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

3

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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 15th of February to the 15th 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 15th 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 6th of March to the
196 3rd of August (median = 4th of May, sd = 32 days), while return ranged from the 7th of May to
197 the 28th of October (median = 10th 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 ± 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, $df = 6$) (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, $df = 4$) (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 ($\Delta AIC = 0.6$, 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 ($\Delta AIC = 1.86$, 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

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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

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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
Total		93	193	190	96

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

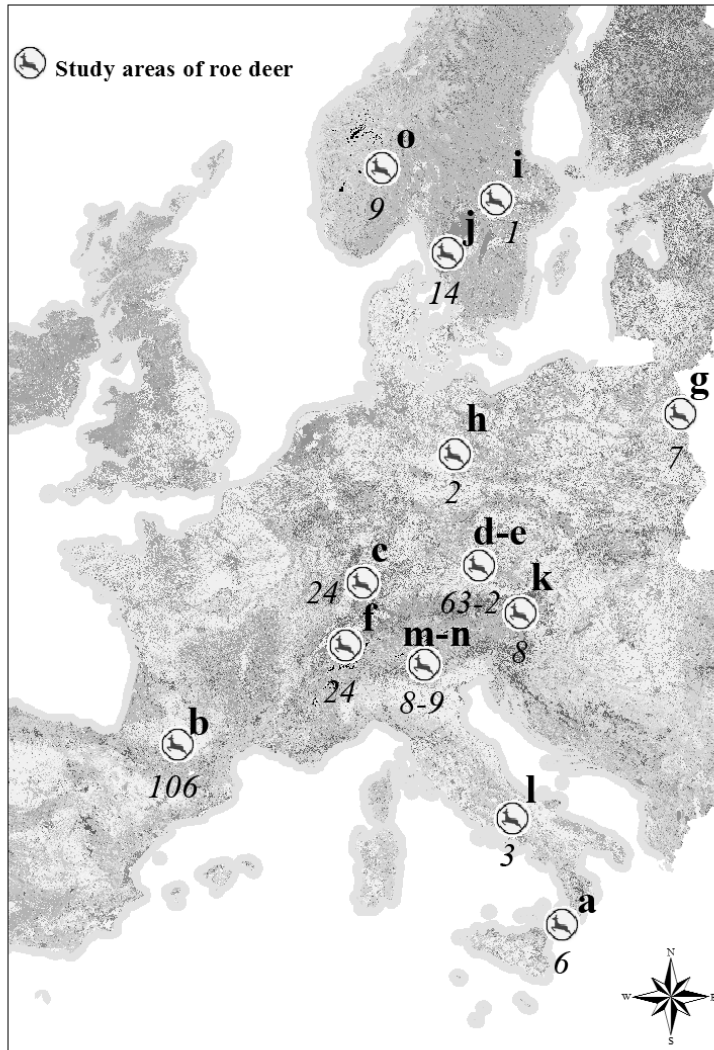


Fig. 2

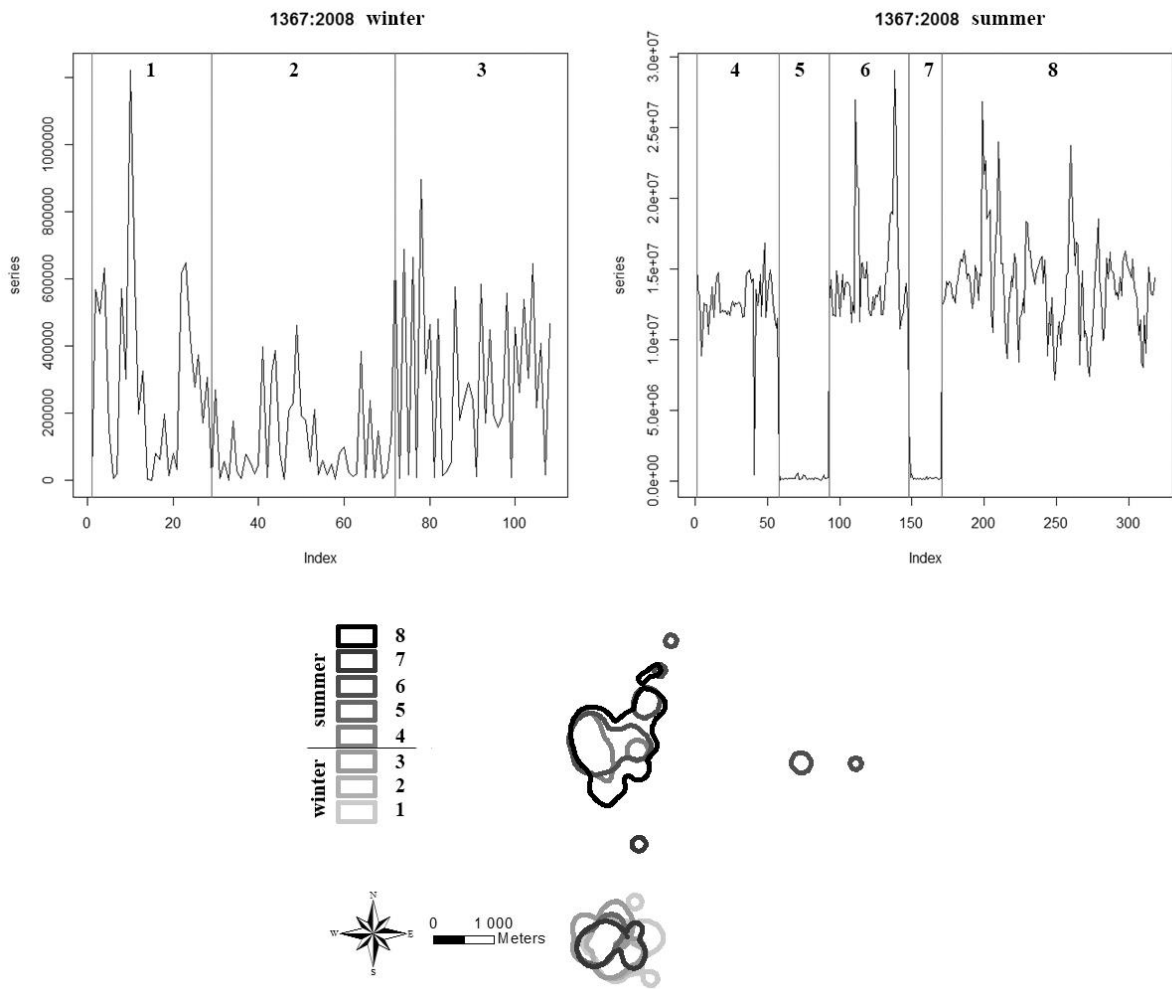


Fig. 3

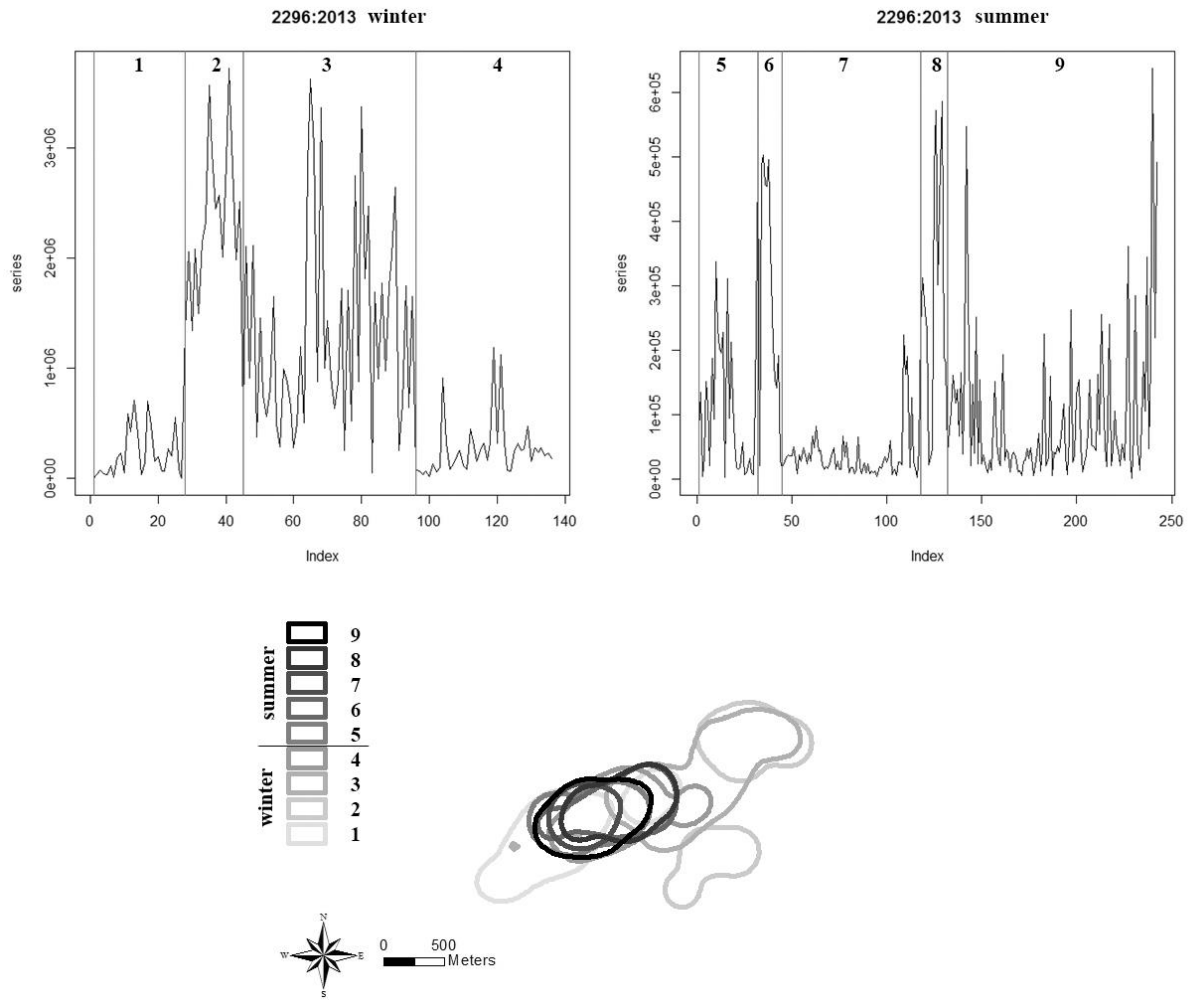


Fig. 4

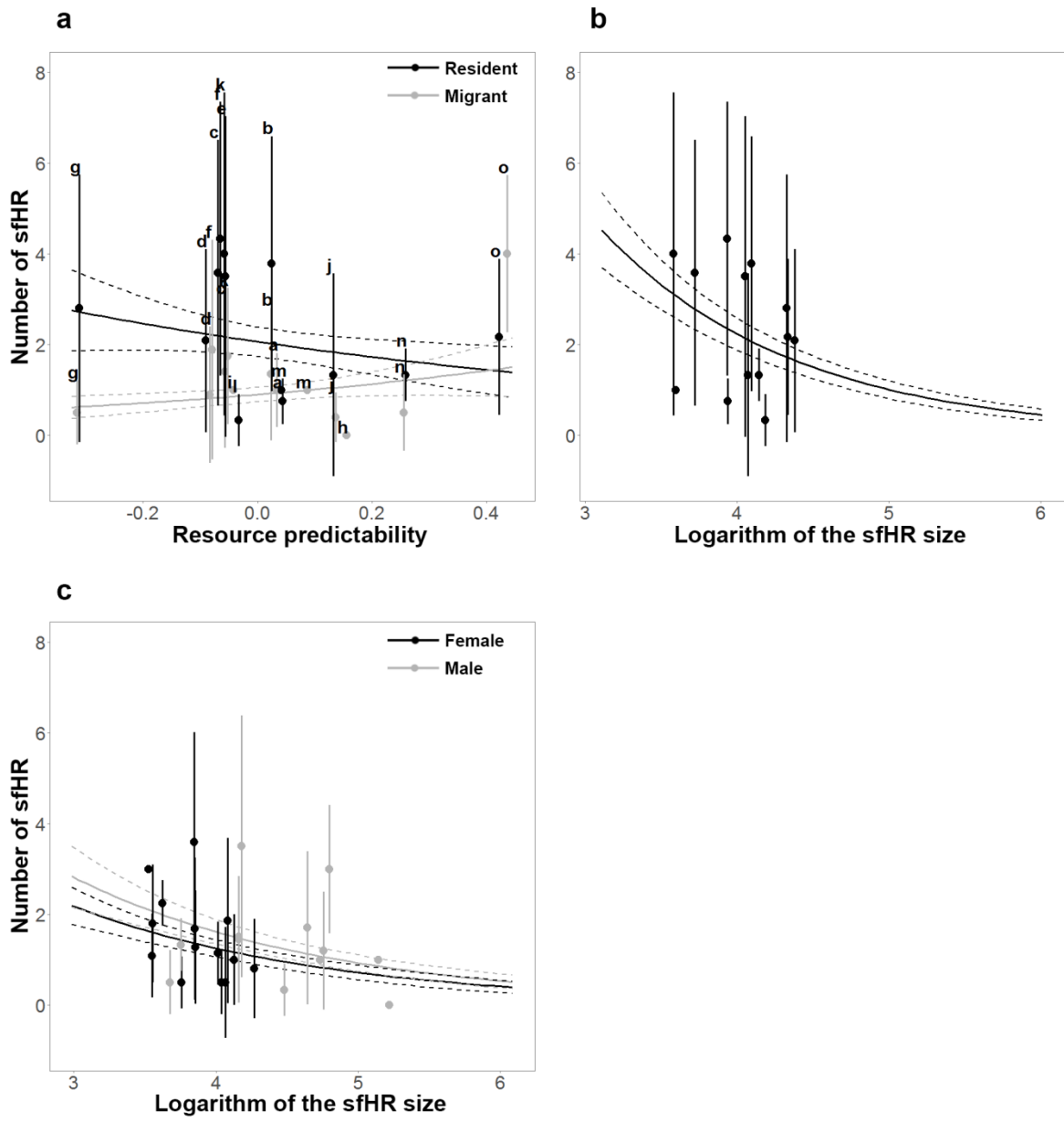


Fig. 5

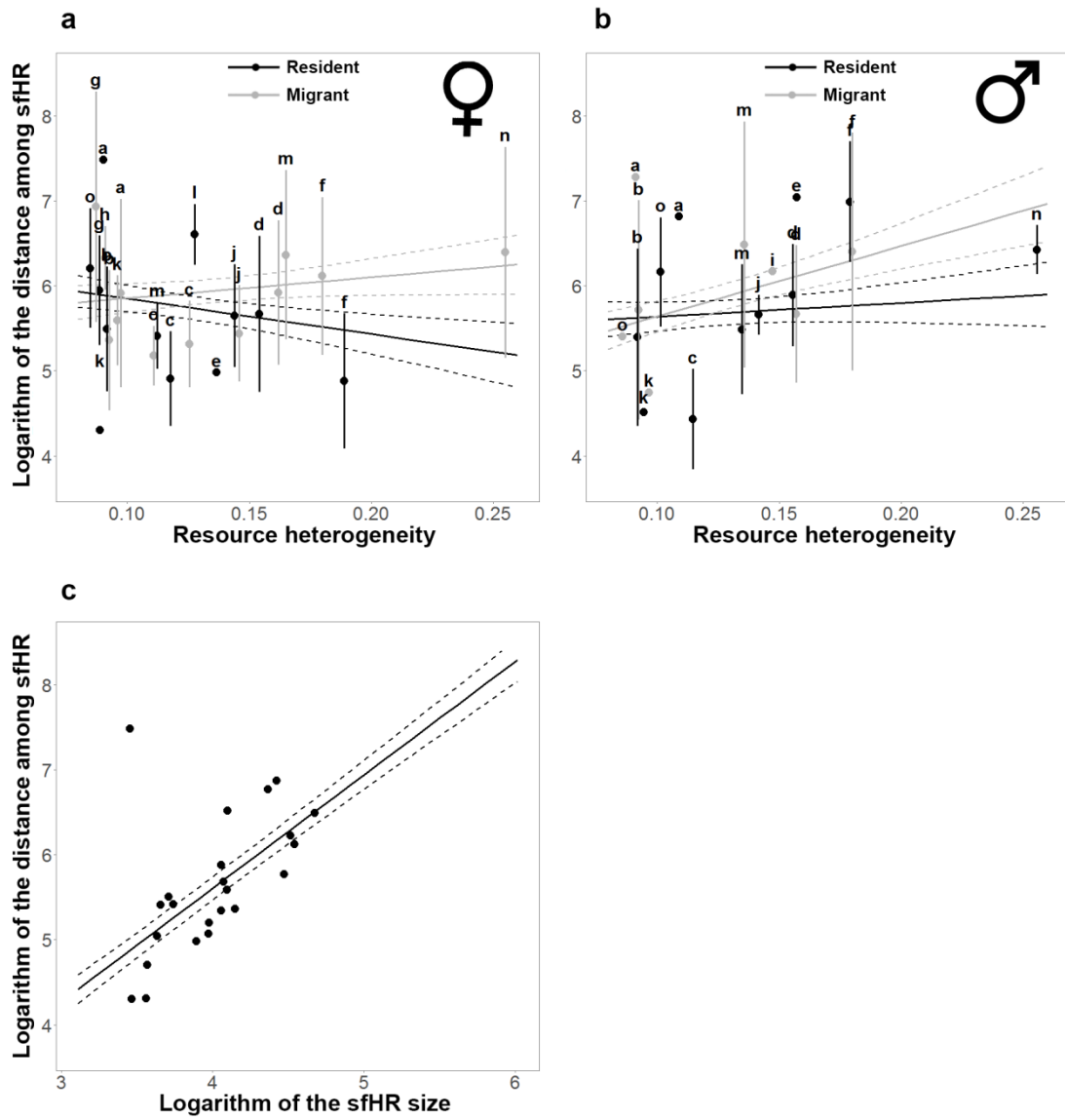
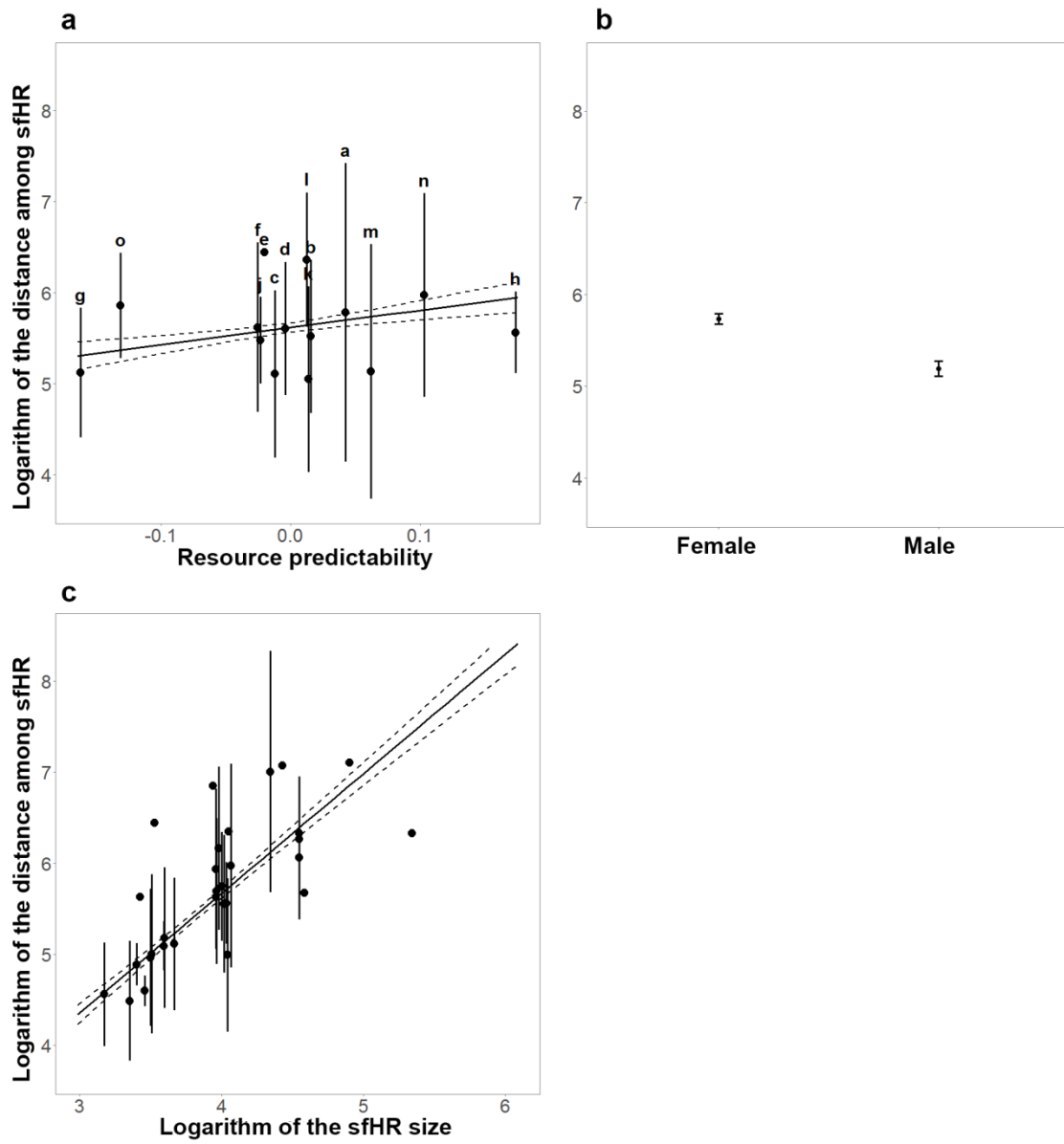
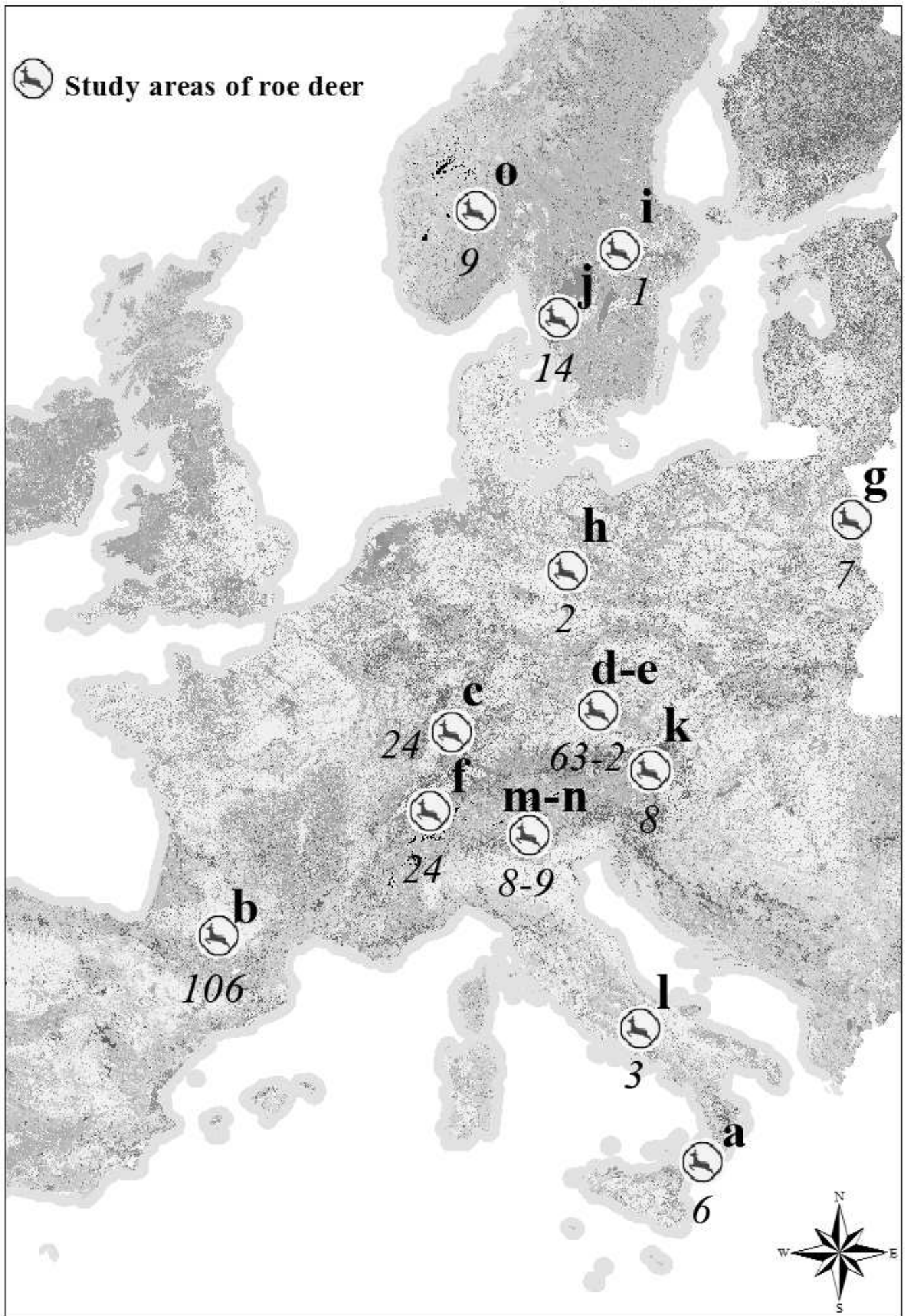
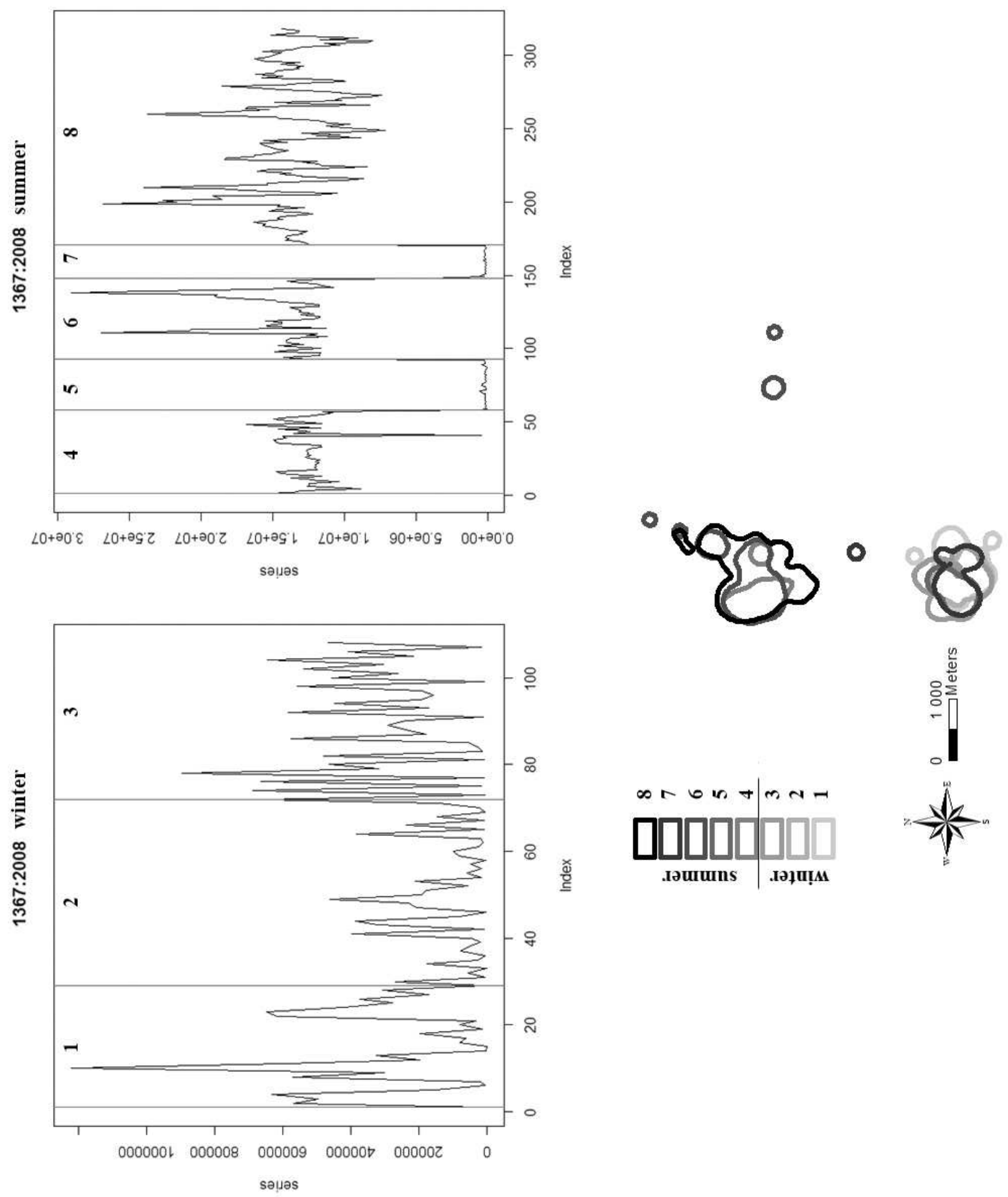


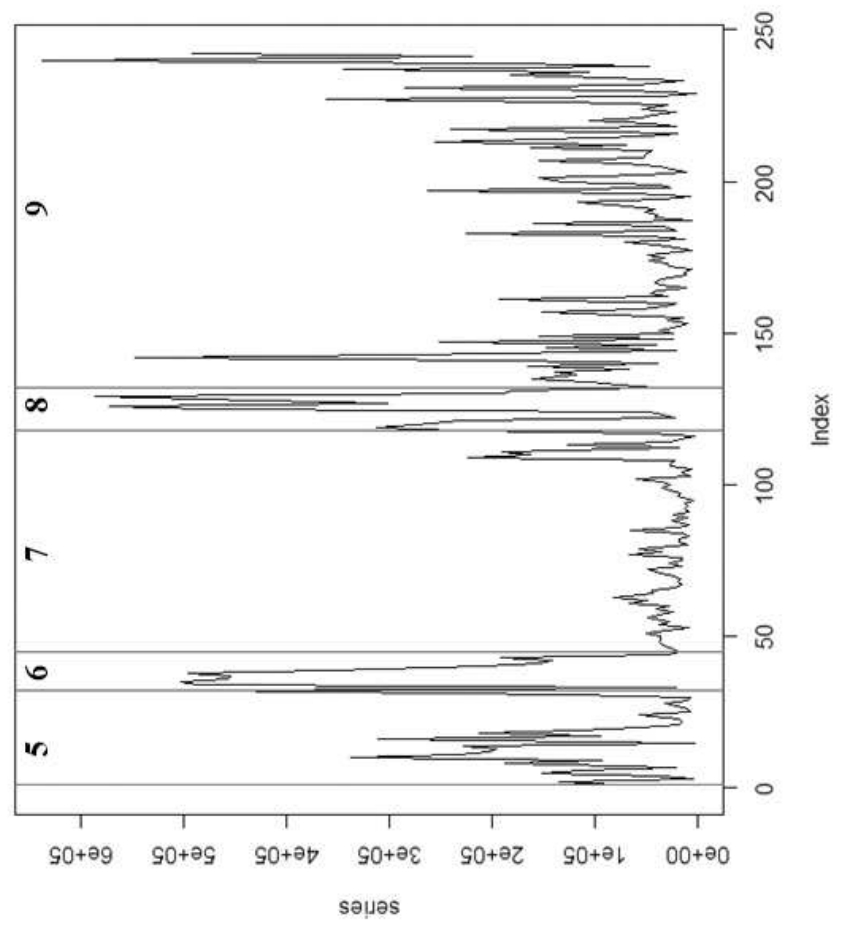
Fig. 6







2296:2013 summer



2296:2013 winter

