky *et al.*, 2006; Seryodkin *et al.*, 2013; Ordiz *et al.*, 2017; Penteriani *et al.*, 2017). Bear movement in Greece increased after denning due to the high energetic requirements in a temporarily resource-poor environment (Clevenger, Purroy & Pelton, 1990) and reached a first peak during the mating season, which was more pronounced in males which roam to mate (Dahle & Swenson, 2003b). A second peak in movement occurred during the hyperphagia season, when bears travelled great distances to store enough fat for hibernation and reproduction (Fernández *et al.*, 2012). However, adult bear movement was reduced towards the late hyperphagia, likely as a preparation to hibernation (Karelus *et al.*, 2017), while sub-adult bear movement continued to increase, probably due to a combination of their lack of experience in coping with the spatio-temporal stochasticity in natural forage production (Baruch-Mordo *et al.*, 2014) and the disturbances caused by hunting activities (Maiorano *et al.*, 2015).

However, some notable differences in circannual bear movement in Greece were recorded compared to other northern populations with less human presence and cooler climatic conditions. Bears in Greece denned for approximately two and a half months, equally long as in Spain (Clevenger, Purroy & Pelton, 1990), but considerably shorter than conspecifics in Scandinavia [i.e. they begin a month later and emerge a month earlier (Manchi & Swenson, 2005)]. Although den entry is generally influenced by reproductive status (Friebe, Swenson & Sandegren, 2001), climatic variability (Delgado *et al.*, 2018), latitude and/or food availability (Manchi & Swenson, 2005), and human activity in late autumn or early spring (such as hunting or winter recreational activities) might cause bears to abandon their denning sites (Linnell *et al.*, 2000) and contribute in the shortened denning duration in the human-dominated landscapes of southern Europe. The mating period of brown bears in Greece was similar to that recorded in bears in similar latitudes (Fernandez-Gil, Naves & Delibes, 2006), but earlier than that recorded for brown bears further north (Dahle & Swenson, 2003a; Dahle & Swenson, 2003b), which could be a consequence of the milder climate in these Mediterranean populations; in fact, the period of oestrus and copulation is partly regulated by climatic conditions (Spady, Lindburg & Durrant, 2007). During post-mating, bear movement in Greece decreased significantly, likely due to a combination of high ambient temperatures, high food availability and high human activity related to increased recreational and agricultural activities (Ordiz *et al.*, 2014; Ordiz *et al.*, 2017).

The predominantly nocturnal movement of adult bears in Greece is considered to be a behavioural adaptation to avoid human activity and has been observed in bears across Europe (Kaczensky *et al.*, 2006; Ordiz *et al.*, 2014; Ordiz *et al.*, 2017)

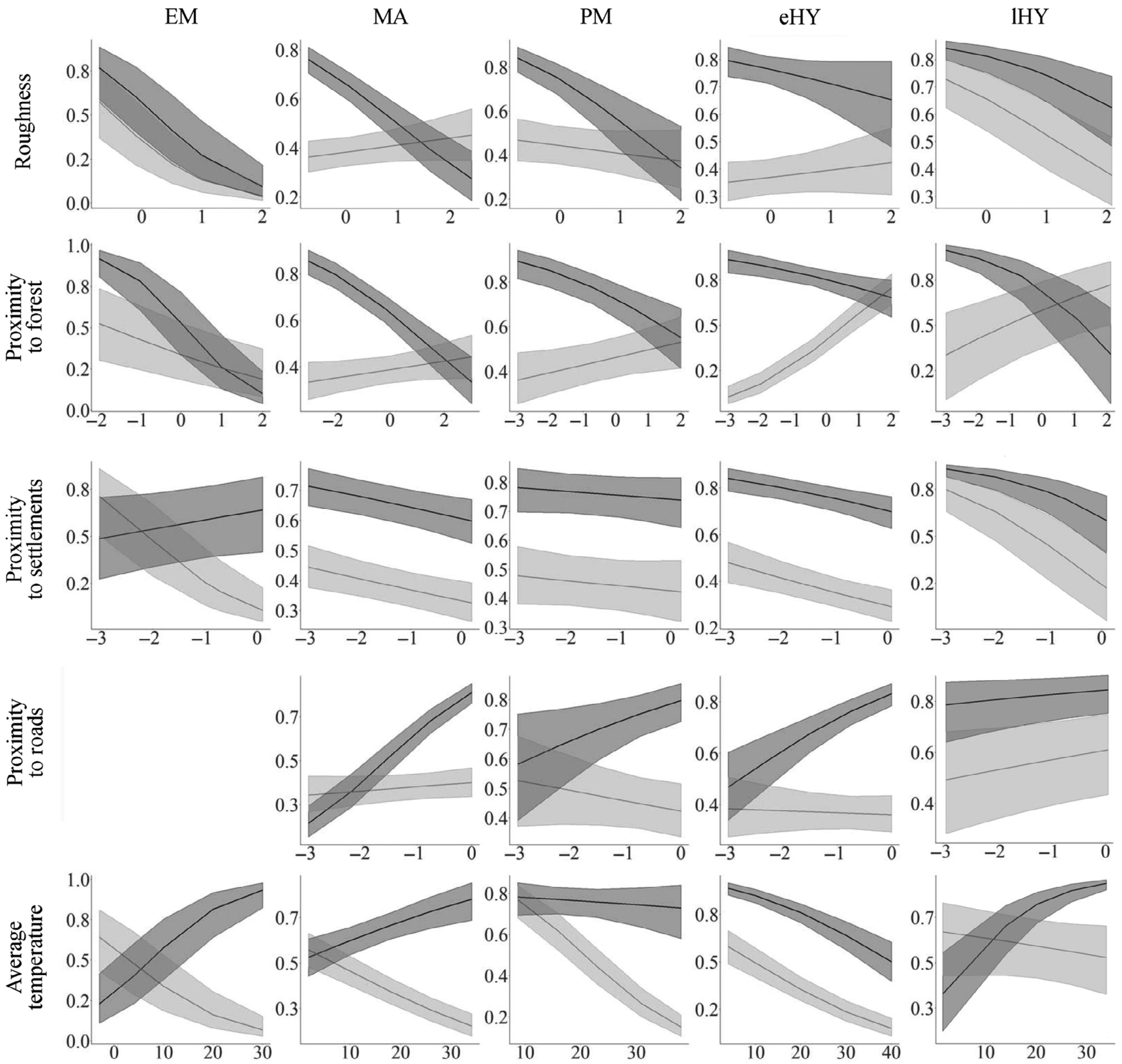

Figure 2 Responses of the most important spatio-temporal variables and their interactions with daylight according to the best-fitting GLMMs predicting bear movement (y-axis) in each season for brown bears in Greece (2003 – 2013). Light grey indicates daytime, and dark grey indicates night-time. X-axes represent km for proximity variables, roughness index for roughness and Celsius degrees for temperature [emergence (EM), mating (MA), post-mating (PM), early hyperphagia (eHY) and late hyperphagia (lHY)].

and in areas of North America with high human activity (Hebblewhite & Merrill, 2008). It was likely also a result of the high ambient temperatures of this Mediterranean landscape, especially in summer, a fact that has been suggested also for other carnivores (Theuerkauf *et al.*, 2007; Hayward & Hayward, 2007). Nevertheless, this predominantly nocturnal movement pattern is interrupted when specific biological functions, such as mating (Fernandez-Gil, Naves & Delibes, 2006) or denning preparation, need to be fulfilled. In contrast, the more diurnal movement patterns of sub-adult bears could have been associated with a higher tolerance towards humans (MacHutchon *et al.*, 1998; Zarzo-Arias *et al.*, 2018) and/or with the efforts to avoid intra-specific competition over food sources (Kaczensky *et al.*, 2006), which may be monopolized by adults at night (Klinka & Reimchen, 2002), when human activity is lower.

Table 2 Descriptive data of GPS-collared bears in Greece (2003–2013), indicating the sample size (i.e. individual bear-year), the average (x) and standard deviation (SD) of the daily activity rates, daily speed, daily tortuosity, daily core area and annual home range (95% MCP) of each age–sex group

	Adult female				Adult male				Sub-adult			
Movement parameter	*N*	x	SD		*N*	x	SD		*N*	x	SD	
Daily activity rate (%)	10	42	25	C	7	59	29	A	5	54	32	B
Daily speed (km/day)	10	3.6	3.1	C	7	10.1	6.0	A	5	4.8	3.8	B
Daily tortuosity (absolute angles)	10	35.2	18.6	C	7	48.9	18.7	B	5	53.7	20.1	A
Daily core area (km^2)	10	0.91	1.16	C	7	2.84	2.39	A	5	1.69	2.53	B
Annual home range (km^2)	9	48.3	28.2	B	5	197.1	69.8	A	5	315.7	255.2	A

Sharing letters indicate no significant differences at $P < 0.05$ between the three bear categories for each movement parameter.

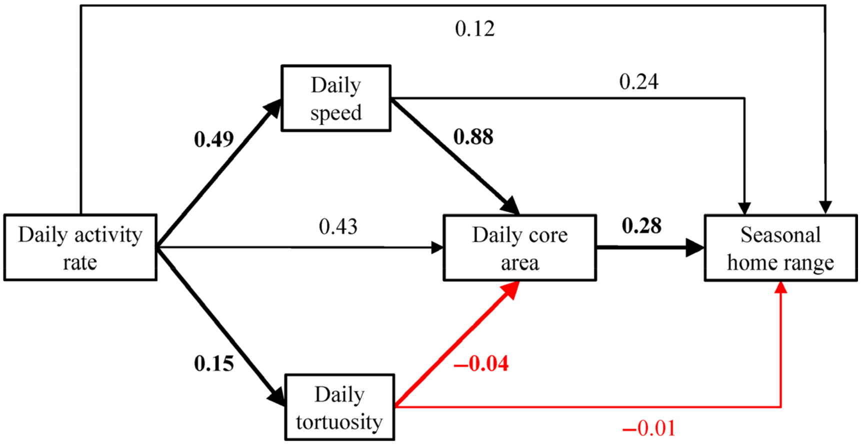

Figure 3 Representation of the causal network used in the piecewise SEM and standardized coefficients for the direct (thick lines) and indirect effects (thin lines). Red line indicates negative effects and black line indicates positive effects. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Factors influencing bear movement

In Greece, daylight appeared to be the most important factor influencing bear movement: bears moved generally more during night-time, although they moved more during daytime when they were close to forests and in rough terrain, especially from mating to early hyperphagia. This movement pattern suggests that such areas were actively used as nutritional and refuge areas (Posillico *et al.*, 2004) during times when human activity is expected to be higher, that is daytime and milder weather seasons. Preference for areas with rough terrain during daytime has been recorded elsewhere in Europe (Martin *et al.*, 2012) and may be associated with better availability of heterogeneous nutritional resources, better denning opportunities and lower human activity (Nellemann *et al.*, 2007). On the other hand, bear movement near settlements and roads was higher during the night than during the day, indicating an active attempt by bears to avoid human activity and mortality risk while using these areas. A similar behaviour has been recorded in several bear populations (Rode, Farley & Robbins, 2006) and various other terrestrial mammals (Tucker *et al.*, 2018). Daylight had also a different effect on bear movement depending on ambient temperatures; when these were high, bears were more active during the night and less active during the day, indicating an attempt to avoid high temperatures, which has been also observed in other large carnivores (Theuerkauf *et al.*, 2003; Rabaiotti & Woodroffe, 2019).

Age-, sex and season-specific differences in movement parameters

Females in Greece had the lowest activity rates, daily speed and tortuosity, and the smallest daily core areas and home ranges, which was likely a result of their effort to seek protection against infanticidal males (Dahle & Swenson, 2003b) and avoid intra-specific competition (Kaczensky *et al.*, 2006), while avoiding at the same time areas with high human activity. Adult males in contrast had the highest activity rates, highest speeds, and largest daily core areas and home ranges, which was likely a result of their need to roam for mating (Lewis & Rachlow, 2011) and their less philopatric behaviour compared to females. The intermediate activity rates of sub-adult males and the high variation in their home ranges were likely a result of their inexperience in utilizing in the best way the available resources (Karelus *et al.*, 2017), higher tolerance of humans (MacHutchon *et al.*, 1998) and an active attempt to avoid intra-specific agonistic interactions (Reimchen, 1998). Large home ranges for sub-adult males have also been recorded in other human-dominated landscapes in Europe [e.g. Serbia (Ćirović *et al.*, 2014), Austria (Kaczensky *et al.*, 2011)]. It should be noted that the high inter-individual variations in average home ranges recorded in our study have been recorded also elsewhere in Europe (Kaczensky *et al.*, 2006), and most likely reflect differences in habitat quality or differences in an individual's ecological condition and perception to risks.

The significant differences in activity rates and other movement parameters between the three bear categories in Greece should be considered a result of the varying effects of experience, reproductive status, energetic requirements, habitat selection, population density and tolerance to human disturbances (McLellan & Hovey, 2001; Dahle & Swenson, 2003a; Ordiz *et al.*, 2014).

Relationship between movement parameters

The causal network linking activity rates and seasonal home range provides an explanation for the smaller home range of bears in southern latitudes with high ambient temperatures and predominantly human-dominated landscapes (Kanellopoulos *et al.*, 2006; Krofel, Filacorda & Jerina, 2010) compared to more northern, colder and wilder parts of their distribution (Dahle & Swenson, 2003a; Dahle & Swenson, 2003b). Although the effects of temperature and human activity in human-dominated landscapes may be counteracted by the scattered distribution of natural resources in space and time, which in turn may force animals to move more frequently (e.g. Morellet *et al.*, 2013), in Greece, movement barriers or the concentration of anthropogenic-related resources (i.e. increased food provisioning) could have a stronger effect, impeding or discouraging movements. This is not uncommon for wildlife in areas with a strong human footprint, where movements may be reduced to a half of their extent compared to wilder areas (Tucker *et al.*, 2018). Furthermore, the negative effects of high temperatures on brown bear movement in Greece should be considered in the actual context of climate change. The effects of climate change are expected to be high in Greece (Giannakopoulos *et al.*, 2009), which could exacerbate the negative effects of human activity and, ultimately, result in home ranges that are too small to meet the biological requirements of the species.

Brown bears in Greece have shown high levels of behavioural plasticity, adapting their movements in space and time to a rapidly changing and ecologically challenging environment. As in the case of brown bears in Scandinavia and Turkey (Kindberg *et al.*, 2011; Cozzi *et al.*, 2016), we suggest that this behavioural trait has been one of the driving forces behind the recent population recovery of the species in the country.

In regard to the management and conservation efforts for bear habitat in Greece, we suggest that these should focus on the linkages between habitat patches, so that bear movement in Greece is not hindered by barriers and bears can maintain home ranges large enough to meet their biological requirements and avoid risks. Furthermore, human–bear coexistence in anthropogenic landscapes often requires wise management planning in space or time (Kaczensky *et al.*, 2006) in order to reduce human–bear conflicts. Bear management in Greece should try to take this premise into account and keep human disturbance at a minimum in refuge and foraging areas (i.e. rough terrain and forested areas). Acknowledging that global warming could push these refuge areas to higher elevations, the increased accessibility of humans to mountain areas (Godde, Price & Zimmermann, 2000), partly a consequence of milder winters, needs to be managed in order to guarantee that bears can cope with it. As it is almost impossible however to restrict human access into bear habitat or closer to human settlements (Penteriani *et al.*, 2019), a separation of humans and bears in time in Greece (i.e. regulating human activities during the night and crepuscular hours) should reduce negative human–bear interactions and increase survival chances.

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Supporting Information

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

Appendix S1. Information about the study area and animals.
Appendix S2. Details on data treatment and analyses.
Appendix S3. Details on results.