



Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore

Ophélie Couriot¹ · A. J. Mark Hewison¹ · Sonia Saïd² · Francesca Cagnacci³ · Simon Chamaillé-Jammes⁴ · John D. C. Linnell⁵ · Atle Mysterud⁶ · Wibke Peters⁷ · Ferdinando Urbano⁸ · Marco Heurich^{9,10} · Petter Kjellander¹¹ · Sandro Nicoloso¹² · Anne Berger¹³ · Pavel Sustr^{14,15} · Max Kroeschel^{10,16} · Leif Soennichsen^{17,18} · Robin Sandfort¹⁹ · Benedikt Gehr²⁰ · Nicolas Morellet¹

Received: 5 April 2017 / Accepted: 27 March 2018 / Published online: 2 April 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Much research on large herbivore movement has focused on the annual scale to distinguish between resident and migratory tactics, commonly assuming that individuals are sedentary at the within-season scale. However, apparently sedentary animals may occupy a number of sub-seasonal functional home ranges (sfHR), particularly when the environment is spatially heterogeneous and/or temporally unpredictable. The roe deer (*Capreolus capreolus*) experiences sharply contrasting environmental conditions due to its widespread distribution, but appears markedly sedentary over much of its range. Using GPS monitoring from 15 populations across Europe, we evaluated the propensity of this large herbivore to be truly sedentary at the seasonal scale in relation to variation in environmental conditions. We studied movement using net square displacement to identify the possible use of sfHR. We expected that roe deer should be less sedentary within seasons in heterogeneous and unpredictable environments, while migratory individuals should be seasonally more sedentary than residents. Our analyses revealed that, across the 15 populations, all individuals adopted a multi-range tactic, occupying between two and nine sfHR during a given season. In addition, we showed that (i) the number of sfHR was only marginally influenced by variation in resource distribution, but decreased with increasing sfHR size; and (ii) the distance between sfHR increased with increasing heterogeneity and predictability in resource distribution, as well as with increasing sfHR size. We suggest that the multi-range tactic is likely widespread among large herbivores, allowing animals to track spatio-temporal variation in resource distribution and, thereby, to cope with changes in their local environment.

Keywords Migration · Residency · Sub-seasonal functional home range · Plasticity · Roe deer

Introduction

Movement is a fundamental characteristic of life which influences the survival and reproduction of organisms and, more generally, individual fitness and population dynamics (Turchin 1991; Revilla and Wiegand 2008). Following the Marginal Value Theorem (Charnov 1976), while foraging,

an individual moves within a patch (sensu Wiens 1976), searching intensively for food, before leaving to search more widely for a new patch when the energetic benefit of the first patch has decreased below the average value of the alternative patches (Charnov 1976; Van Moorter et al. 2009). In slowly regenerating environments, animals should engage in thorough exploration to locate suitable patches. However, in rapidly regenerating environments, individuals are assumed to memorise the value and location of a given patch (Bracis et al. 2015; Riotte-Lambert et al. 2015), returning to previously visited patches periodically. This process leads to the emergence of a stable home range to which individuals restrict their movements to maximise resource acquisition (Brown and Orians 1970; Riotte-Lambert et al. 2015). Therefore, individuals of many species appear to be sedentary at this spatio-temporal scale, occupying a stable home

Communicated by Ilpo Kojola.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-018-4131-5>) contains supplementary material, which is available to authorized users.

✉ Ophélie Couriot
o.couriot@gmail.com

Extended author information available on the last page of the article

range over a long time span (season and year). Site fidelity is widespread in the animal kingdom and has fundamental consequences for ecological processes (Börger et al. 2008).

An individual's lifetime track is an aggregation of successive elementary units with potentially different functionality (Baguette et al. 2014). Indeed, as stated by Van Moorter et al. (2016) "animals do not move for the sake of changing their geographic location, but rather for changing environmental conditions associated with changes in location". In general, an individual decides to move to satisfy its requirements in terms of refuge and resources (Nathan et al. 2008) which encompass changes in environmental space (Van Moorter et al. 2013). For example, since favourable sites for feeding or taking refuge do not necessarily occur at the same location, and since conditions vary in space and time, animals have to move to cope with spatio-temporal heterogeneity in their environment (Pyke 1984; Mueller and Fagan 2008; Chapman et al. 2014). As a result of variation in conditions over time, an animal must shift from one suitable patch to another to fulfil its requirements, in which case it cannot be considered truly sedentary, even at the seasonal scale (Chapin et al. 1980; Barraquand and Benhamou 2008). Indeed, animals may use several spatio-temporally distinct suitable units, particularly in spatially heterogeneous and/or temporally unpredictable environments. While there has been considerable focus in recent years on movements associated with seasonal migration between seasonally distinct home ranges (Cagnacci et al. 2011, 2015; Peters et al. 2017), there has been relatively little work on finer scale movements at the within-season scale. The use of sub-seasonal functional home ranges (sfHR) has previously been described in two African herbivores, the sable antelope (*Hippotragus niger*) and the African savanna buffalo (*Syncerus caffer brachyceros*) (Owen-Smith et al. 2010; Cornélis et al. 2011; Benhamou 2014). However, no study has yet attempted to link the propensity of individuals to adopt this multi-range tactic with spatial and temporal variation in the prevailing environmental conditions.

Here, we used the EURODEER database (<http://www.eurodeer.org>, see "Materials and methods") to analyse space use of roe deer (*Capreolus capreolus*) across widely contrasting environments, from the southern part of their geographic range in Italy to the northern part of their range, in Scandinavia. We focused on the roe deer as it is Europe's most widespread large wild herbivore and is considered highly sedentary over the majority of its range (Hewison et al. 1998). However, this species also exhibits a considerable degree of behavioural plasticity (Jepsen and Topping 2004), and is described as partially migratory in more extreme environments (Cagnacci et al. 2011). Hence, we first analysed whether roe deer are truly sedentary within a given season, or whether they adopt a movement tactic based on the use of a series of sfHR. Second, we hypothesised

that the propensity of an animal to adopt this multi-range tactic should depend on spatio-temporal variations in environmental conditions. More specifically, we predicted that individuals should be less sedentary in spatially heterogeneous compared to homogeneous environments (Mueller and Fagan 2008; Mueller et al. 2011). Analogous to the nomadic movement tactic (Mueller and Fagan 2008), we also expected individuals to be less sedentary in temporally unpredictable environments, or at least in environments where resources vary more markedly over time at the within-season scale, compared to more predictable environments. Finally, we expected that, within a given seasonal range, migratory animals would be more sedentary than residents since they migrate during spring and fall so that they are able to adjust their habitat use to seasonal variations in food resource abundance and/or quality at this scale (Fryxell and Sinclair 1988).

Materials and methods

Study areas and GPS data

This study was based on the database assembled by the EURODEER consortium, a data sharing project to investigate the movement ecology of European deer along environmental gradients (<http://eurodeer.org>, accessed on April 2016). We analysed data on 251 adult roe deer (286 individual-years) from 15 study sites (see Table 1) encompassing widely contrasting environmental conditions (latitude varied from 38.2°N to 60.7°N; longitude varied from 0.9°E to 23.5°E; Fig. 1). Roe deer were captured from 2003 to 2014 using drive nets, net traps or box traps depending on study site. All capture and marking procedures were done in accordance with local and European animal welfare laws. Deer were equipped with GPS collars programmed to obtain a GPS fix with intervals ranging from 10 min to 12 h. To standardise the data for inter-population comparisons, for each individual, we restricted monitoring to the period from the 15th of February to the 15th of November, and retained the two locations per day that were closest to noon and midnight.

Discrimination of individual movement tactics

Of the recently published emerging tools for determining movement tactic (Gurarie et al. 2017; Spitz et al. 2017), we first used a common method proposed by Börger and Fryxell (2012), which has been proven useful for large mammals (Bunnfeld et al. 2011; Bischof et al. 2012), based on the net squared displacement (NSD), i.e. the Euclidean distance between the starting location and all subsequent locations of an individual over time (Turchin 1998), to determine each

Table 1 Number of males, females, migratory individuals, and residents per study site

Study site id	Study site name	Migrants	Residents	Females	Males
a	Aspromonte—Italy	4	2	4	2
b	Aurignac—France	20	86	66	40
c	Baden-Wurttemberg—Germany	5	19	22	2
d	Bavarian Forest National Park—Germany	28	35	36	27
e	Šumava National Park—Czech republic	0	2	1	1
f	Bernese Oberland—Switzerland	9	15	19	5
g	Bialowieza National Park—Poland	2	5	7	0
h	Brandenburg—Germany	2	0	2	0
i	Grimso—Sweden	1	0	0	1
j	Koberg—Sweden	5	9	10	4
k	Leoben—Austria	4	4	5	3
l	Matese—Italy	0	3	3	0
m	Monte Bondone—Italy	4	4	4	4
n	Rendena Giudicarie—Italy	6	3	6	3
o	Østafjells west—Norway	3	6	5	4
	Total	93	193	190	96

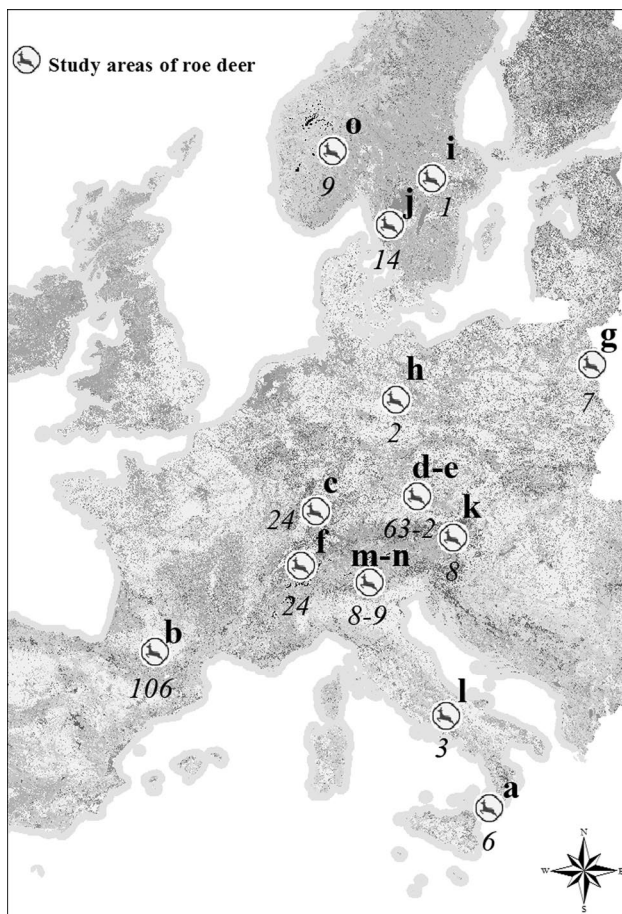


Fig. 1 Location of study sites where roe deer were monitored using GPS collars. Letters correspond to the ‘study site id’ in Table 1, with the corresponding number of individuals in italics

individual’s annual movement tactic: migration, residency or dispersal. We considered two models of range residency, one with a constant NSD (the mean), and one with a linear increase of NSD before reaching an asymptote; we considered one model of migration including approximate dates of departure and return between seasonal ranges, and a model of dispersal with an approximate date of departure (see Bunnefeld et al. 2011 and Börger and Fryxell 2012 for more details on these models). To identify which of these models best described the movement behaviour of a given individual, we used the system of non-linear mixed models proposed by Börger and Fryxell (2012) which links theoretical expectations to movement data. For model selection, as recommended by Börger and Fryxell (2012), we retained the model with the largest concordance correlation (CC), expressing the goodness of fit for each model (Huang et al. 2009). Because the assigned movement tactic using this method did not always closely fit the data, we also visually examined the NSD trajectories to determine each individual’s annual movement tactic by eye (Bischof et al. 2012). We based our visual classification on the patterns of NSD typically observed for migratory individuals, residents and dispersers, following Börger and Fryxell (2012). That is, we assumed that the individual was resident when the NSD was relatively constant, or initially increased linearly before rapidly reaching an asymptote. We assumed that the individual was migratory when the NSD was constant before increasing rapidly during spring to reach a plateau during summer, then decreased during fall, returning to its initial value. Finally, we assumed that the individual had dispersed when the NSD was constant before increasing rapidly to reach a plateau with no further increase or decrease. We then verified that individuals which were classified as dispersers

did not return to their point of departure during subsequent monitoring, after the 15th of November. If they did (53 of 65 animals originally classified as dispersers), these individuals were considered as migratory. We excluded the remaining dispersers ($N=12$) from subsequent analyses as movement patterns during dispersal are governed by different ultimate causes than those involved in range residency or migration (Bowler and Benton 2005; Chapman et al. 2014). After visual reclassification, our data set included 193 residents and 93 migratory individuals. Note that subsequent analyses based on this visual classification of individual movement tactics generated results that were similar to those based on the classification using Borger and Fryxell's (2012) method (not shown).

Subsequently, for each migratory individual, we segmented the NSD using Lavielle's method (1999), which detects change points in a time series, to identify the dates of departure and return from, and to, the winter range (if any) and to define individual-based seasonal ranges. Dates of departure from the winter range ranged from the 6th of March to the 3rd of August (median = 4th of May, $sd=32$ days), while return ranged from the 7th of May to the 28th of October (median = 10th of September, $sd=42$ days). We then used the median departure and return dates across all migratory individuals to establish equivalent seasonal phases for resident individuals. As a result, we subsequently analysed movement behaviour of all deer during the winter period (prior to departure) and the summer period (after departure and prior to return), excluding the 3 days prior to and following departure and return to avoid the transience phase. We did not analyse data from the post-return period, (the second winter), since monitoring periods were too short to characterise individual movement during this period.

Detecting sub-seasonal functional home ranges

We then tested the assumption that roe deer were truly sedentary within the above-defined seasonal periods or, whether their seasonal ranges were composed of several sub-seasonal functional home ranges (sfHR, Benhamou 2014). To do so, we segmented each individual's movement path (i.e. the temporal sequence of locations) for each seasonal period using Lavielle's (1999) method on the mean NSD to identify fine-scale stationary states. Following several studies which have examined variation of weekly home ranges in response to variation in resource distribution (Rivrud et al. 2010; Van Beest et al. 2011; Morellet et al. 2013), we considered 14 locations (i.e. 7 days) as the minimum number required to describe a stationary state. Because this choice of a minimum time span is somewhat arbitrary, we repeated the segmentation approach twice using minimum values of 5 and of 9 days (i.e. 7 ± 2 days) to assess the sensitivity of our results to the length of the temporal window. Finally, we

retained the most parsimonious number of segments comprising each seasonal range for each individual (Figs. 2, 3). We again repeated this step when considering 5 and 9 days as the minimum temporal windows.

We generated a non-linear mixed model describing the use of more than one sfHR within a given season. This model was based on the mean NSD per stationary state (i.e. the number of segments defined by Lavielle's method) for each seasonal period (Supplementary materials, Appendix 1, Eq. A1). To determine whether individuals were truly sedentary, we compared this model with the two models of range residency developed by Börger and Fryxell (2012) used above, adapted for each seasonal period (Supplementary materials, Appendix 1, Eqs. A2, A3), and retained the model with the largest CC (See Supplementary materials, Appendix 1, Table A1).

Describing site-specific environmental conditions

To explore the influence of environmental conditions on the propensity of roe deer to use a number of sfHR within a given season, we described forage resources at each site in terms of spatial heterogeneity and temporal predictability for both the winter and summer periods. To identify the spatial limits of each site, we used the 100% minimum convex polygon of the locations of all GPS monitored individuals at that site to which we added a buffer of 1 kilometre.

To quantify broad-scale site-specific heterogeneity in resource distribution, we used the normalised difference vegetation index (NDVI). NDVI is widely used in ecological research and management as a proxy for biomass (Kerr and Ostrovsky 2003; Pettorelli et al. 2011) and forage quality available for ungulates (Hamel et al. 2009; Borowik et al. 2013; Lendrum et al. 2014; Garrouette et al. 2016) and particularly for roe deer (Morellet et al. 2013; Peters et al. 2017). NDVI was used because of its simplicity, consistent coverage of all study areas, high temporal resolution and demonstrated utility in a variety of ecosystems. Given the linear relationship between NDVI and biomass, a given variation in NDVI should index a similar relative reduction in forage biomass across study sites. Hence, it provides a useful and integrative measure of variation in primary productivity which we assume to be suitable for our purpose of comparing roe deer populations inhabiting widely contrasting environmental conditions.

We obtained weekly values for the NDVI (pixel size = ca. 250 m \times 250 m) from the University of Natural Resources and Life Sciences, Vienna (BOKU) using near real-time filtered products (Whittaker smoother, (Vuolo et al. 2012; Klisch and Atzberger 2016)) of the NDVI time series generated by the NASA Moderate Resolution Imaging Spectroradiometer (MODIS). We used the REFID values, supplied by BOKU, which are the most stable extrapolated values of

Fig. 2 Example of the segmentation approach using Lavielle’s method (1999) on the movement trajectory of a migratory individual (individual 1367 monitored in 2008) during the winter and the summer seasons (top) and the corresponding sub-seasonal functional home ranges (sfHR) (bottom). The X-axis indicates the time in months and the Y-axis shows the net squared displacement (NSD). Vertical lines correspond to cut-off points defining the sequential sfHR

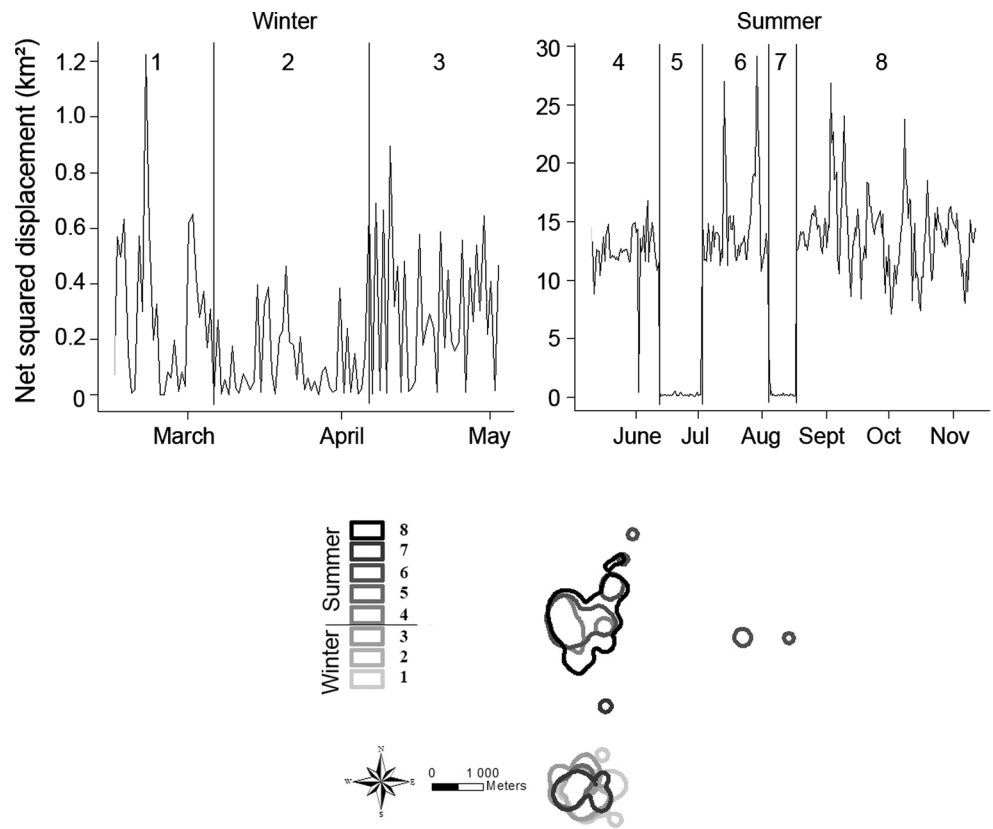
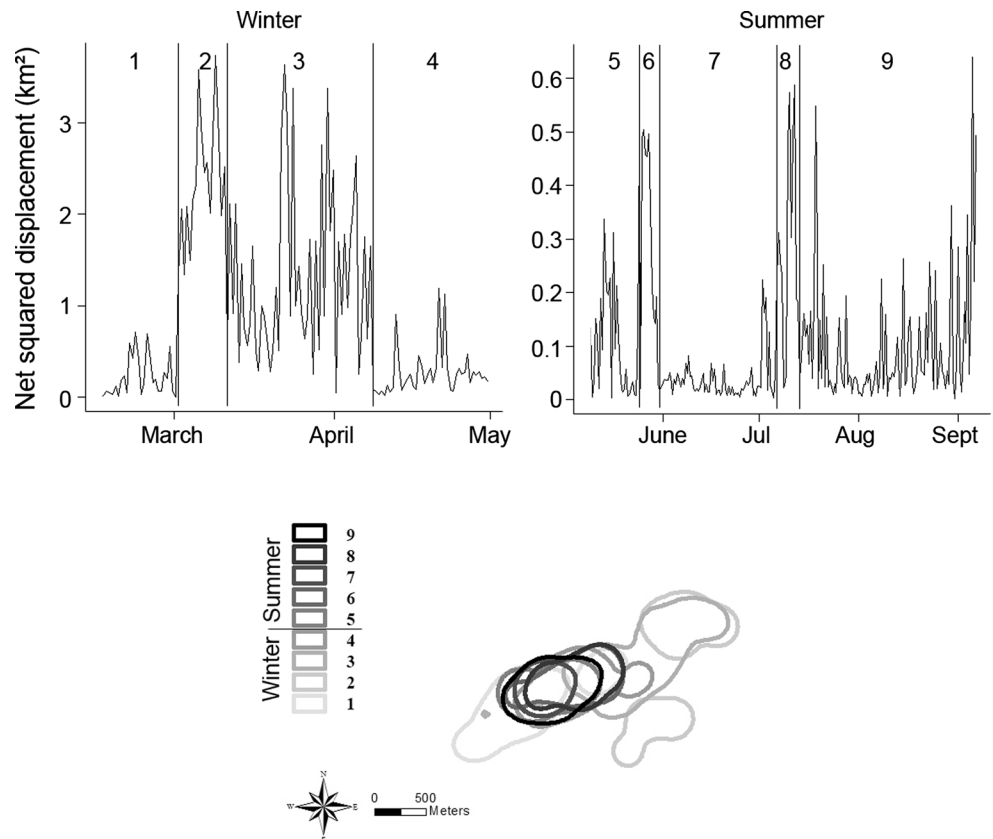


Fig. 3 Example of the segmentation approach using Lavielle’s Method (1999) on the movement trajectory of a resident individual (individual 2296 monitored in 2013), during the winter and the summer seasons (top) and the corresponding sub-seasonal functional home ranges (sfHR) (bottom). The X-axis indicates the time in months and the Y-axis shows the net squared displacement (NSD). Vertical lines correspond to cut-off points defining the sequential sfHR



NDVI (<http://ivfl-info.boku.ac.at/index.php/eo-data-processing/real-time-modis-data-eu-only> for more details).

To describe spatial heterogeneity in resource distribution, we measured spatial heterogeneity of the NDVI at the study site level using the standard deviation of weekly values of the NDVI over all pixels of each study site (Coops et al. 1998; Coops and Culvenor 2000). Then, we averaged these values across weeks for each period to obtain a proxy of spatial heterogeneity per seasonal period, defined above, and per year (from 2003 to 2014) for each study site. Spatial heterogeneity in NDVI ranged from 0.03 (low heterogeneity) to 0.23 (high heterogeneity).

To index temporal predictability in resource distribution, we calculated temporal constancy of the NDVI values across years (i.e. from 2003 to 2014) for each period at a given site following the approach proposed by Colwell (1974). Constancy is a component of temporal predictability (Colwell 1974) that ranges from 0 (no temporal predictability or high temporal variability) to 1 (perfect temporal predictability or high temporal stability). We calculated a value of temporal constancy for each period at each study site across weeks and years (using weekly average values of NDVI across all pixels of a given study site). For this, we built a matrix with NDVI values sorted into 10 equal 0.1 interval classes between 0 and 1 in rows, as indicated by English et al. (2012), and the number of the weeks in columns (irrespective of the year). We counted the number of years for which we observed each class of NDVI for each week, and then we calculated constancy as follows:

$$\text{Constancy} = 1 + \frac{\sum \frac{\sum \text{NDVI}_{ij}}{\sum \sum \text{NDVI}_{ij}} \log\left(\frac{\sum \text{NDVI}_{ij}}{\sum \sum \text{NDVI}_{ij}}\right)}{\log(s)}$$

where i represents the NDVI class, j is the week of the NDVI measure, irrespective of the year, and s is the number of NDVI classes.

As resource heterogeneity was negatively correlated with resource predictability during both seasonal periods ($r = -0.50$, $p < 0.001$ during winter, $r = -0.88$, $p < 0.001$ during summer), we used the residuals of the linear regression between resource predictability and resource heterogeneity to index temporal predictability in resource distribution. Hence, positive values indicate that temporal predictability is higher than expected for a given level of resource heterogeneity.

Statistical analyses

To analyse the link between space use behaviour of roe deer with spatial heterogeneity and temporal predictability in resource distribution, we exploited the extremely marked variation among study sites in environmental conditions,

performing the analyses at the population level. We were unable to analyse within-population (i.e. individual level) variation in these relationships due to the difficulty in measuring the distribution of resources within each study site at a sufficiently fine scale. To describe space use behaviour, we used two individual-based metrics. First, we calculated the number of sfHR used by each individual during each period to describe the degree to which an individual was truly sedentary within a given seasonal range. Second, we calculated the median distance between the centres of all pairs of sfHR for each individual and each period to index the degree of spatial separation among functional ranges (sfHR distance). We log-transformed this quantity to achieve normality.

How many sub-seasonal functional home ranges?

We used generalised linear mixed-effects models (glmm), with a Poisson distribution and a log-link function, to analyse variation in the number of sfHR within an individual's seasonal range (wintering or breeding period) in relation to annual movement tactic (resident vs. migratory), sex (male vs. female, because males are seasonally territorial in this species, Vanpé et al., 2009) and two continuous descriptors of site-specific resource distribution: spatial heterogeneity and temporal predictability. We included the individual's period-specific log-transformed median sfHR size as an additive factor to control for variation in absolute resource availability between individuals (Morellet et al. 2013). Thus, the most complex model contained two three-way interactions among movement tactic, sex and resource heterogeneity and among movement tactic, sex and resource predictability, plus the logarithm of the median sfHR size as a fixed effect, and the study site as a random effect to control for repeated measures (individuals) per population. As the number of sfHR occupied by an individual ranged from 2 to 9, we subtracted 2 from the total number of sfHR per individual per season to conform to a Poisson distribution (Haight 1967). The number of sfHR then ranged from 0 to 7. We estimated sfHR size using fixed-kernel methods considering (i) an ad hoc approach to select the optimal smoothing parameter h for each sfHR estimate and (ii) a constant h set to the overall median of the smoothing parameters estimated by the ad hoc approach for each individual sfHR estimate. Finally, sfHR size was estimated at both 90 and 50% isopleths.

Spatial separation among sub-seasonal functional home ranges

We used linear mixed-effects models (lme) to investigate variation in log-transformed inter-sfHR distance, including period, movement tactic, sex and resource heterogeneity and resource predictability for each study site. We built the

equivalent set of models described above for analysing variation in inter-sfHR distance.

For model selection, we used Akaike's information criterion (AIC, Burnham and Anderson 2002) and the number of parameters to select the most parsimonious model that best described the data. All analyses were performed in R version 3.1.2 (R Development Core Team 2014) using *glmer* and *lmer* functions in the *lme4* library.

Results

Our overall results were robust with respect to the choice of method to estimate sfHR size, the isopleth used (see Supplementary materials, Appendix 1, Figs. A7–A15), and the minimum number of days required to describe a sfHR (see Supplementary materials, Appendix 1, Figs. A1–A6). Thus, in the following, we only present results using the 90% fixed-kernel method based on a constant h and 7 days as the minimum temporal window for a sfHR.

Roe deer use sub-seasonal functional home ranges: the multi-range tactic

All individuals occupied more than one sfHR during a given season. Indeed, the model based on the occupation of more than one sfHR received more support than the two residency models (the CC value was highest for the multi-range model in all 572 cases, corresponding to 286 individuals for the two periods, Supplementary materials, Appendix 1, Table A1). Individuals occupied a sfHR for at least 7 days (by definition, see “Materials and methods”), and up to 186 days during the wintering period (median = 10 days), and for at least 7 days, and up to 223 days, during the breeding period (median = 24 days).

How many sub-seasonal functional home ranges?

The most parsimonious model describing variation in the number of sfHR during the winter period included the two-way interaction between resource predictability and movement tactic and the log-transformed sfHR size ($\Delta\text{AIC} = 0.0$, AIC weight = 0.319, $df = 6$) (Supplementary materials, Appendix 1, Tables A2, A4). During the winter period, the results were partially in accordance with our expectations. First, in accordance with our second prediction, resident individuals occupied 1.5 fewer sfHR in the most predictable study site compared to the most unpredictable one. But contrary to this prediction, migrants tended to occupy one more sfHR in the most predictable study site compared to the most unpredictable one. However, in accordance with our third prediction, except in the most predictable study site where residents and migrants occupied the same number

of sfHR, a resident individual used more sfHR on average than a migrant individual (Fig. 4a). Second, the number of sfHR that individuals used decreased as the median size of the sfHR they occupied increased. Indeed, an individual that occupied a large (sfHR size = 410 ha) sfHR had 4 fewer sfHR than an individual that occupied a small (sfHR size = 22 ha) sfHR (Fig. 4b).

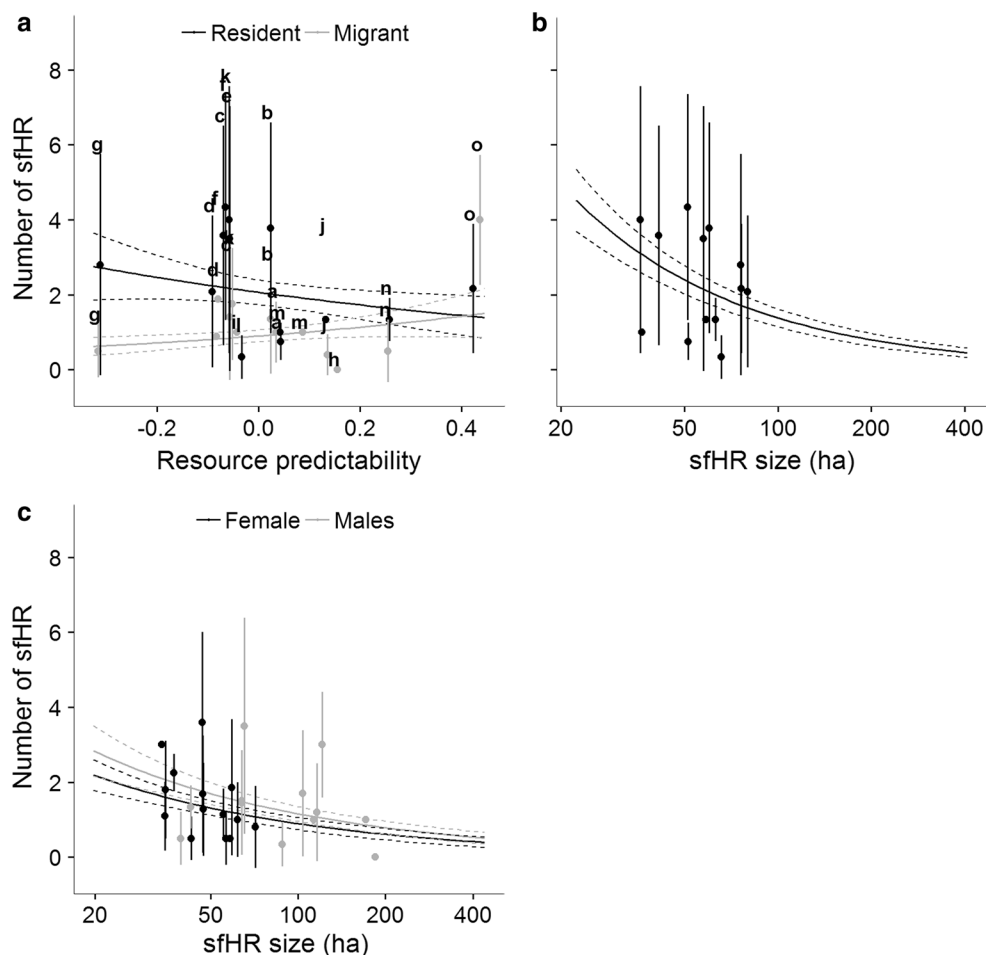
The most parsimonious model describing variation in the number of sfHR during the summer period included sex and the log-transformed sfHR size ($\Delta\text{AIC} = 0.0$, AIC weight = 0.167, $df = 4$) (Supplementary materials, Appendix 1, Tables A2, A4). During the summer period, the difference in the number of sfHR occupied by males and females was low. Indeed, males used, on average, 0.4 sfHR more than females (Fig. 4c). Finally, as above, the number of sfHR that individuals used decreased as the median size of the sfHR they occupied increased. Indeed, an individual that occupied a large (sfHR size = 450 ha) sfHR had 2 sfHR less than an individual that occupied a small (sfHR size = 20 ha) sfHR (Fig. 4c).

Spatial separation among sub-seasonal functional home ranges

The most parsimonious model describing variation in the log-transformed distance among sfHR during the wintering period included the 2 two-way interactions between resource heterogeneity and movement tactic and between resource heterogeneity and sex, with the additive effect of the log-transformed sfHR size ($\Delta\text{AIC} = 0.6$, AIC weight = 0.274, $df = 9$) (Supplementary materials, Appendix 1, Tables A3, A4). First, in accordance with our first prediction, spatial separation between pairs of sfHR during the wintering period increased with increasing resource heterogeneity, except among resident females (Fig. 5a, b). Indeed, when resource heterogeneity was high (resource heterogeneity = 0.26), the distance among sfHR of an individual was, on average, 700 meters (365 meters for resident males and 1050 meters for migratory males), while for an individual living in the least heterogeneous study site (resource heterogeneity = 0.08) it was, on average, 300 meters. However, for resident females, this distance was 350 meters lower when resource heterogeneity was high. Finally, spatial separation among sfHR during the winter period was 3980 meters for an individual which occupied the largest sfHR (median sfHR size = 410 ha) compared to 80 meters for an individual that occupied the smallest sfHR (median sfHR size = 22 ha) (Fig. 5c).

The best model describing variation in the log-transformed inter-sfHR distance during the summer period included resource predictability in addition to sex and the median log-transformed sfHR size ($\Delta\text{AIC} = 1.86$, AIC weight = 0.143, $df = 6$) (Supplementary materials,

Fig. 4 Graphical representation of the best models describing variation in the number of sub-seasonal home ranges (sfHR) during the winter season, as a function of the two-way interaction between resource predictability and movement tactic (a) and the sfHR size (b); and during the summer season as a function of sex and the sfHR size (c). To better visualise the raw data, we plotted the mean number of sfHR for each study site. Dotted lines represent the 95% confidence intervals resulting from the model predictions, error bars represent the standard deviation in number of sfHR, and the letters correspond to the 'study site id' in Table 1. We fixed movement tactic as resident, resource predictability and the sfHR size at their mean when not represented in the figures



Appendix 1, Tables A3, A4). First, contrary to our second prediction, the distance between sfHR was 384 meters in the most predictable study site compared to 200 meters in the most unpredictable one (Fig. 6a). Second, the distance between sfHR was 308 meters for females and 177 meters for males (Fig. 6b). Finally, the spatial separation among sfHR during the summer period was 4450 meters for an individual inhabiting the largest sfHR (median sfHR size = 450 ha) compared to 76 meters for an individual inhabiting the smallest sfHR (median sfHR size = 20 ha) (Fig. 6c).

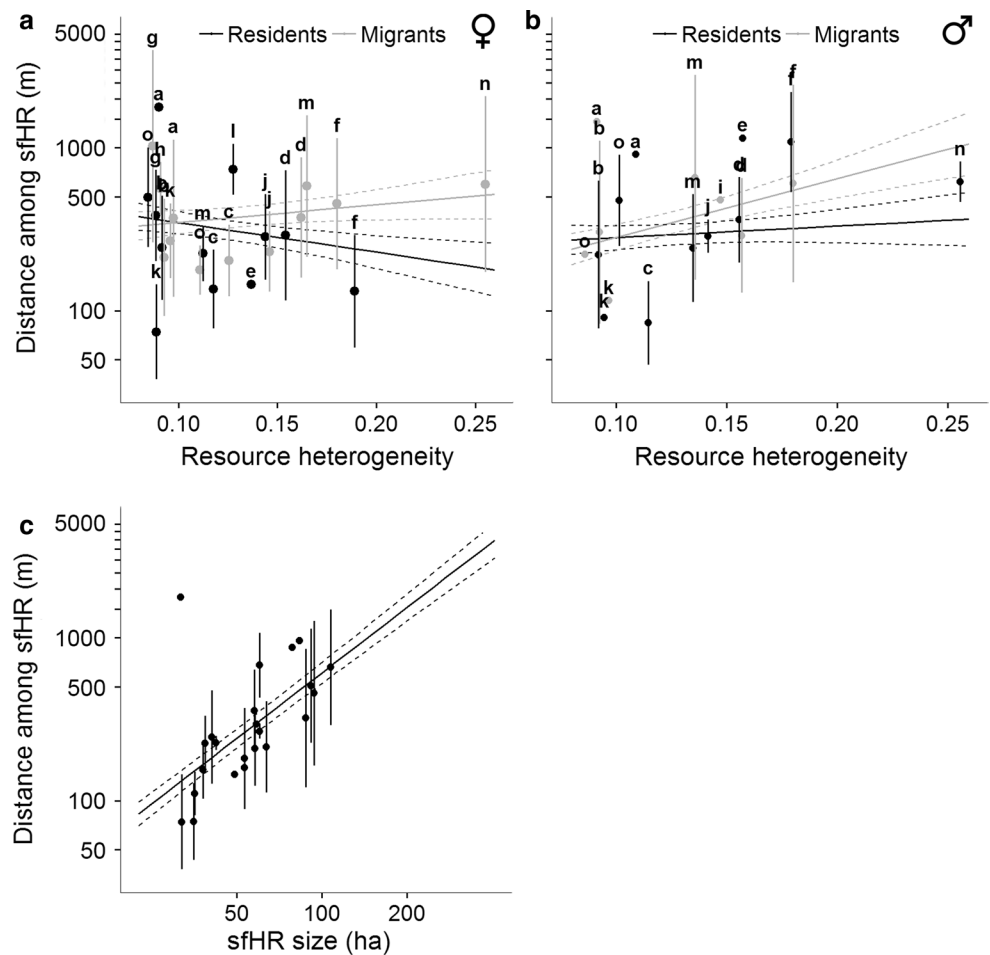
Discussion

Animals are considered sedentary when their routine movements are centred on revisited areas (Papi 1992), leading to the emergence of a stable home range which may be occupied for a season, or for several years (Börger et al. 2008). Sedentary behaviour is a defining feature of the resident movement tactic; however, migratory animals may also be seasonally sedentary within each of their distinct seasonal ranges (Börger et al. 2008; Mueller and Fagan 2008; Van

Moorter et al. 2009). Here, we focused on movements at the within-season scale, when many large herbivores (Börger et al. 2008) and, in particular, roe deer (Hewison et al. 1998), are presumed to be sedentary. Based on a comprehensive analysis of movement behaviour of 15 populations across Europe, we demonstrated that roe deer are never truly sedentary at the seasonal scale. Instead, within any given season, both migratory individuals and residents occupied at least two (and up to nine) spatially distinct sfHR. We suggest that this constitutes an overlooked movement mode, the multi-range tactic, which allows large herbivores to track fine-scaled spatio-temporal variation in the distribution of available resources and, thereby, to cope with changing environmental conditions. Indeed, we found that this space-use behaviour varied in relation to variation in environmental conditions across the European continent.

At the annual scale, we were able to assign a given individual to either a residency or a migratory tactic. However, when we analysed space use behaviour at the finer temporal scale within seasons, we found that all roe deer in this study adopted the multi-range tactic during a given season. A similar pattern of space use behaviour has been documented in two African large herbivores, the sable antelope and the

Fig. 5 Graphical representation of the best model describing variation in the distance among sub-seasonal home ranges (sfHR) during the winter, as a function of the two-way interaction between resource heterogeneity and movement tactic and between resource heterogeneity and sex, represented as a three-way interaction (**a**: females, **b**: males), and the sfHR size (**c**). To better visualise the raw data, we plotted the mean sfHR distance for each study site. Dotted lines represent the 95% confidence intervals resulting from the model predictions, error bars represent the standard deviation of inter-sfHR distance, and the letters correspond to the ‘study site id’ in Table 1. We fixed resource heterogeneity and the sfHR size at their mean, movement tactic as resident and sex as female when not represented in the figures



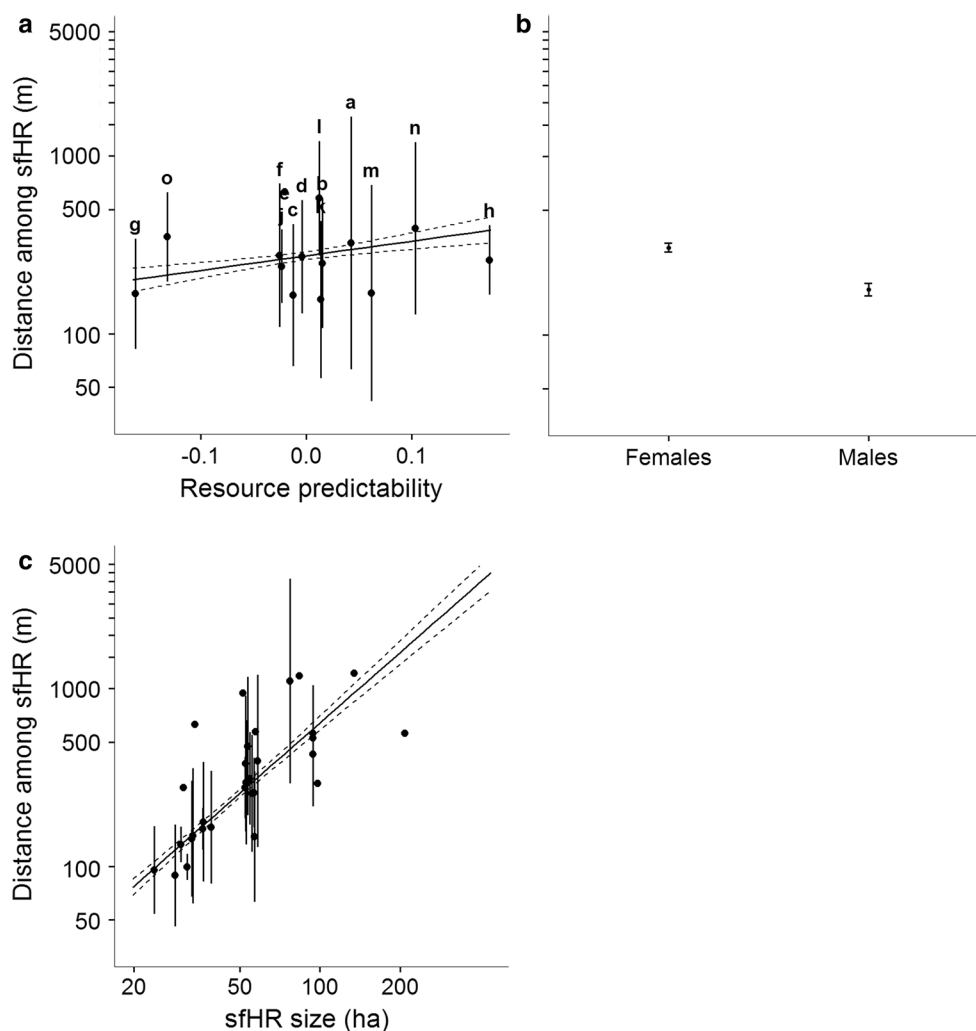
African savannah buffalo (Owen-Smith et al. 2010; Cornélis et al. 2011; Benhamou 2014). These authors showed that the ranges of these animals were composed of several distinct areas which were exploited for several days or weeks. Thus, the use of multiple sfHR to track available food resources seems to be potentially widespread among large herbivores. Here, to understand the proximal drivers of this seasonal space use behaviour, we explored how spatial heterogeneity and temporal predictability of resource distribution influenced variation in the number and the spatial distribution of the sub-seasonal ranges that an individual exploits.

Mueller et al. (2011), focusing on movements at the annual scale, documented longer seasonal migrations among species inhabiting areas where large-scale primary productivity was spatially heterogeneous, but shorter migrations for species inhabiting environments with relatively low spatial heterogeneity. Similarly, but at the seasonal scale, we expected individuals to be less sedentary in heterogeneous environments than in homogeneous environments, occupying a higher number of more spatially distant sfHR. Our analyses only partially supported this prediction as, in heterogeneous study areas, the distance between sfHR was indeed higher compared to homogeneous sites, but only

during winter. Furthermore, the number of sfHR that deer occupied did not vary in relation to resource heterogeneity. One explanation for this discrepancy could be linked to the relatively coarse spatial resolution of the NDVI metric that limits our ability to quantify small-scale variations in resource distribution at a level that is informative for individual animals. Indeed, Van Moorter et al. (2013) have shown that movements at a particular scale are driven by changes in the net profitability of trophic resources at the corresponding scale. As a result, a finer scale measure of spatial heterogeneity could help us to better understand why roe deer use a number of spatially distinct sub-seasonal functional home ranges, even in apparently homogeneous habitats.

Because nomadism is considered to be a response to unpredictability (Mueller and Fagan 2008), we expected roe deer to be less sedentary in unpredictable environments than in predictable environments. We found little support for this prediction. Our results indicated that, while controlling for resource heterogeneity, resource predictability had only a weak effect on the number of sfHR and the distance among sfHR. During summer, roe deer moved slightly further when in predictable environments than in unpredictable ones. During winter, resident roe deer adopted a space use behaviour

Fig. 6 Graphical representation of the best model describing variation in the distance among sub-seasonal home ranges (sfHR) during the summer season, as a function of resource predictability (a), sex (b) and the sfHR size in (c). To better visualise the raw data, we plotted the mean sfHR distance for each study site. Dotted lines represent the 95% confidence intervals resulting from the model predictions, error bars represent the standard deviation of inter-sfHR distance, and the letters correspond to the 'study site id' in Table 1. We fixed resource predictability and the sfHR size at their mean and sex as female when not represented in the figures



that was somewhat similar to a nomadic tactic when in more unpredictable environments, occupying slightly more sfHR than in predictable environments. Migratory individuals, on the contrary, tended to occupy slightly less sfHR in predictable environments than in unpredictable ones. However, these relationships were weak, with the main difference being that resident individuals occupied more sfHR than migrants during winter. Seasonal migration is a tactic designed to cope with seasonal changes in the spatial distribution of resources (Fryxell and Sinclair 1988; Mueller and Fagan 2008). As a result, it seems that migratory individuals do not have to shift their ranges at the finer within-season scale, as they are able to adjust their movements to spatial variation in the distribution of available forage at the larger between-season scale. Given the lack of support for our predictions, we suggest that other factors such as fine-scale variation in forage plant distribution, predation risk, or human disturbance could drive roe deer to switch periodically from one locality to another. Theory also predicts that prey should perform frequent random movements to minimise the probability of

encountering predators (Mitchell and Lima 2002). Indeed, previous studies have shown that herbivores modify their habitat selection or switch location after an encounter with a predator (Latombe et al. 2014; Lone et al. 2016).

From the point of view of landscape complementation (Dunning et al. 1992), an animal's home range must necessarily contain a combination of all non-substitutable resources required for survival and reproduction. Indeed, variation in home range size has previously been shown to reflect variation in resource availability, integrating interactions among local weather, climate and environmental seasonality (Morellet et al. 2013). Hence, all things being equal, animals will occupy larger home ranges when resources are more sparsely distributed in space (Saïd et al. 2005; Van Beest et al. 2011). Our analyses demonstrated strong relationships between sub-seasonal range size with both the number of sfRH and the distance between them. These results indicate that when resources are abundant, deer sequentially exploit a number of short-term functional ranges that are within close proximity. In contrast, when

resources are limiting, deer tend to relocate less frequently, possibly due to the costs of doing so in terms of predation risk, mortality or energy (Hein et al. 2012; Johansson et al. 2014), but move greater distances when they do so to locate a new functional sub-seasonal range. This individual variation in space use is further demonstration of the extensive behavioural plasticity that roe deer express in relation to prevailing environmental conditions (Cagnacci et al. 2011; Morellet et al. 2013; Lone et al. 2016) which has driven the undoubted recent success story of this species across Europe (Linnell et al. 1998).

In conclusion, we suggest that the multi-range tactic is an individual-level behavioural response to cope with spatio-temporal variation in the distribution of resources at the within-seasonal scale. This tactic appears to be ubiquitous in the roe deer, occurring across its entire European distribution, and encompassing a wide gradient of environmental conditions. We suggest that large herbivores may adopt this finer scale tactic when environmental conditions fluctuate spatially and temporally, independently of seasonal variations. In the present context of climate change, predictions of more frequent and intense climatic events (IPCC 2014) may mean that an increasing number of large herbivore populations adopt the multi-range tactic, combining more frequent spasmodic movements interspersed with short periods of sedentarism, to track available resources.

Acknowledgements This paper was conceived and written within the EURODEER collaborative project (paper no. 07 of the EURODEER series; www.eurodeer.org). The coauthors are grateful to all members for their support for the initiative. The EURODEER spatial database is hosted by Fondazione Edmund Mach. For France, we would like to thank the local hunting associations and the Fédération Départementale des Chasseurs de la Haute Garonne for allowing us to work in the Comminges, as well as numerous co-workers and volunteers for their assistance. GPS data collection at the Fondazione Edmund Mach was supported by the Autonomous Province of Trento under grant no. 3479 to F.C. (BECOCERWI—Behavioural Ecology of Cervids in Relation to Wildlife Infections) and project 2C2T. The Norwegian data collection was funded by the Norwegian Environment Agency and the county administration of Buskerud county. J Linnell was also funded by the Research Council of Norway (Grants 212919 and 251112). Financial support for GPS data collection in the Bavarian Forest was provided by the EU-programme INTERREG IV (EFRE Ziel 3) and the Bavarian Forest National Park Administration. The Czech Republic data collection was funded by the Ministry of Education, Youth and Sports of CR within the National Sustainability Program I (NPU I), grant number LO1415. Funding was provided in Białowieża, Poland by the Institute for Zoo and Wildlife Research (IZW), the Mammal Research Institute - Polish Academy of Sciences, the Polish Ministry of Science and Higher Education (grant no NN304172536). We also thank two anonymous reviewers for their constructive comments on an earlier version of this manuscript.

Author contribution statement OC, NM and AJMH formulated the idea. AJMH, FC, JDCL, AM, MH, PK, SN, AB, PS, MK, LS, RS and BG provided data. FU created and updated the database. OC, NM, and AJMH developed the methodology, OC and NM performed the

statistical analyses and wrote the manuscript with assistance from AJMH, SS, FC, SCJ, JDCL, AM, WP, FU, MH, PK, SN, AB, PS, MK, LS, RS and BG commented on and assisted in revising the manuscript.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

Data accessibility Data used for this study are accessible on EURO-DEER website (<http://eurodeer.org>) on demand.


References

- Baguette M, Stevens VM, Clobert J (2014) The pros and cons of applying the movement ecology paradigm for studying animal dispersal. *Mov Ecol* 2(2):13
- Barraquand F, Benhamou S (2008) Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology* 89:3336–3348
- Benhamou S (2014) Of scales and stationarity in animal movements. *Ecol Lett* 17:261–272
- Bischof R, Loe LE, Meisingset EL et al (2012) A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *Am Nat* 180:407–424
- Börger L, Fryxell JM (2012) Quantifying individual differences in dispersal using net squared displacement. In: Clobert J, Baguette M, Benton TJ, Bullock J (eds) *Dispersal ecology and evolution*. Oxford University Press, Oxford, pp 222–230
- Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650
- Borowik T, Pettorelli N, Sönnichsen L, Jedrzejska B (2013) Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *Eur J Wildl Res* 59:675–682
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225
- Bracis C, Gurarie E, Van Moorter B, Goodwin RA (2015) Memory effects on movement behavior in animal foraging. *PLoS ONE* 10:1–21
- Brown JL, Orians GH (1970) Spacing patterns in mobile animals. *Annu Rev Ecol Syst* 1:239–262
- Bunnefeld N, Börger L, van Moorter B et al (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J Anim Ecol* 80:466–476
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, Berlin
- Cagnacci F, Focardi S, Heurich M et al (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* 120:1790–1802
- Cagnacci F, Focardi S, Ghisla A et al (2015) How many routes lead to migration? Comparison of methods to assess and characterise migratory movements. *J Anim Ecol* 85:54–68
- Chapin FS, Johnson DA, McKendrick JD (1980) Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *J Ecol* 68:189–209
- Chapman BB, Hulthén K, Wellenreuther M et al (2014) Patterns of animal migration. In: Hansson L-A, Åkesson S (eds) *Animal*

- movement across scales. Oxford University Press, Oxford, pp 11–35
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136
- Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55:1153
- Coops N, Culvenor D (2000) Utilizing local variance of simulated high spatial resolution imagery to predict spatial pattern of forest stands. *Remote Sens Environ* 71:248–260
- Coops N, Culvenor D, Preston R, Catling P (1998) Procedures for predicting habitat and structural attributes in eucalypt forests using high spatial resolution remotely sensed imagery. *Aust For* 61:244–252
- Cornéllis D, Benhamou S, Janeau G et al (2011) Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes. *J Mammal* 92:1287–1297
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175
- English AK, Chauvenet ALM, Safi K, Pettorelli N (2012) Reassessing the determinants of breeding synchrony in ungulates. *PLoS ONE* 7:e41444
- Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. *Trends Ecol Evol* 3:237–241
- Garrouste EL, Hansen AJ, Lawrence RL (2016) Using NDVI and EVI to map spatiotemporal variation in the biomass and quality of forage for migratory elk in the Greater Yellowstone Ecosystem. *Remote Sens*. <https://doi.org/10.3390/rs8050404>
- Gurarie E, Cagnacci F, Peters W et al (2017) A framework for modeling range shifts and migrations: asking whether, whither, when, and will it return. *J Anim* 86:943–959. <https://doi.org/10.1111/ijlh.12426>
- Haight FA (1967) Handbook of the Poisson distribution. Wiley, Hoboken
- Hamel S, Garel M, Festa-Bianchet M et al (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J Appl Ecol* 46:582–589. <https://doi.org/10.1111/j.1365-2664.2009.01643.x>
- Hein AM, Hou C, Gillooly JF (2012) Energetic and biomechanical constraints on animal migration distance. *Ecol Lett* 15:104–110. <https://doi.org/10.1111/j.1461-0248.2011.01714.x>
- Hewison AJM, Vincent J-P, Reby D (1998) Social organisation of European roe deer. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 189–219
- Huang S, Meng SX, Yang Y (2009) Assessing the goodness of fit of forest models estimated by nonlinear mixed-model methods. *Can J For Res* 39:2418–2436
- IPCC (2014) *Climate Change 2014: Synthesis Report*
- Jepsen JU, Topping CJ (2004) Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. *Can J Zool* 82:1528–1541. <https://doi.org/10.1139/Z04-131>
- Johansson CL, Muijres FT, Hedenström A (2014) The physics of animal locomotion. In: Hansson L-A, Åkesson S (eds) *Animal movement across scales*. Oxford University Press, Oxford, pp 232–258
- Kerr JT, Ostrovsky M (2003) From space to species: ecological applications for remote sensing. *Trends Ecol Evol* 18:299–305
- Klisch A, Atzberger C (2016) Operational drought monitoring in Kenya using MODIS NDVI time series. *Remote Sens* 8:267
- Latombe G, Fortin D, Parrott L (2014) Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *J Anim Ecol* 83:185–198
- Lavielle M (1999) Detection of multiple changes in a sequence of dependent variables. *Stoch Process Appl* 83:79–102
- Lendrum PE, Anderson CR, Monteith KL et al (2014) Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. *Mamm Biol* 79:369–375
- Linnell JDC, Duncan P, Andersen R (1998) The European roe deer: a portrait of a successful species. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 11–22
- Lone K, Mysterud A, Gobakken T et al (2016) Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. *Oikos* 126:624–632
- Mitchell WA, Lima SL (2002) Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* 99:249–259
- Morellet N, Bonenfant C, Börger L et al (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *J Anim Ecol* 82:1326–1339
- Mueller T, Fagan WF (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117:654–664
- Mueller T, Olson KA, Dressler G et al (2011) How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob Ecol Biogeogr* 20:683–694
- Nathan R, Getz WM, Revilla E et al (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci* 105:19052–19059
- Owen-Smith N, Fryxell JM, Merrill EH (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philos Trans R Soc Lond* 365:2267–2278
- Papi F (1992) *Animal homing*. Chapman and Hall, London
- Peters W, Hebblewhite M, Mysterud A et al (2017) Migration in geographic and ecological space by a large herbivore. *Ecol Monogr* 87:297–320
- Pettorelli N, Ryan S, Mueller T et al (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Clim Res* 46:15–27. <https://doi.org/10.3354/cr00936>
- Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575
- Revilla E, Wiegand T (2008) Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. *Proc Natl Acad Sci USA* 105:19120–19125
- Riotte-Lambert L, Benhamou S, Chamaillé-Jammes S (2015) How memory-based movement leads to nonterritorial spatial segregation. *Am Nat* 185:E103–E116
- Rivrud IM, Loe LE, Mysterud A (2010) How does local weather predict red deer home range size at different temporal scales? *J Anim Ecol* 79:1280–1295
- Saïd S, Gaillard J-M, Duncan P et al (2005) Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *J Zool* 267:301–308
- Spitz DB, Hebblewhite M, Stephenson TR (2017) “MigrateR”: extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography (Cop)* 40:788–799
- R Development Core Team (2014) *R: a language and environment for statistical computing*
- Turchin P (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253–1266
- Turchin P (1998) *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland
- Van Beest FM, Rivrud IM, Loe LE et al (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J Anim Ecol* 80:771–785

- Van Moorter B, Visscher D, Benhamou S et al (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* 118:641–652
- Van Moorter B, Bunnefeld N, Panzacchi M et al (2013) Understanding scales of movement: animals ride waves and ripples of environmental change. *J Anim Ecol* 82:770–780
- Van Moorter B, Rolandsen CM, Basille M, Gaillard J-M (2016) Movement is the glue connecting home ranges and habitat selection. *J Anim Ecol* 85:21–31
- Vanpé C, Gaillard J, Morellet N et al (2009) Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J Mammal* 90:661–665
- Vuolo F, Mattiuzzi M, Klisch A, Atzberger C (2012) Data service platform for MODIS Vegetation Indices time series processing at BOKU Vienna: current status and future perspectives. *SPIE Proc* 8538:85380A
- Wiens JA (1976) Population responses to patchy environments. *Annu Rev Ecol Syst* 7:81–120

Affiliations

Ophélie Couriot¹  · A. J. Mark Hewison¹ · Sonia Saïd² · Francesca Cagnacci³ · Simon Chamaillé-Jammes⁴ · John D. C. Linnell⁵ · Atle Mysterud⁶ · Wibke Peters⁷ · Ferdinando Urbano⁸ · Marco Heurich^{9,10} · Petter Kjellander¹¹ · Sandro Nicoloso¹² · Anne Berger¹³ · Pavel Sustr^{14,15} · Max Kroeschel^{10,16} · Leif Soennichsen^{17,18} · Robin Sandfort¹⁹ · Benedikt Gehr²⁰ · Nicolas Morellet¹

A. J. Mark Hewison
mark.hewison@inra.fr

Sonia Saïd
sonia.said@oncfs.gouv.fr

Francesca Cagnacci
cagnacci.fem@gmail.com

Simon Chamaillé-Jammes
simon.chamaillé@cefe.cnrs.fr

John D. C. Linnell
john.linnell@nina.no

Atle Mysterud
atle.mysterud@ibv.uio.no

Wibke Peters
wibkepeters@gmail.com

Ferdinando Urbano
ferdi.urbano@gmail.com

Marco Heurich
marco.heurich@npv-bw.bayern.de

Petter Kjellander
petter.kjellander@slu.se

Sandro Nicoloso
nicoloso@dream-italia.it

Anne Berger
berger@izw-berlin.de

Pavel Sustr
krakononasumave@gmail.com

Max Kroeschel
max.kroeschel@wildlife.uni-freiburg.de

Leif Soennichsen
leif.soennichsen@gmx.de

Robin Sandfort
robin.sandfort@boku.ac.at

Benedikt Gehr
benedikt.gehr@ieu.uzh.ch

Nicolas Morellet
nicolas.morellet@inra.fr

¹ CEFS, Université de Toulouse, INRA, Castanet Tolosan, France

² Office National de la Chasse et de la Faune Sauvage, Direction Recherche et Expertise, Unité Ongulés Sauvages, Monfort 01330, Birieux, France

³ Biodiversity and Molecular Ecology Department, Research and Innovation Centre, Fondazione Edmund Mach, Via Mach 1, 38010 San Michele all'Adige, TN, Italy

⁴ CNRS, Univ Montpellier, EPHE, IRD, Univ Paul Valéry Montpellier 3, 34293 Montpellier, France

⁵ Norwegian Institute for Nature Research, PO Box 5685, Torgard, NO-7485 Trondheim, Norway

⁶ Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Blindern, P.O. Box 1066, NO-0316 Oslo, Norway

⁷ Bavarian State Institute of Forestry (LWF), Hans-Carl-von-Carlowitz-Platz 1, 85354 Freising, Germany

⁸ Freelance Consultant, Milan, Italy

⁹ Department of Conservation and Research, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

¹⁰ Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany

¹¹ Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

¹² Research, Ecology and Environment Dimension (D.R.E.Am. Italia), Via Enrico Bindi 14, 51100 Pistoia, PT, Italy

¹³ Leibniz-Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

¹⁴ Department of Biodiversity Research, Global Change Research Institute CAS, Academy of Sciences of the Czech Republic, Brno, Czech Republic

¹⁵ Šumava National Park, Vimperk, Czech Republic

¹⁶ Forest Research Institute of Baden-Wuerttemberg, Wildlife Ecology, Wonnhaldestraße 4, 79100 Freiburg, Germany

- ¹⁷ Mammal Research Institute, Polish Academy of Sciences, ul. Stoczek 1, 17-230 Białowieża, Poland
- ¹⁸ Leibniz Institute for Zoo and Wildlife Research (IZW), Forschungsverbund Berlin e.V. Alfred-Kowalke-Straße 17, 10315 Berlin, Germany
- ¹⁹ Department of Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria
- ²⁰ Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Germany