



**HAL**  
open science

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

Ophélie Couriot, A.J. Mark Hewison, Sonia Said, Francesca Cagnacci, Simon Chamaille-Jammes, John Linnell, Atle Mysterud, Wibke Peters, Ferdinando Urbano, Marco Heurich, et al.

### ► To cite this version:

Ophélie Couriot, A.J. Mark Hewison, Sonia Said, Francesca Cagnacci, Simon Chamaille-Jammes, et al. Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia*, 2018, 187 (1), pp.47-60. 10.1007/s00442-018-4131-5 . hal-02311434

**HAL Id: hal-02311434**

**<https://hal.science/hal-02311434>**

Submitted on 13 Mar 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

[Click here to view linked References](#)

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

3

4 Ophélie Couriot, A. J. Mark Hewison, Sonia Saïd, Francesca Cagnacci, Simon Chamailé-  
5 Jammes, John D. C. Linnell, Atle Mysterud, Wibke Peters, Ferdinando Urbano, Marco  
6 Heurich, Petter Kjellander, Sandro Nicoloso, Anne Berger, Pavel Sustr, Max Kroeschel, Leif  
7 Soennichsen, Robin Sandfort, Benedikt Gehr and Nicolas Morellet

8

9 Ophélie Couriot, CEFS, Université de Toulouse, INRA, Castanet Tolosan, France, email:  
10 o.couriot@gmail.com, tel. +33 (0) 561 28 51 25, corresponding author

11 A. J. Mark Hewison, CEFS, Université de Toulouse, INRA, Castanet Tolosan, France, email:  
12 mark.hewison@inra.fr

13 Sonia Saïd, Office National de la Chasse et de la Faune Sauvage, Direction Recherche et  
14 Expertise, Unité Ongulés Sauvages, « Monfort » 01330 Birieux, France, email:  
15 sonia.said@oncfs.gouv.fr

16 Francesca Cagnacci, Biodiversity and Molecular Ecology Department, Research and  
17 Innovation Centre, Fondazione Edmund Mach, Via Mach 1, 38010 San Michele all'Adige,  
18 TN, Italy, email: cagnacci.fem@gmail.com

19 Simon Chamailé-Jammes, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS  
20 - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, 34293 Montpellier  
21 Cedex 5, France, email: simon.chamaille@cefe.cnrs.fr

22 John D. C. Linnell, Norwegian Institute for Nature Research, PO Box 5685 Torgard, NO-  
23 7485 Trondheim, Norway, email: john.linnell@nina.no

24 Atle Mysterud, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo,  
25 Blindern, P.O. Box 1066, 0316 Oslo, Norway, email: atle.mysterud@ibv.uio.no

26 Wibke Peters, Bavarian State Institute of Forestry (LWF), Hans-Carl-von-Carlowitz-Platz 1,  
27 85354 Freising, Germany, email: wibkepeters@gmail.com

28 Ferdinando Urbano, Freelance Eurodeer Database Manager, Milan, Italy, email:  
29 ferdi.urbano@gmail.com

30 Marco Heurich, Bavarian Forest National Park, Department of Conservation and Research,  
31 Freyunger Str. 2, 94481 Grafenau, Germany & Chair of Wildlife Ecology and Management,  
32 University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany, email:  
33 marco.heurich@npv-bw.bayern.de

34 Petter Kjellander, Grimsö Wildlife Research Station, Department of Ecology, Swedish  
35 University of Agricultural Sciences, Riddarhyttan, Sweden, email: petter.kjellander@slu.se

36 Sandro Nicoloso, Research, Ecology and Environment Dimension (D.R.E.Am. Italia), Via  
37 Enrico Bindi 14, 51100 Pistoia, PT, Italy, email: nicoloso@dream-italia.it

38 Anne Berger, Leibniz-Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17,  
39 10315 Berlin, Germany, email: berger@izw-berlin.de

40 Pavel Sustr, Department of Biodiversity Research, Global Change Research Centre, Academy  
41 of Sciences of the Czech Republic, Brno, Czech Republic, Šumava National Park, Vimperk,  
42 Czech Republic, email: krakonosnasumave@gmail.com

43 Max Kroeschel, Chair of Wildlife Ecology and Management, University of Freiburg,  
44 Tennenbacher Straße 4, 79106 Freiburg, Germany & Forest Research Institute of Baden-  
45 Wuerttemberg, Wildlife Ecology, Wonnhaldestraße 4, 79100 Freiburg, Germany, email:  
46 max.kroeschel@wildlife.uni-freiburg.de

47 Leif Soennichsen, Mammal Research Institute, Polish Academy of Sciences, Białowieża,  
48 Poland, email: l\_soennichsen@ibs.bialowieza.pl

49 Robin Sandfort, Institute of Wildlife Biology and Game Management, Department of  
50 Integrative Biology and Biodiversity Research, University of Natural Resources and Life  
51 Sciences, Vienna, email: robin.sandfort@boku.ac.at  
52 Benedikt Gehr, Department of Evolutionary Biology and Environmental Studies, University  
53 of Zurich, Winterthurerstrasse 190, 8057 Zurich, email: benedikt.gehr@ieu.uzh.ch  
54 Nicolas Morellet, CEFS, Université de Toulouse, INRA, Castanet Tolosan, France, email:  
55 nicolas.morellet@inra.fr

Author contributions: 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.

56 **Abstract**

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

77

78 **Key words:** migration, residency, sub-seasonal functional home range, plasticity, roe deer

79

## 80 **Introduction**

81 Movement is a fundamental characteristic of life which influences the survival and  
82 reproduction of organisms and, more generally, individual fitness and population dynamics  
83 (Turchin 1991; Revilla and Wiegand 2008). Following the Marginal Value Theorem  
84 (Charnov 1976), while foraging, an individual moves within a patch (sensu Wiens 1976),  
85 searching intensively for food, before leaving to search more widely for a new patch when the  
86 energetic benefit of the first patch has decreased below the average value of the alternative  
87 patches (Charnov 1976; Van Moorter et al. 2009). In slowly regenerating environments,  
88 animals should engage in thorough exploration to locate suitable patches. However, in rapidly  
89 regenerating environments, individuals are assumed to memorise the value and location of a  
90 given patch (Bracis et al. 2015; Riotte-Lambert et al. 2015), returning to previously visited  
91 patches periodically. This process leads to the emergence of a stable home range to which  
92 individuals restrict their movements in order to maximise resource acquisition (Brown and  
93 Orians 1970; Riotte-Lambert et al. 2015). Therefore, individuals of many species appear to be  
94 sedentary at this spatio-temporal scale, occupying a stable home range over a long time span  
95 (season and year). Site fidelity is widespread in the animal kingdom and has fundamental  
96 consequences for ecological processes (Börger et al. 2008).

97 An individual's lifetime track is an aggregation of successive elementary units with  
98 potentially different functionality (Baguette et al. 2014). Indeed, as stated by Van Moorter et  
99 al. (2016) "animals do not move for the sake of changing their geographic location, but rather  
100 for changing environmental conditions associated with changes in location". In general, an  
101 individual decides to move in order to satisfy its requirements in terms of refuge and  
102 resources (Nathan et al. 2008) which encompass changes in environmental space (Van  
103 Moorter et al. 2013). For example, since favourable sites for feeding or taking refuge do not  
104 necessarily occur at the same location, and since conditions vary in space and time, animals

105 have to move to cope with spatio-temporal heterogeneity in their environment (Pyke 1984;  
106 Mueller and Fagan 2008; Chapman et al. 2014). As a result of variation in conditions over  
107 time, an animal must shift from one suitable patch to another in order to fulfil its  
108 requirements, in which case it cannot be considered truly sedentary, even at the seasonal scale  
109 (Chapin et al. 1980; Barraquand and Benhamou 2008). Indeed, animals may use several  
110 spatio-temporally distinct suitable units, particularly in spatially heterogeneous and/or  
111 temporally unpredictable environments. While there has been considerable focus in recent  
112 years on movements associated with seasonal migration between seasonally distinct home  
113 ranges (Cagnacci et al. 2011; Cagnacci et al. 2015; Peters et al. 2017), there has been  
114 relatively little work on finer scale movements at the within season scale. The use of sub-  
115 seasonal functional home ranges (sfHR) has previously been described in two African  
116 herbivores, the sable antelope (*Hippotragus niger*) and the African savanna buffalo (*Syncerus*  
117 *caffer brachyceros*) (Owen-Smith et al. 2010; Cornélis et al. 2011; Benhamou 2014).  
118 However, no study has yet attempted to link the propensity of individuals to adopt this multi-  
119 range tactic with spatial and temporal variation in the prevailing environmental conditions.

120 Here, we used the EURODEER database (<http://www.eurodeer.org>, see methods) to  
121 analyse space use of roe deer (*Capreolus capreolus*) across widely contrasting environments,  
122 from the southern part of their geographic range in Italy to the northern part of their range, in  
123 Scandinavia. We focused on the roe deer as it is Europe's most widespread large wild  
124 herbivore and is considered highly sedentary over the majority of its range (Hewison et al.  
125 1998). However, this species also exhibits a considerable degree of behavioural plasticity  
126 (Jepsen and Topping 2004), and is described as partially migratory in more extreme  
127 environments (Cagnacci et al. 2011). Hence, we first analysed whether roe deer are truly  
128 sedentary within a given season, or whether they adopt a movement tactic based on the use of  
129 a series of sfHR. Secondly, we hypothesised that the propensity of an animal to adopt this

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



## 140 **Material and methods**

### 141 *Study areas and GPS data*

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

154

### 155 *Discrimination of individual movement tactics*

156 Of the recently published emerging tools for determining movement tactic (Gurarie et al.  
157 2017; Spitz et al. 2017), we first used a common method proposed by Börger and Fryxell  
158 (2012), which has been proven useful for large mammals (Bunnefeld et al. 2011; Bischof et  
159 al. 2012), based on the net squared displacement (NSD), *i.e.* the Euclidian distance between  
160 the starting location and all subsequent locations of an individual over time (Turchin 1998), to  
161 determine each individual's annual movement tactic: migration, residency or dispersal. We  
162 considered two models of range residency, one with a constant NSD (the mean), and one with  
163 a linear increase of NSD before reaching an asymptote; we considered one model of  
164 migration including approximate dates of departure and return between seasonal ranges, and a

165 model of dispersal with an approximate date of departure (see Bunnefeld et al. 2011 and  
166 Börger and Fryxell 2012 for more details on these models). In order to identify which of these  
167 models best described the movement behaviour of a given individual, we used the system of  
168 non-linear mixed models proposed by Börger and Fryxell (2012) which links theoretical  
169 expectations to movement data. For model selection, as recommended by Börger and Fryxell  
170 (2012), we retained the model with the largest concordance correlation (CC), expressing the  
171 goodness of fit for each model (Huang et al. 2009). Because the assigned movement tactic  
172 using this method did not always closely fit the data, we also visually examined the NSD  
173 trajectories to determine each individual's annual movement tactic by eye (Bischof et al.  
174 2012). We based our visual classification on the patterns of NSD typically observed for  
175 migratory individuals, residents and dispersers, following Börger and Fryxell (2012). That is,  
176 we assumed that the individual was resident when the NSD was relatively constant, or  
177 initially increased linearly before rapidly reaching an asymptote. We assumed that the  
178 individual was migratory when the NSD was constant before increasing rapidly during spring  
179 to reach a plateau during summer, then decreased during fall, returning to its initial value.  
180 Finally, we assumed that the individual had dispersed when the NSD was constant before  
181 increasing rapidly to reach a plateau with no further increase or decrease. We then verified  
182 that individuals which were classified as dispersers did not return to their point of departure  
183 during subsequent monitoring, after the 15<sup>th</sup> of November. If they did (53 of 65 animals  
184 originally classified as dispersers), these individuals were considered as migratory. We  
185 excluded the remaining dispersers (N = 12) from subsequent analyses as movement patterns  
186 during dispersal are governed by different ultimate causes than those involved in range  
187 residency or migration (Bowler and Benton 2005; Chapman et al. 2014). After visual  
188 reclassification, our data set included 193 residents and 93 migratory individuals. Note that  
189 subsequent analyses based on this visual classification of individual movement tactics

190 generated results that were similar to those based on the classification using Borger and  
191 Fryxell's (2012) method (not shown).

192 Subsequently, for each migratory individual, we segmented the NSD using Lavielle's  
193 method (Lavielle 1999), which detects change points in a time series, to identify the dates of  
194 departure and return from, and to, the winter range (if any) and to define individual-based  
195 seasonal ranges. Dates of departure from the winter range ranged from the 6<sup>th</sup> of March to the  
196 3<sup>rd</sup> of August (median = 4<sup>th</sup> of May, sd = 32 days), while return ranged from the 7<sup>th</sup> of May to  
197 the 28<sup>th</sup> of October (median = 10<sup>th</sup> of September, sd = 42 days). We then used the median  
198 departure and return dates across all migratory individuals to establish equivalent seasonal  
199 phases for resident individuals. As a result, we subsequently analysed movement behaviour of  
200 all deer during the winter period (prior to departure) and the summer period (after departure  
201 and prior to return), excluding the three days prior to and following departure and return to  
202 avoid the transience phase. We did not analyse data from the post-return period, (the second  
203 winter), since monitoring periods were too short to characterise individual movement during  
204 this period.

205

### 206 *Detecting sub-seasonal functional home ranges*

207 We then tested the assumption that roe deer were truly sedentary within the above defined  
208 seasonal periods or, whether their seasonal ranges were composed of several sub-seasonal  
209 functional home ranges (sfHR, Benhamou 2014). To do so, we segmented each individual's  
210 movement path (*i.e.* the temporal sequence of locations) for each seasonal period using  
211 Lavielle's (1999) method on the mean NSD to identify fine scale stationary states. Following  
212 several studies which have examined variation of weekly home ranges in response to variation  
213 in resource distribution (Rivrud et al. 2010; Van Beest et al. 2011; Morellet et al. 2013), we  
214 considered 14 locations (*i.e.* 7 days) as the minimum number required to describe a stationary

215 state. Because this choice of a minimum time span is somewhat arbitrary, we repeated the  
216 segmentation approach twice using minimum values of 5 and of 9 days (*i.e.*  $7\pm 2$  days) to  
217 assess the sensitivity of our results to the length of the temporal window. Finally, we retained  
218 the most parsimonious number of segments comprising each seasonal range for each  
219 individual (Figs. 2 & 3). We again repeated this step when considering 5 and 9 days as the  
220 minimum temporal windows.

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

229

### 230 *Describing site-specific environmental conditions*

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

237 To quantify broad scale site-specific heterogeneity in resource distribution, we used  
238 the normalized difference vegetation index (NDVI). NDVI is widely used in ecological  
239 research and management as a proxy for biomass (Kerr and Ostrovsky 2003; Pettorelli et al.

240 2011) and forage quality available for ungulates (Hamel et al. 2009; Borowik et al. 2013;  
241 Lendrum et al. 2014; Garrouette et al. 2016) and particularly for roe deer (Morellet et al. 2013;  
242 Peters et al. 2017). NDVI was used because of its simplicity, consistent coverage of all study  
243 areas, high temporal resolution and demonstrated utility in a variety of ecosystems. Given the  
244 linear relationship between NDVI and biomass, a given variation in NDVI should index a  
245 similar relative reduction in forage biomass across study sites. Hence, it provides a useful and  
246 integrative measure of variation in primary productivity which we assume to be suitable for  
247 our purpose of comparing roe deer populations inhabiting widely contrasting environmental  
248 conditions.

249 We obtained weekly values for the NDVI (pixel size = ca. 250m x 250m) from the  
250 University of Natural Resources and Life Sciences, Vienna (BOKU) using near real-time  
251 filtered products (Whittaker smoother, (Vuolo et al. 2012; Klisch and Atzberger 2016)) of the  
252 NDVI time series generated by the NASA Moderate Resolution Imaging Spectroradiometer  
253 (MODIS). We used the REFMID values, supplied by BOKU, which are the most stable  
254 extrapolated values of NDVI ([http://ivfl-info.boku.ac.at/index.php/eo-data-processing/real-](http://ivfl-info.boku.ac.at/index.php/eo-data-processing/real-time-modis-data-eu-only)  
255 [time-modis-data-eu-only](http://ivfl-info.boku.ac.at/index.php/eo-data-processing/real-time-modis-data-eu-only) for more details).

256 To describe spatial heterogeneity in resource distribution, we measured spatial  
257 heterogeneity of the NDVI at the study site level using the standard deviation of weekly  
258 values of the NDVI over all pixels of each study site (Coops et al. 1998; Coops and Culvenor  
259 2000). Then, we averaged these values across weeks for each period to obtain a proxy of  
260 spatial heterogeneity per seasonal period, defined above, and per year (from 2003 to 2014) for  
261 each study site. Spatial heterogeneity in NDVI ranged from 0.03 (low heterogeneity) to 0.23  
262 (high heterogeneity).

263 To index temporal predictability in resource distribution, we calculated temporal  
264 constancy of the NDVI values across years (*i.e.* from 2003 to 2014) for each period at a given

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

$$274 \quad Constancy = 1 + \frac{\sum \frac{\sum NDVI_{ij}}{\sum \sum NDVI_{ij}} \log\left(\frac{\sum NDVI_{ij}}{\sum \sum NDVI_{ij}}\right)}{\log(s)}$$

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

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

283

### 284 *Statistical analyses*

285 To analyse the link between space use behaviour of roe deer with spatial heterogeneity and  
286 temporal predictability in resource distribution, we exploited the extremely marked variation  
287 among study sites in environmental conditions, performing the analyses at the population  
288 level. We were unable to analyse within-population (*i.e.* individual level) variation in these

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

296

### 297 *How many sub-seasonal functional home ranges?*

298 We used Generalised Linear Mixed-Effects Models (glmm), with a Poisson distribution and a  
299 log-link function, to analyse variation in the number of sfHR within an individual's seasonal  
300 range (wintering or breeding period) in relation to annual movement tactic (resident vs.  
301 migratory), sex (male vs. female, because males are seasonally territorial in this species,  
302 Vanpé *et al.*, 2009) and two continuous descriptors of site-specific resource distribution:  
303 spatial heterogeneity and temporal predictability. We included the individual's period-specific  
304 log-transformed median sfHR size as an additive factor to control for variation in absolute  
305 resource availability between individuals (Morellet *et al.* 2013). Thus, the most complex  
306 model contained two three-way interactions among movement tactic, sex and resource  
307 heterogeneity and among movement tactic, sex and resource predictability, plus the logarithm  
308 of the median sfHR size as a fixed effect, and the study site as a random effect to control for  
309 repeated measures (individuals) per population. As the number of sfHR occupied by an  
310 individual ranged from 2 to 9, we subtracted 2 from the total number of sfHR per individual  
311 per season in order to conform to a Poisson distribution (Haight 1967). The number of sfHR  
312 then ranged from 0 to 7. We estimated sfHR size using fixed-kernel methods considering (i)  
313 an ad hoc approach to select the optimal smoothing parameter  $h$  for each sfHR estimate and

314 (ii) a constant  $h$  set to the overall median of the smoothing parameters estimated by the ad hoc  
315 approach for each individual sfHR estimate. Finally, sfHR size was estimated at both 90%  
316 and 50% isopleths.

317

### 318 *Spatial separation among sub-seasonal functional home ranges*

319 We used Linear Mixed-Effects models (lme) to investigate variation in log-transformed inter-  
320 sfHR distance, including period, movement tactic, sex and resource heterogeneity and  
321 resource predictability for each study site. We built the equivalent set of models described  
322 above for analysing variation in inter-sfHR distance.

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

327

## 328 **Results**

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

334

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

336 All individuals occupied more than one sfHR during a given season. Indeed, the model based  
337 on the occupation of more than one sfHR received more support than the two residency  
338 models (the CC value was highest for the multi-range model in all 572 cases, corresponding



339 to 286 individuals for the two periods, Supplementary materials, Appendix 1, Table A1).  
340 Individuals occupied a sfHR for at least 7 days (by definition, see Methods), and up to 186  
341 days during the wintering period (median = 10 days), and for at least 7 days, and up to 223  
342 days, during the breeding period (median = 24 days).

343

#### 344 *How many sub-seasonal functional home ranges?*

345 The most parsimonious model describing variation in the number of sfHR during the winter  
346 period included the two-way interaction between resource predictability and movement tactic  
347 and the log-transformed sfHR size ( $\Delta\text{AIC} = 0.0$ , AIC weight = 0.319,  $\text{df} = 6$ ) (Supplementary  
348 materials, Appendix 1, Table A2 & A4). During the winter period, the results were partially in  
349 accordance with our expectations. Firstly, in accordance with our second prediction, resident  
350 individuals occupied 1.5 fewer sfHR in the most predictable study site compared to the most  
351 unpredictable one. But contrary to this prediction, migrants tended to occupy one more sfHR  
352 in the most predictable study site compared to the most unpredictable one. However, in  
353 accordance with our third prediction, except in the most predictable study site where residents  
354 and migrants occupied the same number of sfHR, a resident individual used more sfHR on  
355 average than a migrant individual (Fig. 4a). Secondly, the number of sfHR that individuals  
356 used decreased as the median size of the sfHR they occupied increased. Indeed, an individual  
357 that occupied a large (sfHR size = 410 ha) sfHR had 4 fewer sfHR than an individual that  
358 occupied a small (sfHR size = 22 ha) sfHR (Fig. 4b).

359 The most parsimonious model describing variation in the number of sfHR during the  
360 summer period included sex and the log-transformed sfHR size ( $\Delta\text{AIC} = 0.0$ , AIC weight =  
361 0.167,  $\text{df} = 4$ ) (Supplementary materials, Appendix 1, Table A2 & A4). During the summer  
362 period, the difference in the number of sfHR occupied by males and females was low. Indeed,  
363 males used, on average, 0.4 sfHR more than females (Fig. 4c). Finally, as above, the number

364 of sfHR that individuals used decreased as the median size of the sfHR they occupied  
365 increased. Indeed, an individual that occupied a large (sfHR size = 450 ha) sfHR had 2 sfHR  
366 less than an individual that occupied a small (sfHR size = 20 ha) sfHR (Fig. 4c).

367

### 368 *Spatial separation among sub-seasonal functional home ranges*

369 The most parsimonious model describing variation in the log-transformed distance among  
370 sfHR during the wintering period included the two two-way interactions between resource  
371 heterogeneity and movement tactic and between resource heterogeneity and sex, with the  
372 additive effect of the log-transformed sfHR size ( $\Delta\text{AIC} = 0.6$ , AIC weight = 0.274,  $df = 9$ )  
373 (Supplementary materials, Appendix 1, Table A3 & A4). First, in accordance with our first  
374 prediction, spatial separation between pairs of sfHR during the wintering period increased  
375 with increasing resource heterogeneity, except among resident females (Fig. 5a and b).  
376 Indeed, when resource heterogeneity was high (resource heterogeneity = 0.26), the distance  
377 among sfHR of an individual was, on average, 700 meters (365 meters for resident males and  
378 1050 meters for migratory males), while for an individual living in the least heterogeneous  
379 study site (resource heterogeneity = 0.08) it was, on average, 300 meters. However, for  
380 resident females, this distance was 350 meters lower when resource heterogeneity was high.  
381 Finally, spatial separation among sfHR during the winter period was 3980 meters for an  
382 individual which occupied the largest sfHR (median sfHR size = 410 ha) compared to 80  
383 meters for an individual that occupied the smallest sfHR (median sfHR size = 22 ha) (Fig. 5c).

384 The best model describing variation in the log-transformed inter-sfHR distance during  
385 the summer period included resource predictability in addition to sex and the median log-  
386 transformed sfHR size ( $\Delta\text{AIC} = 1.86$ , AIC weight = 0.143,  $df = 6$ ) (Supplementary materials,  
387 Appendix 1, Table A3 & A4). Firstly, contrary to our second prediction, the distance between  
388 sfHR was 384 meters in the most predictable study site compared to 200 meters in the most

389 unpredictable one (Fig. 6a). Secondly, the distance between sfHR was 308 meters for females  
390 and 177 meters for males (Fig. 6b). Finally, the spatial separation among sfHR during the  
391 summer period was 4450 meters for an individual inhabiting the largest sfHR (median sfHR  
392 size = 450 ha) compared to 76 meters for an individual inhabiting the smallest sfHR (median  
393 sfHR size = 20 ha) (Fig. 6c).

394

## 395 **Discussion**

396 Animals are considered sedentary when their routine movements are centred on revisited  
397 areas (Papi 1992), leading to the emergence of a stable home range which may be occupied  
398 for a season, or for several years (Börger et al. 2008). Sedentary behaviour is a defining  
399 feature of the resident movement tactic, however, migratory animals may also be seasonally  
400 sedentary within each of their distinct seasonal ranges (Börger et al. 2008; Mueller and Fagan  
401 2008; Van Moorter et al. 2009). Here, we focused on movements at the within-season scale,  
402 when many large herbivores (Börger et al. 2008) and, in particular, roe deer (Hewison et al.  
403 1998), are presumed to be sedentary. Based on a comprehensive analysis of movement  
404 behaviour of 15 populations across Europe, we demonstrated that roe deer are never truly  
405 sedentary at the seasonal scale. Instead, within any given season, both migratory individuals  
406 and residents occupied at least two (and up to nine) spatially distinct sfHR. We suggest that  
407 this constitutes an overlooked movement mode, the multi-range tactic, which allows large  
408 herbivores to track fine-scaled spatio-temporal variation in the distribution of available  
409 resources and, thereby, to cope with changing environmental conditions. Indeed, we found  
410 that this space-use behaviour varied in relation to variation in environmental conditions across  
411 the European continent.

412         At the annual scale, we were able to assign a given individual to either a residency or a  
413 migratory tactic. However, when we analysed space use behaviour at the finer temporal scale

414 within seasons, we found that all roe deer in this study adopted the multi-range tactic during a  
415 given season. A similar pattern of space use behaviour has been documented in two African  
416 large herbivores, the sable antelope and the African savannah buffalo (Owen-Smith et al.  
417 2010; Cornélis et al. 2011; Benhamou 2014). These authors showed that the ranges of these  
418 animals were composed of several distinct areas which were exploited for several days or  
419 weeks. Thus, the use of multiple sfHR to track available food resources seems to be  
420 potentially widespread among large herbivores. Here, to understand the proximal drivers of  
421 this seasonal space use behaviour, we explored how spatial heterogeneity and temporal  
422 predictability of resource distribution influenced variation in the number and the spatial  
423 distribution of the sub-seasonal ranges that an individual exploits.

424 Mueller et al. (2011), focusing on movements at the annual scale, documented longer  
425 seasonal migrations among species inhabiting areas where large-scale primary productivity  
426 was spatially heterogeneous, but shorter migrations for species inhabiting environments with  
427 relatively low spatial heterogeneity. Similarly, but at the seasonal scale, we expected  
428 individuals to be less sedentary in heterogeneous environments than in homogeneous  
429 environments, occupying a higher number of more spatially distant sfHR. Our analyses only  
430 partially supported this prediction as, in heterogeneous study areas, the distance between  
431 sfHR was indeed higher compared to homogeneous sites, but only during winter.  
432 Furthermore, the number of sfHR that deer occupied did not vary in relation to resource  
433 heterogeneity. One explanation for this discrepancy could be linked to the relatively coarse  
434 spatial resolution of the NDVI metric that limits our ability to quantify small-scale variations  
435 in resource distribution at a level that is informative for individual animals. Indeed, Van  
436 Moorter et al. (2013) have shown that movements at a particular scale are driven by changes  
437 in the net profitability of trophic resources at the corresponding scale. As a result, a finer-scale  
438 measure of spatial heterogeneity could help us to better understand why roe deer use a number

439 of spatially distinct sub-seasonal functional home ranges, even in apparently homogeneous  
440 habitats.

441 Because nomadism is considered to be a response to unpredictability (Mueller and  
442 Fagan 2008), we expected roe deer to be less sedentary in unpredictable environments than in  
443 predictable environments. We found little support for this prediction. Our results indicated  
444 that, while controlling for resource heterogeneity, resource predictability had only a weak  
445 effect on the number of sfHR and the distance among sfHR. During summer, roe deer moved  
446 slightly further when in predictable environments than in unpredictable ones. During winter,  
447 resident roe deer adopted a space use behaviour that was somewhat similar to a nomadic tactic  
448 when in more unpredictable environments, occupying slightly more sfHR than in predictable  
449 environments. Migratory individuals, on the contrary, tended to occupy slightly less sfHR in  
450 predictable environments than in unpredictable ones. However, these relationships were weak,  
451 with the main difference being that resident individuals occupied more sfHR than migrants  
452 during winter. Seasonal migration is a tactic designed to cope with seasonal changes in the  
453 spatial distribution of resources (Fryxell and Sinclair 1988; Mueller and Fagan 2008). As a  
454 result, it seems that migratory individuals do not have to shift their ranges at the finer within-  
455 season scale, as they are able to adjust their movements to spatial variation in the distribution  
456 of available forage at the larger between-season scale. Given the lack of support for our  
457 predictions, we suggest that other factors such as fine-scale variation in forage plant  
458 distribution, predation risk, or human disturbance could drive roe deer to switch periodically  
459 from one locality to another. Theory also predicts that prey should perform frequent random  
460 movements to minimise the probability of encountering predators (Mitchell and Lima 2002).  
461 Indeed, previous studies have shown that herbivores modify their habitat selection or switch  
462 location after an encounter with a predator (Latombe et al. 2014; Lone et al. 2016).

463 From the point of view of landscape complementation (Dunning et al. 1992), an  
464 animal's home range must necessarily contain a combination of all non-substitutable  
465 resources required for survival and reproduction. Indeed, variation in home range size has  
466 previously been shown to reflect variation in resource availability, integrating interactions  
467 among local weather, climate and environmental seasonality (Morellet et al. 2013). Hence, all  
468 things being equal, animals will occupy larger home ranges when resources are more sparsely  
469 distributed in space (Saïd et al. 2005; Van Beest et al. 2011). Our analyses demonstrated  
470 strong relationships between sub-seasonal range size with both the number of sfRH and the  
471 distance between them. These results indicate that when resources are abundant, deer  
472 sequentially exploit a number of short-term functional ranges that are within close proximity.  
473 In contrast, when resources are limiting, deer tend to relocate less frequently, possibly due to  
474 the costs of doing so in terms of predation risk, mortality or energy (Hein et al. 2012;  
475 Johansson et al. 2014), but move greater distances when they do so to locate a new functional  
476 sub-seasonal range. This individual variation in space use is further demonstration of the  
477 extensive behavioural plasticity that roe deer express in relation to prevailing environmental  
478 conditions (Cagnacci et al. 2011; Morellet et al. 2013; Lone et al. 2016) which has driven the  
479 undoubted recent success story of this species across Europe (Linnell et al. 1998).

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

488 combining more frequent spasmodic movements interspersed with short periods of  
489 sedentarism, to track available resources.

490

## 491 **Acknowledgments**

492 This study was conducted within the EURODEER collaborative project. The co-authors are  
493 grateful to all members for their support for the initiative. The EURODEER data base is  
494 hosted by Fondazione Edmund Mach. For France, we would like to thank the local hunting  
495 associations and the Fédération Départementale des Chasseurs de la Haute Garonne for  
496 allowing us to work in the Comminges, as well as numerous co-workers and volunteers for  
497 their assistance. The Norwegian data collection was funded by the Norwegian Environment  
498 Agency and the county administration of Buskerud county. J Linnell was also funded by the  
499 Research Council of Norway (grants 212919 and 251112). Financial support for GPS data  
500 collection in the Bavarian Forest was provided by the EU-programme INTERREG IV (EFRE  
501 Ziel 3) and the Bavarian Forest National Park Administration. We also thank two anonymous  
502 reviewers for their constructive comments on an earlier version of this manuscript.

503

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

506

## 507 **Data accessibility**

508 Data used for this study are accessible on EURODEER website (<http://eurodeer.org>) on  
509 demand.

510

## 511 **References**

512 Baguette M, Stevens VM, Clobert J (2014) The pros and cons of applying the movement

513 ecology paradigm for studying animal dispersal. *Mov Ecol* 2:2:13.

514 Barraquand F, Benhamou S (2008) Animal movements in heterogeneous landscapes:  
515 identifying profitable places and homogeneous movement bouts. *Ecology* 89:3336–3348.

516 Benhamou S (2014) Of scales and stationarity in animal movements. *Ecol Lett* 17:261–272.

517 Bischof R, Loe LE, Meisingset EL, et al (2012) A migratory northern ungulate in the pursuit  
518 of spring: jumping or surfing the green wave? *Am Nat* 180:407–424.

519 Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home  
520 range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650.

521 Börger L, Fryxell JM (2012) Quantifying individual differences in dispersal using net squared  
522 displacement. In: Clobert J, Baguette M, Benton TJ, Bullock J (eds) *Dispersal Ecology  
523 and Evolution*, Oxford Uni. pp 222–230

524 Borowik T, Pettorelli N, Sönning L, Jedrzejewska B (2013) Normalized difference  
525 vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and  
526 field habitats. *Eur J Wildl Res* 59:675–682.

527 Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies:  
528 relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225.

529 Bracis C, Gurarie E, Van Moorter B, Goodwin RA (2015) Memory effects on movement  
530 behavior in animal foraging. *PLoS One* 10:1–21.

531 Brown JL, Orians GH (1970) Spacing patterns in mobile animals. *Annu Rev Ecol Syst* 1:239–  
532 262.

533 Bunnefeld N, Börger L, van Moorter B, et al (2011) A model-driven approach to quantify  
534 migration patterns: individual, regional and yearly differences. *J Anim Ecol* 80:466–476.

535 Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: A practical  
536 information-theoretic approach* (2nd ed). Springer

537 Cagnacci F, Focardi S, Ghisla A, et al (2015) How many routes lead to migration?



538 Comparison of methods to assess and characterise migratory movements. *J Anim Ecol*  
539 85:54–68.

540 Cagnacci F, Focardi S, Heurich M, et al (2011) Partial migration in roe deer: migratory and  
541 resident tactics are end points of a behavioural gradient determined by ecological factors.  
542 *Oikos* 120:1790–1802.

543 Chapin FS, Johnson DA, McKendrick JD (1980) Seasonal movement of nutrients in plants of  
544 differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *J Ecol*  
545 68:189–209.

546 Chapman BB, Hulthén K, Wellenreuther M, et al (2014) Patterns of animal migration. In:  
547 Hansson L-A, Åkesson S (eds) *Animal movement across scales*. Oxford University  
548 Press, pp 11–35

549 Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9:129–  
550 136.

551 Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena.  
552 *Ecology* 55:1153.

553 Coops N, Culvenor D (2000) Utilizing local variance of simulated high spatial resolution  
554 imagery to predict spatial pattern of forest stands. *Remote Sens Environ* 71:248–260.

555 Coops N, Culvenor D, Preston R, Catling P (1998) Procedures for predicting habitat and  
556 structural attributes in eucalypt forests using high spatial resolution remotely sensed  
557 imagery. *Aust For* 61:244–252.

558 Cornélis D, Benhamou S, Janeau G, et al (2011) Spatiotemporal dynamics of forage and water  
559 resources shape space use of West African savanna buffaloes. *J Mammal* 92:1287–1297.

560 Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in  
561 complex landscapes. *Oikos* 65:169–175.

562 English AK, Chauvenet ALM, Safi K, Pettorelli N (2012) Reassessing the determinants of

563 breeding synchrony in Ungulates. PLoS One 7:e41444.

564 Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores.  
565 Trends Ecol Evol 3:237–241.

566 Garrouste EL, Hansen AJ, Lawrence RL (2016) Using NDVI and EVI to map spatiotemporal  
567 variation in the biomass and quality of forage for migratory elk in the Greater  
568 Yellowstone Ecosystem. Remote Sens. doi: 10.3390/rs8050404

569 Gurarie E, Cagnacci F, Peters W, et al (2017) A framework for modeling range shifts and  
570 migrations: Asking whether, whither, when, and will it return. J Anim 943–959. doi:  
571 10.1111/ijlh.12426

572 Haight FA (1967) Handbook of the Poisson distribution. Wiley

573 Hamel S, Garel M, Festa-Bianchet M, et al (2009) Spring Normalized Difference Vegetation  
574 Index (NDVI) predicts annual variation in timing of peak faecal crude protein in  
575 mountain ungulates. J Appl Ecol 46:582–589. doi: 10.1111/j.1365-2664.2009.01643.x

576 Hein AM, Hou C, Gillooly JF (2012) Energetic and biomechanical constraints on animal  
577 migration distance. Ecol Lett 15:104–110. doi: 10.1111/j.1461-0248.2011.01714.x

578 Hewison AJM, Vincent J-P, Reby D (1998) Social organisation of European roe deer. In:  
579 Andersen R, Duncan P, Linnell JDC (eds) The European roe deer: The Biology of  
580 Success. Scandinavian University Press, Oslo, pp 189–219

581 Huang S, Meng SX, Yang Y (2009) Assessing the goodness of fit of forest models estimated  
582 by nonlinear mixed-model methods. Can J For Res 39:2418–2436.

583 IPCC (2014) Climate change 2014: Synthesis Report.

584 Jepsen JU, Topping CJ (2004) Modelling roe deer (*Capreolus capreolus*) in a gradient of  
585 forest fragmentation: behavioural plasticity and choice of cover. Can J Zool 82:1528–  
586 1541. doi: Doi 10.1139/Z04-131

587 Johansson CL, Muijres FT, Hedenström A (2014) The physics of animal locomotion. In:

588       Hansson L-A, Åkesson S (eds) Animal movement across scales. Oxford University  
589       Press, pp 232–258

590   Kerr JT, Ostrovsky M (2003) From space to species: Ecological applications for remote  
591       sensing. *Trends Ecol Evol* 18:299–305.

592   Klisch A, Atzberger C (2016) Operational drought monitoring in Kenya using MODIS NDVI  
593       time series. *Remote Sens* 8:267.

594   Latombe G, Fortin D, Parrott L (2014) Spatio-temporal dynamics in the response of woodland  
595       caribou and moose to the passage of grey wolf. *J Anim Ecol* 83:185–198.

596   Lavielle M (1999) Detection of multiple changes in a sequence of dependent variables. *Stoch*  
597       *Process their Appl* 83:79–102.

598   Lendrum PE, Anderson CR, Monteith KL, et al (2014) Relating the movement of a rapidly  
599       migrating ungulate to spatiotemporal patterns of forage quality. *Mamm Biol* 79:369–375.

600   Linnell JDC, Duncan P, Andersen R (1998) The European roe deer: A portrait of a successful  
601       species. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: The*  
602       *Biology of Success*. Scandinavian University Press, Oslo, pp 11–22

603   Lone K, Mysterud A, Gobakken T, et al (2016) Temporal variation in habitat selection breaks  
604       the catch-22 of spatially contrasting predation risk from multiple predators. *Oikos*  
605       126:624–632.

606   Mitchell WA, Lima SL (2002) Predator-prey shell games: large-scale movement and its  
607       implications for decision-making by prey. *Oikos* 99:249–259.

608   Morellet N, Bonenfant C, Börger L, et al (2013) Seasonality, weather and climate affect home  
609       range size in roe deer across a wide latitudinal gradient within Europe. *J Anim Ecol*  
610       82:1326–1339.

611   Mueller T, Fagan WF (2008) Search and navigation in dynamic environments - from  
612       individual behaviors to population distributions. *Oikos* 117:654–664.

613 Mueller T, Olson KA, Dressler G, et al (2011) How landscape dynamics link individual- to  
614 population-level movement patterns: a multispecies comparison of ungulate relocation  
615 data. *Glob Ecol Biogeogr* 20:683–694.

616 Nathan R, Getz WM, Revilla E, et al (2008) A movement ecology paradigm for unifying  
617 organismal movement research. *Proc Natl Acad Sci* 105:19052–19059.

618 Owen-Smith N, Fryxell JM, Merrill EH (2010) Foraging theory upscaled: the behavioural  
619 ecology of herbivore movement. *Philos Trans R Soc London* 365:2267–2278.

620 Papi F (1992) *Animal homing*. Chapman & Hall

621 Peters W, Hebblewhite M, Musterud A, et al (2017) Migration in geographic and ecological  
622 space by a large herbivore. *Ecol Monogr* 87:297–320.

623 Pettorelli N, Ryan S, Mueller T, et al (2011) The Normalized Difference Vegetation Index  
624 (NDVI): Unforeseen successes in animal ecology. *Clim Res* 46:15–27. doi:  
625 10.3354/cr00936

626 Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575.

627 R Development Core Team (2014) *R: a language and environment for statistical computing*.

628 Revilla E, Wiegand T (2008) Individual movement behavior, matrix heterogeneity, and the  
629 dynamics of spatially structured populations. *Proc Natl Acad Sci USA* 105:19120–  
630 19125.

631 Riotte-Lambert L, Benhamou S, Chamailé-Jammes S (2015) How Memory-Based Movement  
632 Leads to Nonterritorial Spatial Segregation. *Am Nat* 185:E103-16.

633 Rivrud IM, Loe LE, Mysterud A (2010) How does local weather predict red deer home range  
634 size at different temporal scales? *J Anim Ecol* 79:1280–1295.

635 Saïd S, Gaillard J-M, Duncan P, et al (2005) Ecological correlates of home-range size in  
636 spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *J*  
637 *Zool* 267:301–308.

638 Spitz DB, Hebblewhite M, Stephenson TR (2017) “MigrateR”: extending model-driven  
639 methods for classifying and quantifying animal movement behavior. *Ecography (Cop)*  
640 40:788–799.

641 Turchin P (1991) Translating foraging movements in heterogeneous environments into the  
642 spatial distribution of foragers. *Ecology* 72:1253–1266.

643 Turchin P (1998) Quantitative analysis of movement: measuring and modeling population  
644 redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts,  
645 USA

646 Van Beest FM, Rivrud IM, Loe LE, et al (2011) What determines variation in home range  
647 size across spatiotemporal scales in a large browsing herbivore? *J Anim Ecol* 80:771–  
648 785.

649 Van Moorter B, Bunnefeld N, Panzacchi M, et al (2013) Understanding scales of movement:  
650 animals ride waves and ripples of environmental change. *J Anim Ecol* 82:770–780.

651 Van Moorter B, Rolandsen CM, Basille M, Gaillard J-M (2016) Movement is the glue  
652 connecting home ranges and habitat selection. *J Anim Ecol* 85:21–31.

653 Van Moorter B, Visscher D, Benhamou S, et al (2009) Memory keeps you at home: a  
654 mechanistic model for home range emergence. *Oikos* 118:641–652.

655 Vanpé C, Gaillard J, Morellet N, et al (2009) Age-Specific Variation in Male Breeding  
656 Success of a Territorial Ungulate Species, the European Roe Deer. *J Mammal* 90:661–  
657 665.

658 Vuolo F, Mattiuzzi M, Klisch A, Atzberger C (2012) Data service platform for MODIS  
659 Vegetation Indices time series processing at BOKU Vienna: current status and future  
660 perspectives. *SPIE Proc* 8538:85380A.

661 Wiens JA (1976) Population responses to patchy environments. *Annu Rev Ecol Syst* 7:81–  
662 120.

663

## 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	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
<b>Total</b>		<b>93</b>	<b>193</b>	<b>190</b>	<b>96</b>

644 **Figure legends**

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

648 **Fig. 2** Example of the segmentation approach using Lavielle’s Method (1999) on the  
649 movement trajectory of a migratory individual (individual 1367 monitored in 2008) during the  
650 winter and the summer seasons (top) and the corresponding sub-seasonal functional home  
651 ranges (sfHR) (bottom). The X-axis indicates the chronological order of successive locations  
652 and the Y-axis shows the Net Squared Displacement (NSD). Vertical lines correspond to cut-  
653 off points defining the sequential sfHR

654 **Fig. 3** Example of the segmentation approach using Lavielle’s Method (1999) on the  
655 movement trajectory of a resident individual (individual 2296 monitored in 2013), during the  
656 winter and the summer seasons (top) and the corresponding sub-seasonal functional home  
657 ranges (sfHR) (bottom). The X-axis indicates the chronological order of successive locations  
658 and the Y-axis shows the Net Squared Displacement (NSD). Vertical lines correspond to cut-  
659 off points defining the sequential sfHR

660 **Fig. 4** Graphical representation of the best models describing variation in the number of sub-  
661 seasonal home ranges (sfHR) during the winter season, as a function of the two-way  
662 interaction between resource predictability and movement tactic (a) and the log-transformed  
663 sfHR size (b) ; and during the summer season as a function of sex and the log-transformed  
664 sfHR size (c). In order to better visualize the raw data, we plotted the mean number of sfHR  
665 for each study site. Dotted lines represent the 95% confidence intervals resulting from the  
666 model predictions, error bars represent the standard deviation in number of sfHR, and the  
667 letters correspond to the ‘study site id’ in Table 1. We fixed movement tactic as resident,

668 resource predictability and the log-transformed sfHR size at their mean when not represented  
669 in the figures

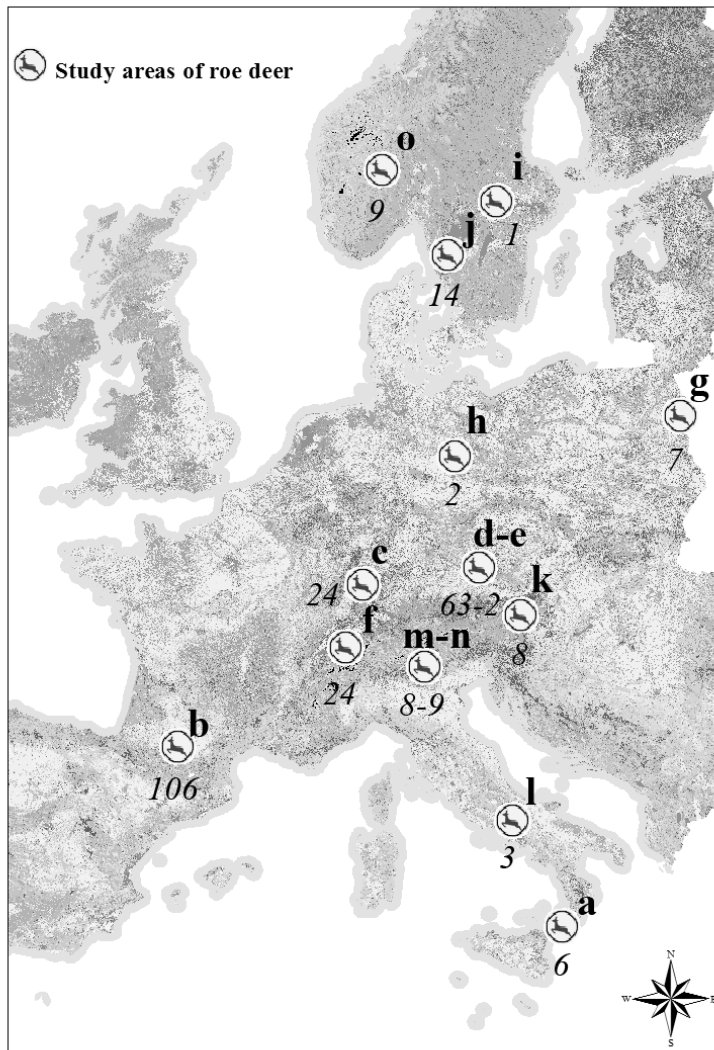
670 **Fig. 5** Graphical representation of the best model describing variation in the log-transformed  
671 distance among sub-seasonal home ranges (sfHR) during the winter, as a function of the two-  
672 way interaction between resource heterogeneity and movement tactic and between resource  
673 heterogeneity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

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

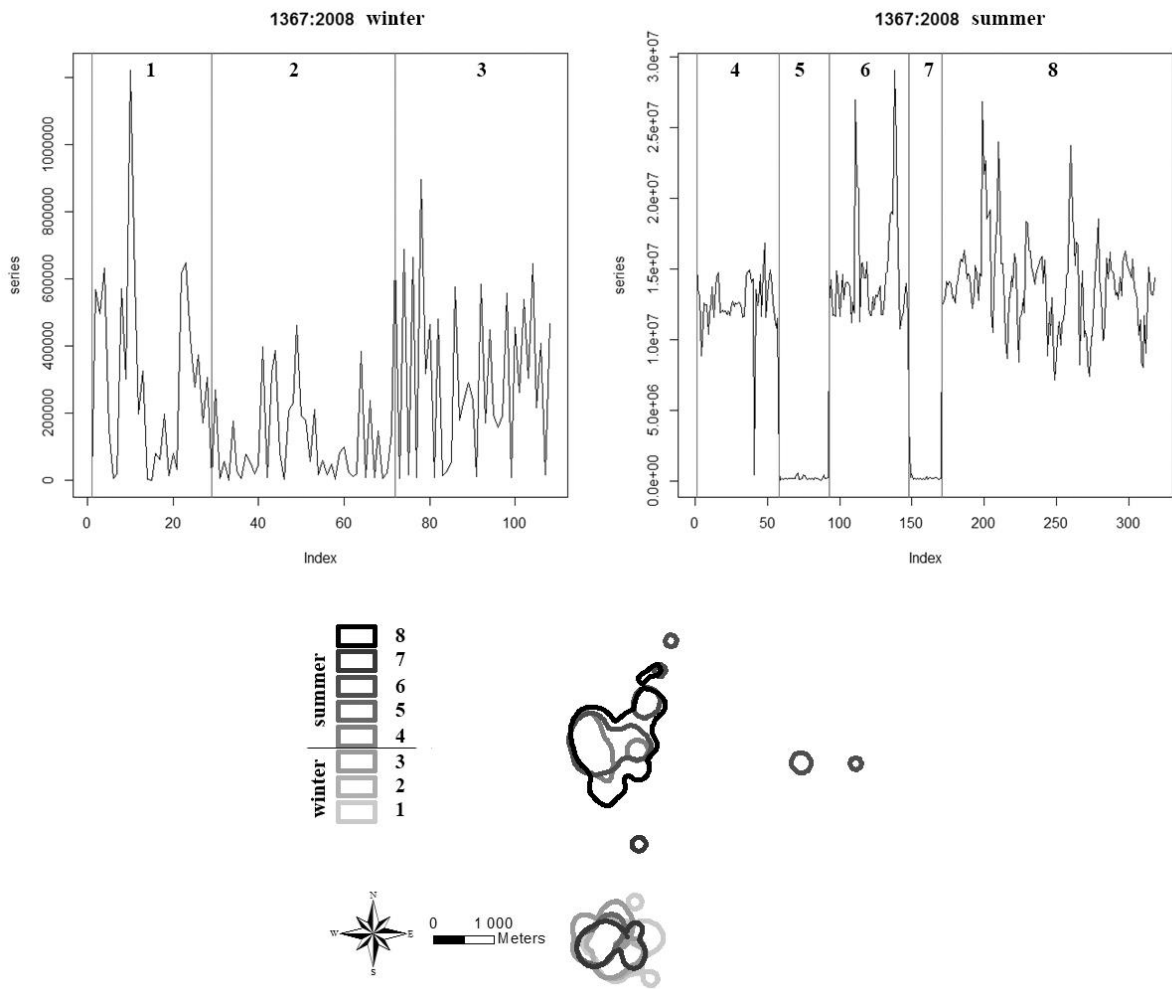
689



**Fig. 1**



**Fig. 2**



**Fig. 3**

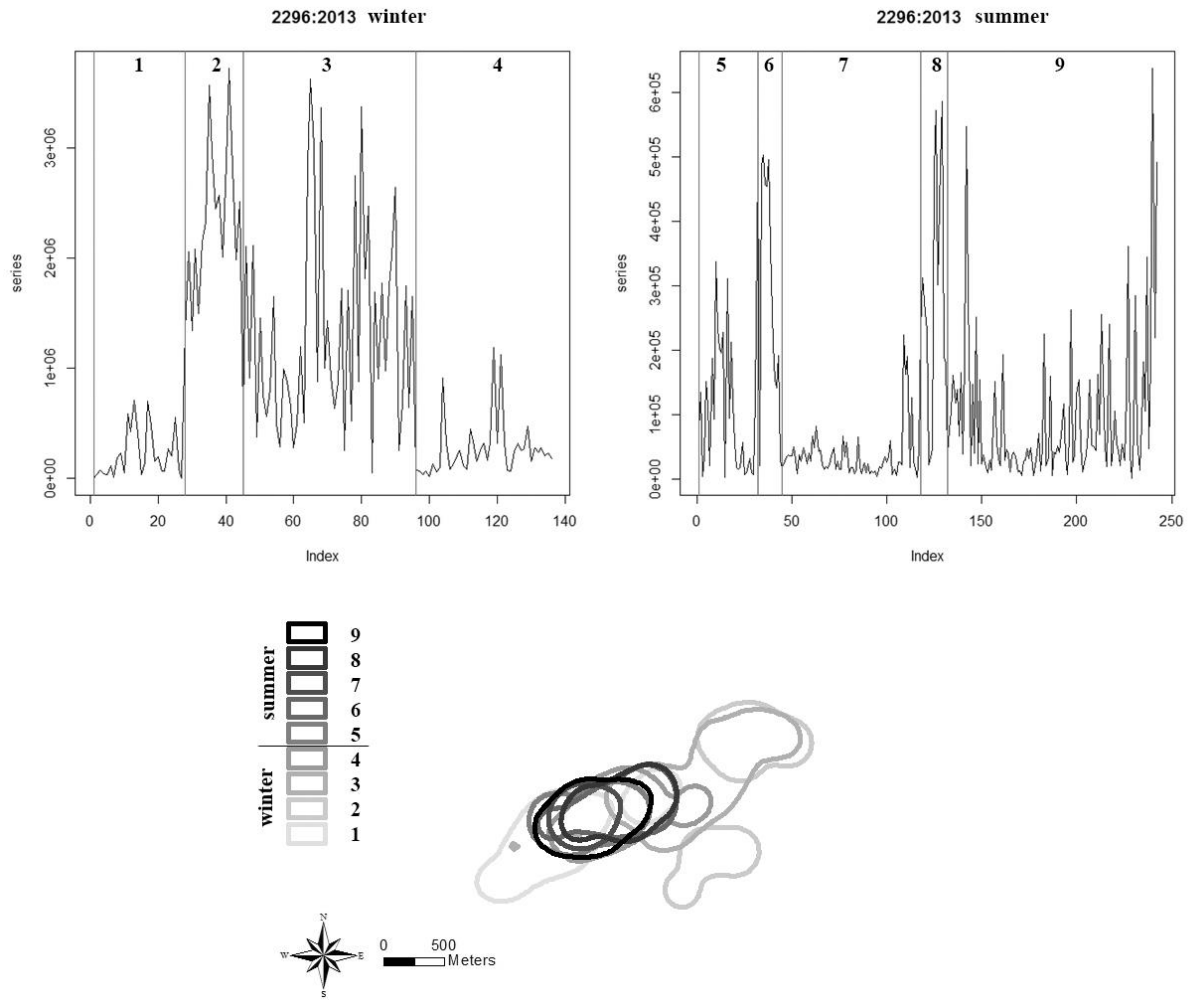


Fig. 4

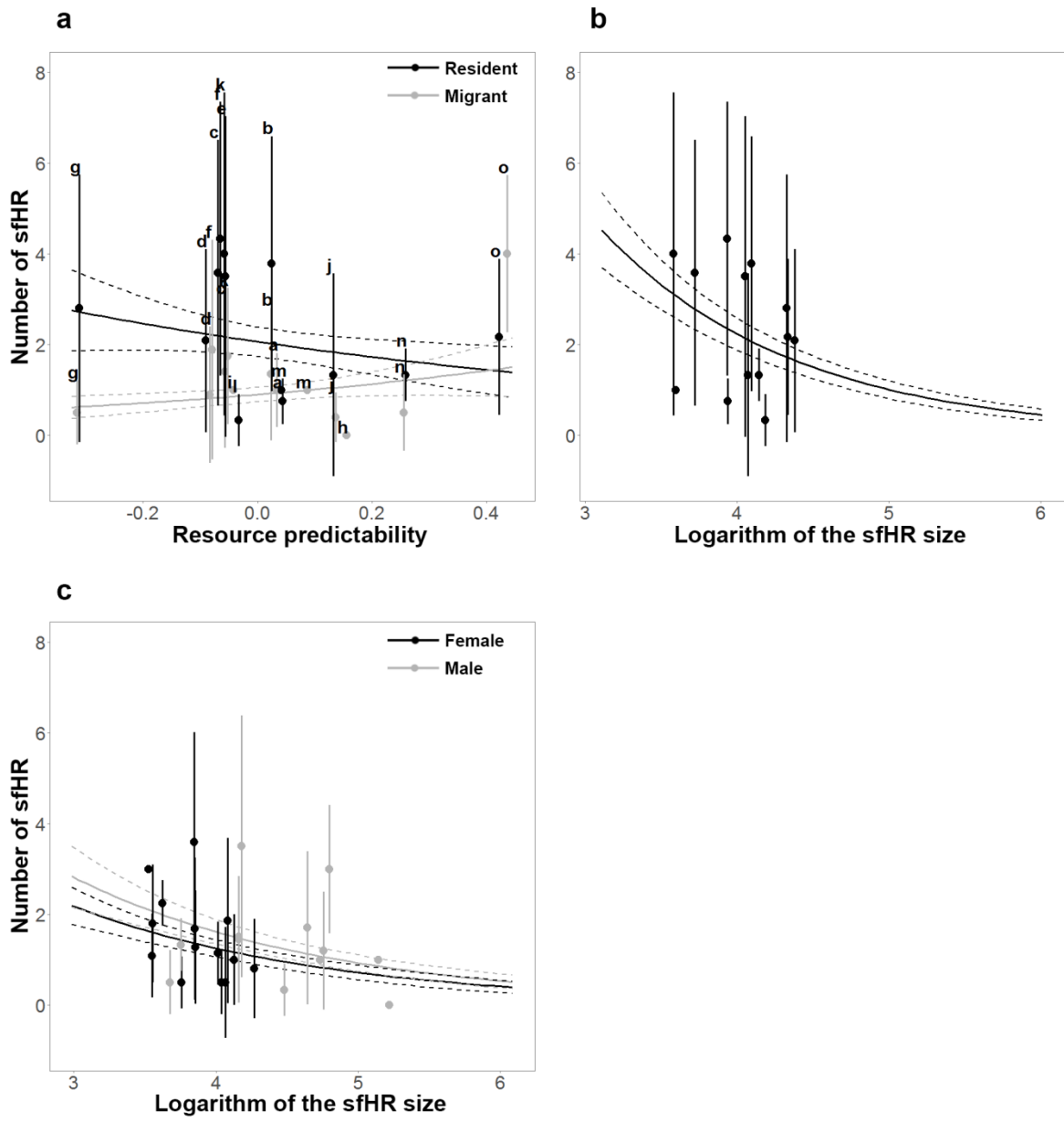
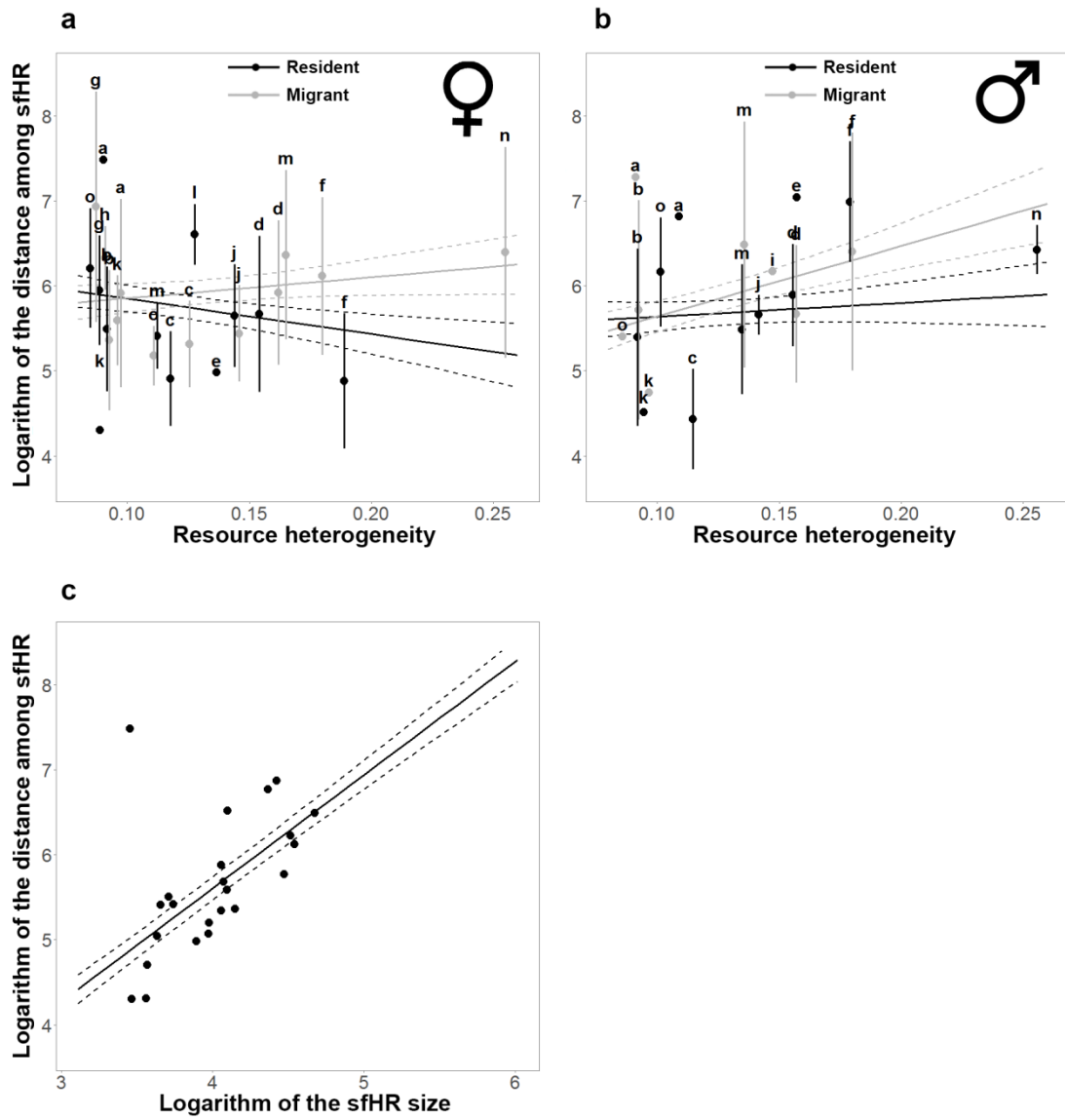
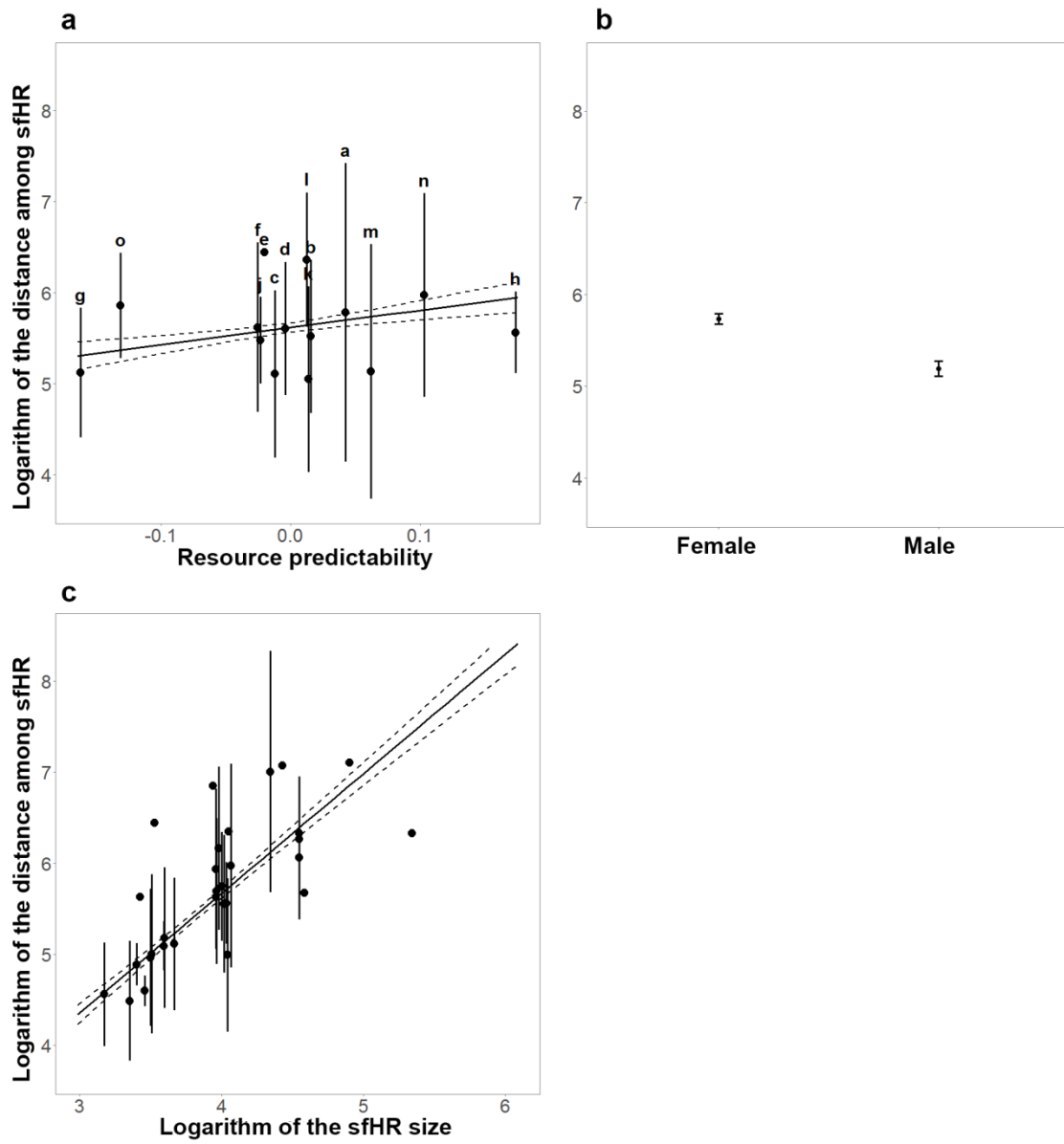
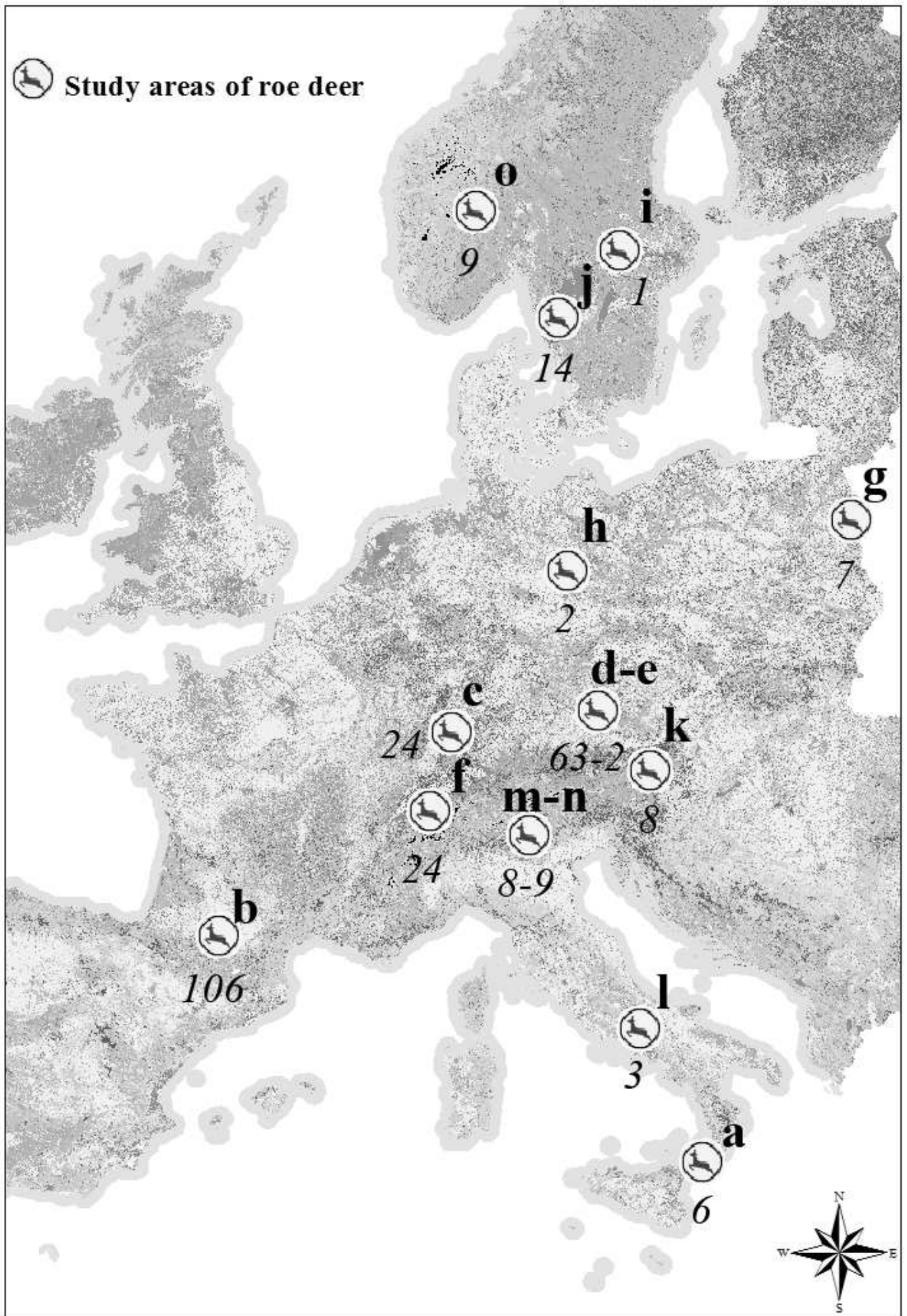


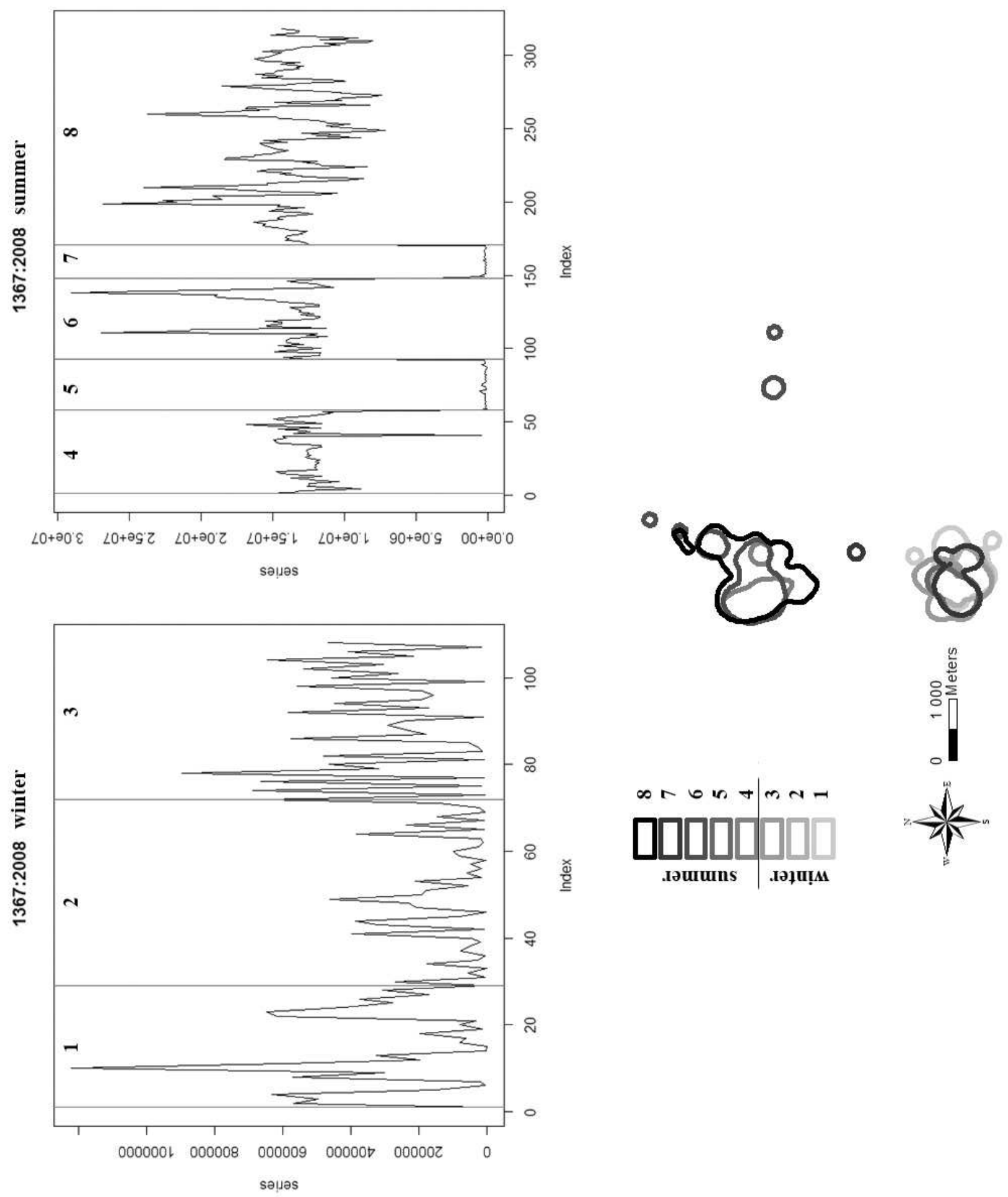
Fig. 5



**Fig. 6**

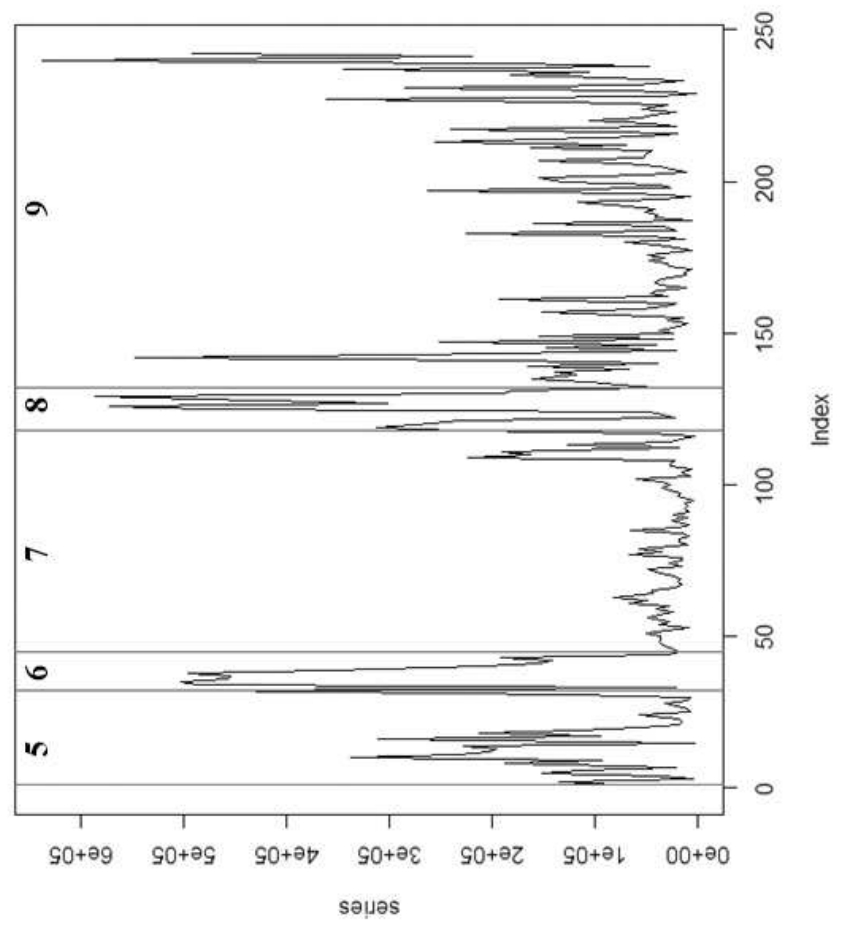








2296:2013 summer



2296:2013 winter

