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

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Abstract:

Much research on large herbivore movement has focused on the annual scale to distinguish between resident and migratory tactics, and assumes 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 not impacted 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.

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

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Abstract

Much research on large herbivore movement has focused on the annual scale to distinguish between resident and migratory tactics, and assumes 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 not impacted 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.

Key words: migration, residency, sub-seasonal functional home range, spatial heterogeneity, temporal predictability

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). Individuals are assumed to memorise the value and location of a given patch (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 in order 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 range over a long time span (season, 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 in order 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 in order 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; Cagnacci et al. 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 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. Secondly, 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 heterogeneous compared to homogeneous environments (Mueller and Fagan 2008; Mueller et al. 2011). Analogously to the nomadic movement tactic (Mueller and Fagan 2008), we also expected individuals to be less sedentary in unpredictable environments, or at least in environments where resources vary more markedly over time at the within-seasonal 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).

Material 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 minutes to 12 hours. In order 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

First, we used the method proposed by Börger and Fryxell (2012), based on the net squared displacement (NSD), i.e. the Euclidian distance between the starting location and all subsequent locations of an individual over time (Turchin 1998), to determine each 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). In order to identify which of these models best described the movement behaviour of a given individual, we used the system of nonlinear 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 when the NSD was relatively constant or increased linearly initially before rapidly reaching an asymptote, the individual was resident. 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, we assumed that the individual was migratory. Finally, when the NSD was constant before increasing rapidly to reach a plateau with no further increase or decrease, we assumed that the individual had dispersed. 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 (Lavielle 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 three 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 was 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. We arbitrarily considered 14 locations (i.e. 7 days) as the minimum number required to describe a stationary state. We retained the most parsimonious number of segments comprising each seasonal range for each individual.

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, above) for each seasonal period (Supplementary materials, Appendix S1, Eq.1). 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 S1, Eq. 2 & 3)., and retained the model with the largest concordance correlation (CC) coefficient (See Supplementary materials, Appendix S2).

Describing site-specific environmental conditions

In order 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 normalized difference vegetation index (NDVI) which is widely considered to be a reliable index of plant productivity in general, and a good proxy of spatio-temporal variation in resource availability for herbivores in particular (Hamel et al. 2009; Pettorelli et al. 2011; Borowik et al. 2013). We obtained weekly values for the NDVI (pixel size = ca. 250m x 250m) 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 REFMID values, supplied by BOKU, which are the most stable extrapolated values of 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 the 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:

$$\text{Constancy} = 1 + \Sigma(\Sigma(\text{NDVI})ij / \Sigma\Sigma(\text{NDVI})ij * \log(\Sigma(\text{NDVI})ij / \Sigma\Sigma(\text{NDVI})ij)) / \log(s)$$

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.

First, we used cumulative link mixed models, which are appropriate for ordinal data (clmm, Christensen 2015a), 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 among individuals (Morellet et al. 2013). For that, we calculated sfHR size using the fixed kernel method with the 90% isopleths. 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 preliminary analyses showed that all individuals occupied at least two sfHR per season, but that most individuals used less than six, we analysed the number of sfHR as a categorical variable with five modalities from two to six or more (Supplementary material, Appendix S6). Note, to simplify interpretation, we only present results contrasting the probabilities of occupying ‘2’ or ‘6 or more’ sfHR (we present complete results in Supplementary material, Appendix S7 & S8).

Second, we used linear mixed-effects models (lmer) 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).

Results

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 each period). Individuals occupied a sfHR for at least 7 days (by definition, see 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 (from two to six or more) during the winter period included movement tactic and the log-transformed sfHR size (ΔAIC = 0.0, AIC weight = 0.413, df = 7) (Supplementary materials, Appendix S3 & S5).

During the winter period, the results were partially in accordance with our expectations. First, in accordance with our prediction, migratory individuals occupied fewer sfHR than resident individuals: for migrants, the probability of occupying '2' sfHR was 331% higher than the probability of occupying '6 or more' sfHR, while for resident individuals the probability of occupying '2' sfHR was 29% lower than the probability of occupying '6 or more' sfHR (Fig. 2a). Second, the number of sfHR that individuals used decreased as the median size of the sfHR they occupied increased. Indeed, the probability of occupying '6 or more' sfHR was 92% lower than the probability of occupying '2' sfHR for an individual occupying a large (sfHR size = 410 ha) sfHR, whereas it was 771% higher for an individual occupying a small (sfHR size = 22 ha) sfHR (Fig. 2b).

The most parsimonious model describing variation in the number of sfHR (from two to six or more) during the summer period included sex and the log-transformed sfHR size (ΔAIC = 0.92, AIC weight = 0.148, df = 7) (Supplementary materials, Appendix S3 & S5). During the summer period, both sexes had a much higher probability of using 2 sfHR than '6 or more' sfHR, but this difference was slightly more marked among females (the probability of using '6 or more' sfHR was 98% lower than the probability of using 2 sfHR) than among males (the probability of using '6 or more' sfHR was 96% lower than the probability of using 2 sfHR) (Fig. 3a). Finally, as above, the number of sfHR that individuals used decreased as the median size of the sfHR they occupied increased. Indeed, the probability of occupying '6 or more' sfHR was 99% lower than the probability of occupying '2' sfHR for an individual occupying a large (sfHR size = 450 ha) sfHR, whereas it was 620% higher for an individual occupying a small (sfHR size = 20 ha) sfHR (Fig. 3b).

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 two 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 (ΔAIC = 0.6, AIC weight = 0.274, df = 9) (Supplementary materials, Appendix S4 & S5). First, in accordance with our prediction, spatial separation between pairs of sfHR during the wintering period increased with increasing resource heterogeneity, except among resident females (Fig. 4a and b). Indeed, when resource heterogeneity was high (resource heterogeneity = 0.26), the log-transformed inter-sfHR distance was, on average, 13% (5% for resident males and 27% for migratory males) higher than for an individual living in the least heterogeneous study site (resource heterogeneity = 0.08). However, for resident females, this distance was 13% lower when resource heterogeneity was high. Finally, spatial separation among sfHR during the winter period was 87% higher for an individual which occupied the largest sfHR (median sfHR size = 410 ha) compared to an individual occupying the smallest sfHR (median sfHR size = 22 ha) (Fig. 4c).

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 (ΔAIC = 1.86, AIC weight = 0.143, df = 6) (Supplementary materials, Appendix S4 & S5). First, contrary to our prediction, the distance between sfHR was 12% higher in the most predictable study site compared to the most unpredictable one (Fig. 5a). Secondly, the distance between sfHR was 10% higher for females than for males (Fig. 5b). Finally, the spatial separation among sfHR during the summer period was 94% higher for an individual inhabiting the largest sfHR (median sfHR size = 450 ha) compared to an individual inhabiting the smallest sfHR (median sfHR size = 20 ha) (Fig. 5c).

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, whether or not they migrate. 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 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 within season temporal scale, we found that all roe deer in this study, covering widely contrasting environmental conditions, 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, the 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 primary productivity was spatially heterogeneous at a large-scale, but shorter migrations for species inhabiting environments with relatively low spatial heterogeneity. In an analogous fashion, 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 individuals. 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 no effect on variation in the number of sfHR, and only a very weak effect on the distance among sfHR, and this only during summer. During this period, roe deer adopted a space use behaviour that was somewhat more similar to a nomadic tactic when in more predictable environments, moving further among sub-seasonal functional ranges than in unpredictable environments. Given the lack of support for our predictions, we suggest that other factors such as predation risk or human disturbance could drive roe deer to switch periodically from one locality to another. Theory 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).

Finally, as expected, migratory individuals occupied fewer sfHR than resident individuals. 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 within seasons, as they are able to adjust their movements to spatial variation in the distribution of available forage at the between-season scale.

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 when this occurs 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 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.

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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 EURODEER website (http://eurodeer.org) on demand.

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Tables

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	Brandeburg - 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	NINA west - Norway	3	6	5	4
	Total	**93**	**193**	**190**	**96**

Figure legends

Figure 1: Location of study sites where roe deer were monitored using GPS collars. Letters correspond to the 'study site id' in Table 1.

Figure 2: Graphical representation of the best model describing variation in the number of sub-seasonal home ranges (sfHR) during the winter period, represented here by the probability of occupying either '2' or '6 or more' sfHR (for simplification, intermediate values of sfHR are excluded from the graph, see Supplementary material, Appendix S7), as a function of movement tactic (a) and the log-transformed sfHR size (b). Dotted lines represent the 95% confidence intervals resulting from the model predictions. We fixed the log-transformed sfHR size at the mean and movement tactic as residency when not represented in the following figures.

Figure 3: Graphical representation of the best model describing variation in the number of sub-seasonal home ranges (sfHR) during the summer period, represented here by the probability of occupying either '2' or '6 or more' sfHR (for simplification, intermediate values of sfHR are excluded from the graph, see Supplementary material, Appendix S8), as a function of sex (a) and the log-transformed ssHR size (b). Dotted lines represent the 95% confidence intervals resulting from the model predictions. We fixed the log-transformed sfHR size at the mean and sex as female when not represented in the following figures.

Figure 4: Graphical representation of the best model describing variation in the log-transformed distance among sub-seasonal home ranges (sfHR) during the winter period, 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 log-transformed median sfHR size (c). In order to better visualize the raw data, we plotted the mean log-transformed 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 log-transformed inter-sfHR distance, and the letters correspond to the ‘study site id’ in Table 1. We fixed resource heterogeneity and the log-transformed sfHR size at the mean, movement tactic as residency and sex as female when not represented in the following figures.

Figure 5: Graphical representation of the best model describing variation in the log-transformed distance among sub-seasonal home ranges (sfHR) during the summer period, as a function of resource predictability (a), sex (b) and the log-transformed median sfHR size (c). In order to better visualize the raw data, we plotted the mean log-transformed 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 log-transformed inter-sfHR distance, and the letters correspond to the ‘study site id’ in Table 1. We fixed resource predictability and the log-transformed sfHR size at the mean and sex as female when not represented in the following figures.

Fig. 1

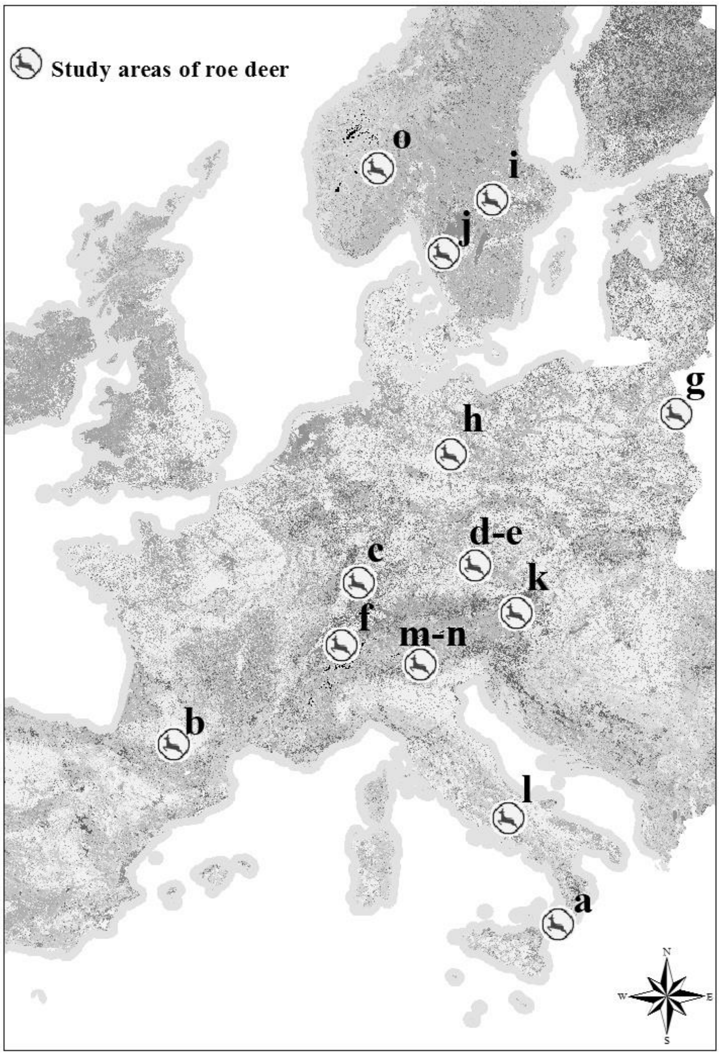


Fig. 2

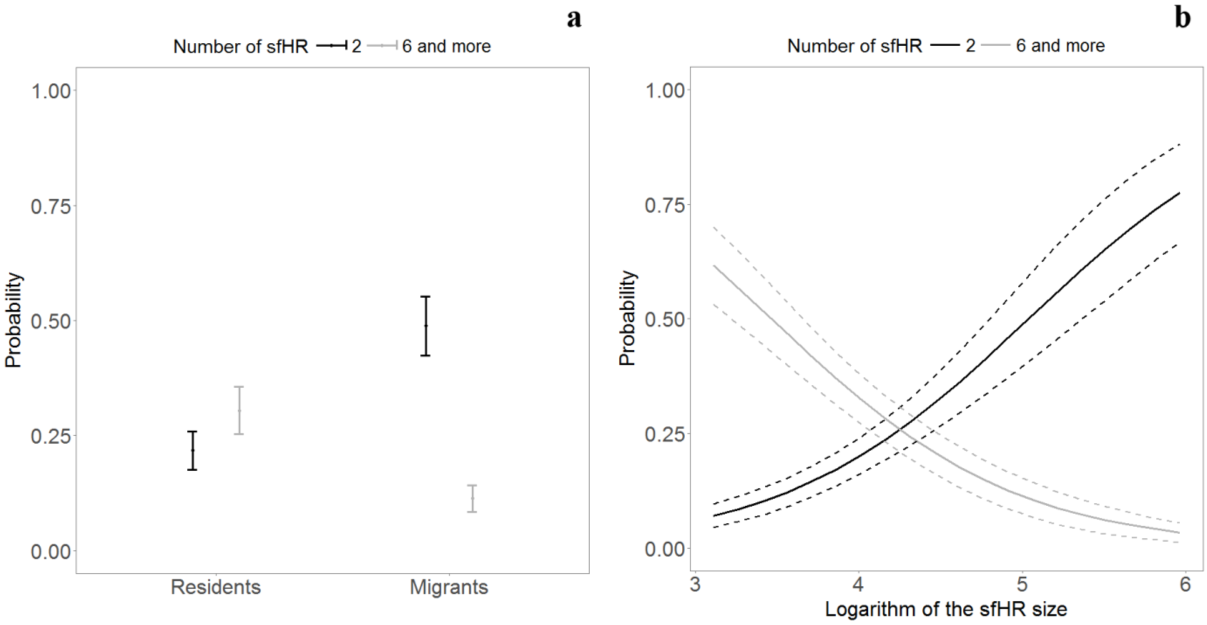

a
Number of sfHR
2
6 and more
Probability
1.00
0.75
0.50
0.25
0.00
Residents
Migrants
b
Number of sfHR
2
6 and more
Probability
1.00
0.75
0.50
0.25
0.00
3
4
5
6
Logarithm of the sfHR size

Fig. 3

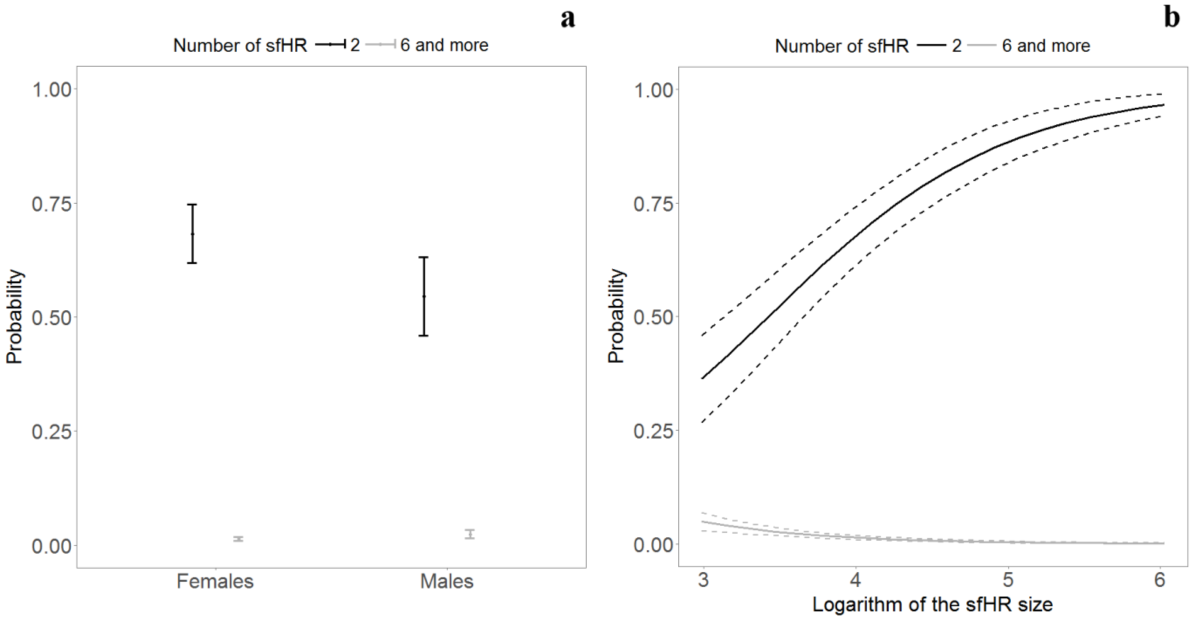

a
Number of sfHR
2
6 and more
Probability
1.00
0.75
0.50
0.25
0.00
Females
Males
b
Number of sfHR
2
6 and more
Probability
1.00
0.75
0.50
0.25
0.00
3
4
5
6
Logarithm of the sfHR size

Fig. 4

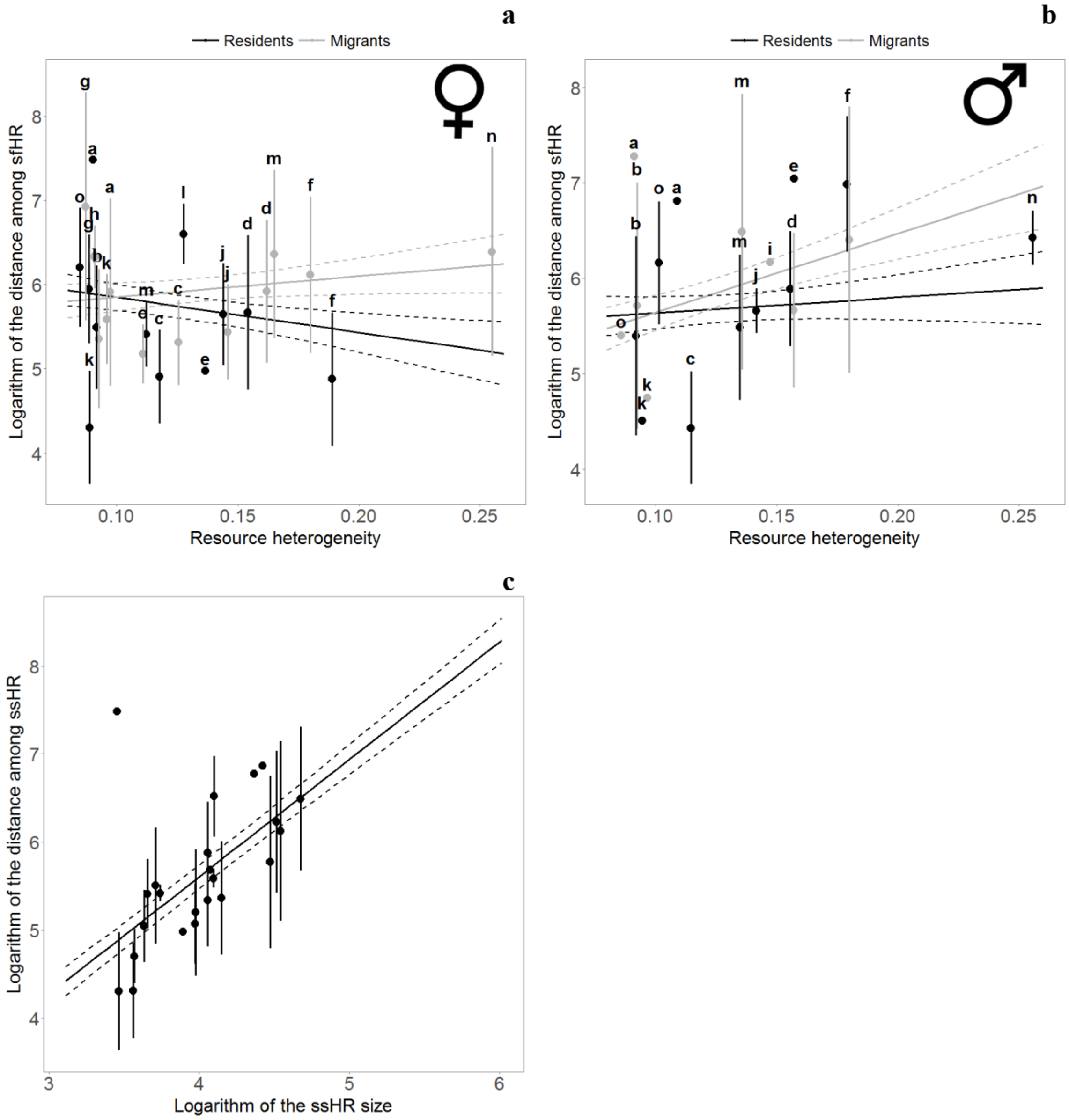
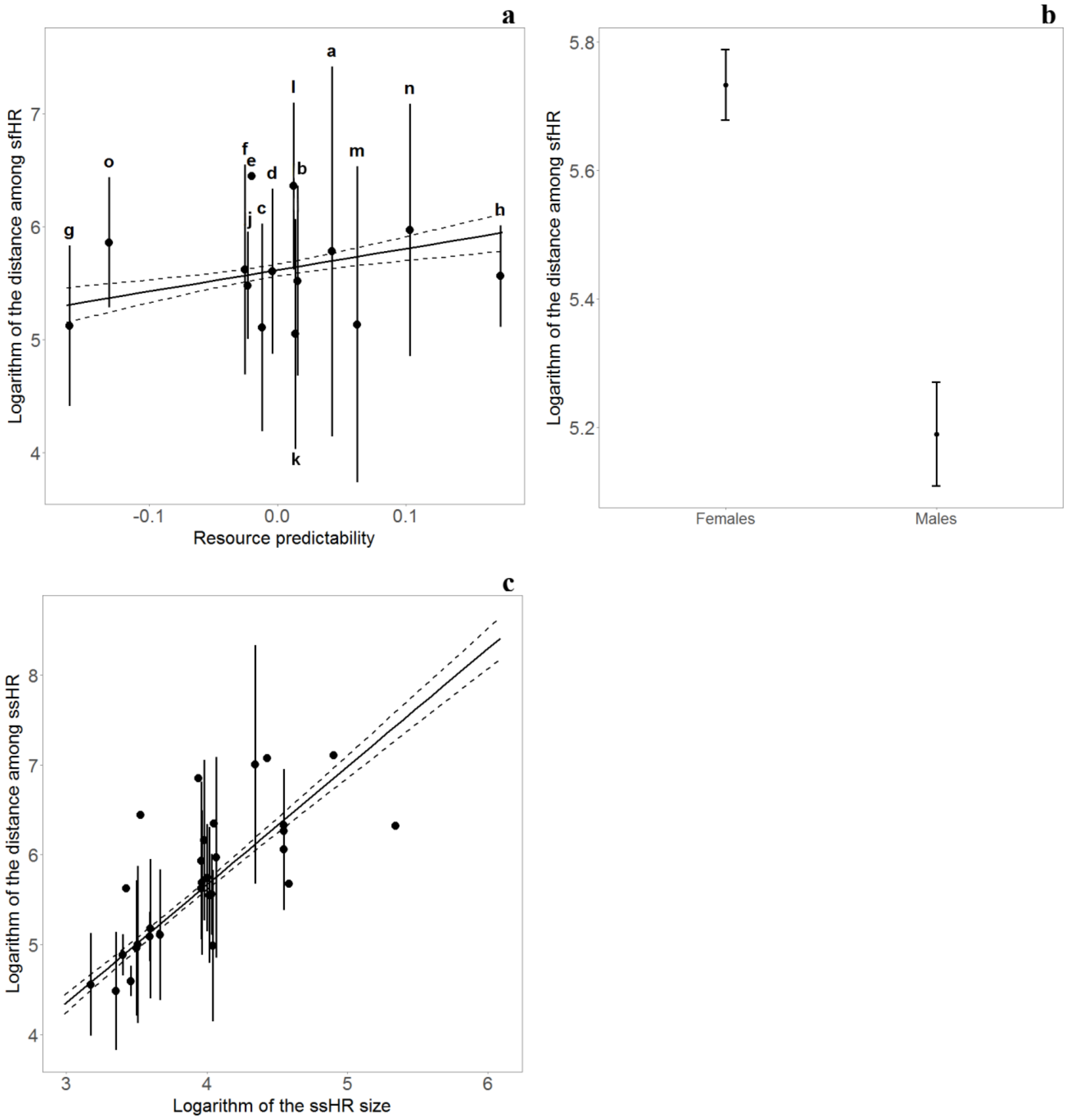

a
Residents
Migrants
Logarithm of the distance among sfHR
Resource heterogeneity
0.10
0.15
0.20
0.25
4
5
6
7
8
♀
g
a
o
a
h
g
b
k
l
m
c
e
c
k
e
j
j
d
d
m
f
f
n
b
Residents
Migrants
Logarithm of the distance among sfHR
Resource heterogeneity
♂
a
b
b
o
a
m
e
f
m
i
j
d
n
o
k
k
c
c
Logarithm of the distance among ssHR
Logarithm of the ssHR size
3
4
5
6

Fig. 5


a
Logarithm of the distance among sfHR
Resource predictability
-0.1
0.0
0.1
4
5
6
7
a
b
c
d
e
f
g
h
j
k
l
m
n
o
b
Logarithm of the distance among sfHR
5.2
5.4
5.6
5.8
Females
Males
c
Logarithm of the distance among ssHR
Logarithm of the ssHR size
3
4
5
6
4
5
6
7
8

Supplementary Material