1   **Title:** Movement and space-use responses of a large herbivore to experimental alteration of

2   resource availability

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15 **Abstract**

16 Resource acquisition is a key factor governing patterns of animal movement. While the link

17 between spatio-temporal resource patterns and movement behaviour has been widely

18 documented for migration, our understanding of home ranging behaviour in relation to resource

19 dynamics has been limited by challenges of quantifying resource heterogeneity at fine spatio-

20 temporal scales. In this study, we addressed this issue by analysing the movement responses of a

21 resident large herbivore in response to an *in situ* manipulation of a high-quality, concentrated

22 food resource. Specifically, we fitted roe deer (*Capreolus capreolus*) with GPS collars in the

23 Eastern Italian Alps and recorded their fine-scale movement responses to an alteration of feeding

24 site accessibility, for a total of 25 animal-years. The experiment involved identifying, for each

25 animal, a familiar feeding site, whose accessibility was transitorily restricted (i.e., closed) while

26 maintaining the availability of forage at alternative feeding sites. First, we tested whether

27 individuals altered their spatial behaviour to track dynamical changes in resource availability.

28 Experimental closure led to larger, spatially-shifted home ranges, resulting from more

29 exploratory movements. Individual roe deer compensated the loss of their familiar feeding site

30 by using alternative ones, and by doing so maintained their overall use of these concentrated

31 resources. Our results demonstrate that roe deer actively track resource dynamics, and rapidly

32 adjust their space-use and movement behaviour in response to changes in resource availability.

33 Second, we showed that individual resource preferences mediate these behavioural adjustments:

34 individuals characterized by a high preference for feeding sites exhibited larger space-use shifts

35 and stronger changes in resource use in response to the resource manipulation. In contrast, sex

36 had relatively minor influence on the observed patterns. Third, we investigated the role of site

37 familiarity in roe deer foraging decisions. We found that space-use and resource use during the

2

38   post-closure period were restored to pre-closure patterns, thereby providing evidence for the

39   inherent benefits of site familiarity to animals maintaining a home range. Together, our results

40   establish the connections between movement, space-use, individual preference, and the spatio-

41   temporal pattern of resources in deer home ranging behaviour.

42

43   **Key-words:** *Capreolus capreolus*; concentrated resource; familiarity; home range; *in situ*

44   experiment; resource preference; roe deer; supplemental feeding site.

45

46   **Introduction**

47   Animals move to change the environmental context they experience (Van Moorter,

48   Rolandsen, Basille, & Gaillard, 2016), including abiotic conditions, the presence of predators

49   and competitors, and the availability of resources. Because foraging efficiency can be linked to

50   individual fitness (Stephens & Krebs, 1986), food acquisition is thought to be a primary driver

51   underlying animal movements (e.g., Mueller & Fagan, 2008). Consequently, space-use

52   represents the geographic realization of optimizing fitness as a function of resource availability

53   and acquisition costs (Mitchell & Powell, 2004).

54   Food resources are usually dynamic in both space and time (Wiens, 1976). In the case of

55   herbivores, animals typically feed on resources distributed in patches, which are characterized by

56   important temporal variations in quantity and quality (Owen-Smith, Fryxell, & Merrill, 2010). In

57   this context, Mueller et al. (2011) have shown that strong spatio-temporal gradients in resource

58   availability at either landscape or regional scales appear to drive migration and nomadism tactics.

59   In many herbivore populations, however, individuals show a high year-round fidelity to a

60   spatially-localized home range. It has been suggested that the foraging benefits of site

61 familiarity, where resources are constant or predictable, are responsible for the formation of a

62 stable home range (see Fagan et al., 2013 for a review). While the home range has traditionally

63 been perceived as a relatively static space-use tactic, recent evidence suggests that animals have

64 sub-seasonal home ranges (Benhamou 2014), i.e. focus their movements into particular areas in

65 response to seasonal variation in local resource availability. For example, Couriot et al. (2018)

66 have shown that in roe deer (*Capreolus capreolus*) sub-seasonal home ranges are a ubiquitous

67 behavioural tactic across a wide ecological gradient.

68   The link between movement behaviour and resource dynamics is less clear when

69 observing home ranging behaviour than migration or nomadism (Mueller & Fagan, 2008),

70 because of the difficulty to quantify spatio-temporal variability in resource heterogeneity at small

71 spatial scales (Couriot et al., 2018). In this study, we address this issue by experimentally

72 manipulating the spatio-temporal patterns of food availability within home ranges. *In situ* food

73 manipulation experiments have a long history in the study of population dynamics, with a

74 primary focus on understanding the numerical response to food supplementation (e.g., Krebs,

75 1971), and of animal communities (e.g., Brown & Munger, 1985). Although these field

76 experiments have provided fundamental insights in animal ecology, they have seldom been

77 combined with the emerging technological capabilities of animal tracking (Cagnacci, Boitani,

78 Powell, & Boyce, 2010) to investigate the implications of food availability on individual

79 movements and space-use. In a rare example of field experiment in large herbivores, Kilpatrick

80 and Stober (2002) showed that white-tailed deer (*Odocoileus virginianus*) shifted their core-area

81 i.e., familiar areas of use, in response to novel food supplementation. In a second experiment,

82 van Overveld and Matthysen (2010) demonstrated that the individual variability in responses to

83 an alteration of resource distribution are personality-dependent in great tits (*Parus major*). Our

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84 research builds upon these two studies by investigating the spatial responses of a large herbivore,

85 roe deer, to an experimental *in situ* manipulation of a high-quality, concentrated food resource in

86 relation to both individual resource preferences and site familiarity.

87   Observational studies have suggested that, as browsers with limited fat reserves

88 (Andersen, Gaillard, Linnell, & Duncan, 2000), roe deer exhibit a tight association between

89 movement and resource dynamics (Ossi et al. 2017) with a strong plasticity to adapt its resource

90 acquisition at different spatio-temporal scales (De Groeve et al., 2019; Morellet et al., 2013;

91 Peters et al., 2017). In contrast to group-living ungulates, the foraging decisions of roe deer are

92 expected to be clearly expressed at the level of individuals. The experiment was conducted

93 during winter, when food scarcity limits roe deer foraging performance, and individuals are most

94 inclined to adjust their spatial behaviour to continue meeting their energy requirements (Ossi,

95 Gaillard, Hebblewhite, & Cagnacci, 2015).

96   We tagged roe deer in the Eastern Italian Alps with GPS units and followed their

97 movements during transitory alterations of food availability at supplemental feeding sites (FS),

98 i.e. discrete resource patches with an identifiable resource value distinguishable from the

99 vegetation matrix (Mitchell & Powell, 2004; Wiens, 1976). The experiment therefore mimics –

100 on free-ranging animals – the variation in the availability of concentrated, high-reward resources

101 akin to watering holes for savannah ungulates (Owen-Smith, 2004) and feral horses (*Equus*

102 *ferus*; Rozen-Rechels et al. 2015), or fruit trees for hornbills (*Ceratogymna atrata* and *C.*

103 *cylindricus*; Holbrook et al. 2002), forest chimpanzees (*Pan troglodytes*; Normand et al. 2009)

104 and other frugivorous primates.

105   In large herbivores, and roe deer in particular, our initial hypothesis states that individuals

106 alter their movement behaviours and consequently space-use patterns to track dynamics in

5

107   resource availability (H1; Table 1). We predicted that the loss of a key foraging resource should

108   lead to larger (P1.1), and spatially-shifted (P1.2) home ranges, resulting from more explorative

109   movements (P1.3). Furthermore, we predicted that roe deer reduced the intensity of use of the

110   familiar FS when food accessibility was prevented (P1.4a) and compensated for this loss by

111   using other accessible FS (P1.4b).

112   We further hypothesized that the behavioural adjustments to changes in resource

113   availability would vary between individuals (H2; Table 1). In particular, because roe deer males

114   have been shown to maintain a high year-round fidelity to their summer territory (Linnell &

115   Andersen, 1998), we predicted that they would respond less markedly to the experiment than

116   females (P2.1). We also predicted the responsiveness of roe deer to be positively influenced by

117   the individual's prior preference for FS (P2.2).

118   If the spatial patterns of roe deer home ranges result from the foraging benefits of site

119   familiarity (Riotte-lambert, Benhamou, & Chamaillé-Jammes, 2015; Van Moorter et al., 2009),

120   animals should strive to use familiar areas and resources when accessible (H3; Table 1).

121   Accordingly, we predicted that when initial conditions of food accessibility are re-established

122   after perturbation, the initial space-use patterns would be restored (P3.1), following a return to

123   high use of the familiar FS (P3.2).

124

125   **Materials and methods**

126   *Study area*

127   Roe deer is the primary large herbivore in the study area (7-8 individuals km^{-2}), located in

128   the north-eastern Italian Alps (Argentario range, Autonomous Province of Trento). The area is

129   characterized by a continental climate (mean temperature of January: 1.0 °C; July: 21.0 °C; mean

130   annual rainfall: 966 m) with occasional snow cover, and is largely forested (80%). It

131   encompasses four hunting reserves in which selective hunting occurs between September and

132   December (see Appendix S1 for further details).

133   Supplemental feeding management of roe deer is conducted year-round at > 50 distinct

134   feeding sites (FS; Appendix S2: Fig. S2.1). FS are typically wooden hopper dispensers that

135   provide a continuous supply of corn accessible through a tray (Fig. 1a). They are managed by

136   private hunters for roe deer but are also attended sporadically by red deer (*Cervus elaphus*).

137

138   *Experimental design*

139   We took advantage of roe deer use of a focal, identifiable resource – the FS – to design an

140   *in situ* experimental manipulation of resource availability. We created three successive

141   experimental phases of the availability of this resource – pre-closure, closure and post-closure –

142   by physically managing the accessibility of food at the FS. During the closure phase, access to

143   forage at FS was transitorily restricted by placing wooden boards obstructing the tray; these were

144   then removed again in the post-closure phase (Fig. 1).

145   The experiment was conducted between January and April, when roe deer use of

146   supplemental feeding is the most intense (Ossi et al., 2017), for three consecutive winters (2017,

147   2018 and 2019). We implemented the experiment on 18 individuals, including five recaptures

148   and two deployments spanning two winters, leading to a total of 25 animal-years (21 adults: 15

149   females, 6 males; 4 yearlings: 2 females, 2 males; sample size n=4, 11 and 10 in 2017, 2018 and

150   2019 respectively; see Appendix S2 for details). The animal-year was our sampling unit, on the

151   assumption that the same individual may respond independently to manipulations in different

152   years. Roe deer were captured using baited box traps (n=16) or net drives (n=3), and were fitted

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153   with GPS-GSM radio collars programmed to acquire hourly GPS locations for a year, after

154   which they were released via a drop-off mechanism. Radio-collared roe deer moved an average

155   of 61.2 m per hour. This value of the average hourly movement distance *(l)* was subsequently

156   utilized in the analyses described below.

157   For all captured animals, we assumed a post-capture response in ranging behaviour. We

158   therefore considered the first re-visitation of the capture location as the sign of resettlement in

159   the original range and we used this time as the earliest possible onset of the experimental pre-

160   closure phase. Although not all the individuals were manipulated at the same time, we avoided

161   interference between capture operations and FS manipulations and between co-occurring

162   different manipulation phases (i.e. ensuring that co-occurring manipulations occurred in separate

163   areas).

164   During the *pre-closure phase*, we assessed the use of FS by radio-collared roe deer. We

165   identified the "main" FS (M) for each individual as the site with the largest number of locations

166   within a radius l during this initial phase, and considered it as the FS to which an individual is

167   most familiar. During the *closure phase*, corn was made inaccessible at M for a duration of about

168   15 days, depending on personnel availabilities (min=14.0 days, max=18.1, mean=15.5). M was

169   then re-opened, thereby initiating the *post-closure phase*. During both pre- and post-closure

170   phases, corn was available *ad libitum* at M. All "other" (O) managed FS – i.e., that were

171   provisioned at least once in the month prior to the experiment – had corn available *ad libitum*

172   throughout the experiment.

173

174   *Data preparation*

8

175   To ensure meaningful comparisons between animal-years, we homogenized the durations

176   of each experimental phase to the minimum length of the closure phase (i.e., 14 days).

177   Specifically, we truncated the movement data by removing initial excess positions for the pre-

178   closure and closure phases, and terminal excess positions for the post-closure phase. GPS

179   acquisition success was extremely high (99.57 % during the experiment) and we did not

180   interpolate missing fixes in the collected data.

181   The analyses of space-use and movement behaviour were based on spatially-explicit, raw

182   movement trajectories. The analyses of resource use relied on spatially-implicit, state time series

183   derived from the underlying movement data. To this end, we created an initial time series, for

184   each animal, by intersecting the relocations with three spatial domains: vegetation (the matrix;

185   V), main FS (M) and other FS (O). We converted FS locations (M and O) into areas by buffering

186   them. To investigate the sensitivity of buffer choice we considered six buffer sizes: l (i.e., 61.2

187   m) multiplied by 0.5, 1, 1.5, 2, 3 and 4. We associated all locations falling outside M and O to

188   the state V. The three-state time series was then converted into three single-state

189   presence/absence time series.

190

191   *Preference for feeding sites*

192   We calculated each individual's preference for FS (h_{FS}) as the relative use of FS over

193   natural vegetation during the pre-closure phase (i.e., the proportion of GPS fixes classified as

194   either M or O). Because preference is considered to be temporally dynamic (Beyer et al., 2010),

195   we chose to evaluate h_{FS} for each year separately in case individuals were manipulated in two

196   separate years. This reasoning allowed for the influence of individual condition and of the

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197   relative quality and quantity of vegetation resources on h_{FS}. We included h_{FS} in all space-use,

198   movement, and resource use analyses described below.

199   The variability of h_{FS} across animal-years was maximal when FS attendance was defined

200   as a GPS location within a 61.2 m distance (i.e., the population mean hourly step length) from

201   the FS (interquartile range=0.278, mean=0.343; Appendix S3: Table S3.1). Accordingly, the

202   results described below are based on this definition (see Appendix S7 for sensitivity analysis). At

203   this scale, h_{FS} did not differ consistently between sex (mean for females=0.346; mean for

204   males=0.336; t-test: p-value=0.901).

205

206   *Analysis*

207   We analysed how the experimental manipulation, and its interaction with both preference

208   for FS and sex, affected roe deer space-use, movement behaviour, and resource use.

209   *Space-use:* We assessed the changes of home range and core area sizes (P1.1), and of

210   space-use overlap (P1.2, P3.1) between experimental phases. We calculated utilization

211   distributions, (UD; *sensu* Worton 1989) for each animal-year and experimental phase using a

212   Gaussian kernel density estimation. After visual inspection, we chose to compute the UDs at a

213   spatial resolution of 10 m and with a fixed bandwidth, set to half the average hourly movement

214   distance (i.e. $l/2$=30.6 m).

215   For home range and core area sizes, we calculated the area (in hectares) corresponding to

216   the 95% and 50% UD contours, respectively, for each experimental phase (*Phase*; three levels;

217   reference level: *Pre-closure*). We then analysed the log-transformed areas using a linear mixed-

218   effect model (LMM) with five fixed effects: *Phase*, h_{FS}, *Sex* (categorical predictor; reference

219   level: *Female*), and two interaction terms (*Phase:h_{FS}* and *Phase:Sex*). We included animal-year

10

220   (*ind*) as random effect (intercept). In all analyses, interaction terms were dropped when

221   statistically non-significant (p-value>0.05).

222   For space-use patterns, we estimated the overlaps for three pairs of UDs – pre- and post-

223   closure, pre-closure and closure, and closure and post-closure (*Contrast*; three levels; reference

224   level: Pre-/Closure) – using the volume of intersection statistic (VI; Fieberg and Kochany 2005).

225   VI ranges between 0 (no overlap) and 1 (complete overlap). We then analysed the logit-

226   transformed overlaps using an LMM with *Contrast*, h_{FS}, *Sex*, *Contrast:h_{FS}* and *Contrast:Sex* as

227   fixed effects, and *ind* as random intercept.

228   *Movement behaviour*: We investigated the movement responses of roe deer to the

229   experiment (P1.3) by analysing the changes in hourly step length (Euclidean distance between

230   two successive relocations) and turning angle θ_t (angle between two successive movement

231   steps). Turning angles range between $-\pi$ and π, and were symmetric around 0. We analysed the

232   log-transformed step length, s_t, and the logit-transformed absolute turning angle, $\varphi_t =$

233    $log\left(\frac{|\theta_t|}{1-|\theta_t|}\right)$ using LMMs with *Phase*, h_{FS}, *Sex*, *Phase:h_{FS}* and *Phase:Sex* as fixed effects, and

234   *ind* as random intercept. Because step length was characterized by strong serial autocorrelation at

235   short lags and at circadian periodicities (a common pattern in movement trajectories; Fieberg,

236   Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010), we also included step length measured at

237   lags 1, 2 and 24 h (i.e., $s_{t-1}, s_{t-2}, s_{t-24}$) as fixed effects to reduce the autocorrelation of the

238   model residuals.

239   *Resource use*: To test whether the experiment led to a transitory change in resource use

240   (P1.4a-b, P3.2), we fitted separate mixed-effect logistic regression models to the three single-

241   state presence/absence time series ($u_{M,t}$, $u_{O,t}$ and $u_{V,t}$) using *Phase*, h_{FS}, *Sex*, *Phase:h_{FS}* and

242   *Phase:Sex* as fixed effects, and *ind* as random intercept. The pre-closure level for *Phase* was

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243   dropped for u_V to avoid circularity ($h_{FS} = 1 - \bar{u}_{V,t\,Pre-closure}$). We also included the response

244   variables measured at lags 1, 2 and 24 h (e.g., $u_{M,t-1}, u_{M,t-2}, u_{M,t-24}$) as fixed effects to reduce

245   the autocorrelation of the model residuals. However, for the sake of conciseness and clarity, we

246   omit these response lags when visualizing resource use predictions. Because the model results

247   were consistent regardless of the inclusion of the response lags (Appendix S6: Table S6.2), this

248   decision had no impact on the interpretation. Two animal-years were excluded from the analyses

249   of resource use due to the absence of suitable O-state: F4-2017 did not seem to have visited any

250   other FS (O) prior to the experiment; and F16-2016 had two distinct, highly-used FS during pre-

251   closure, but only the second most visited FS could be manipulated (due to stakeholder

252   acceptance). While the use of O was more variable when including these two outliers, the

253   general patterns remained unchanged (Appendix S6: Table S6.3).

254   *Software*: All analyses were conducted in the R environment (R Development Core

255   Team, 2016). We used the packages adehabitatLT and adehabitatHR (Calenge 2006) for the

256   spatial analyses, fitted all mixed-effect models via Maximum Likelihood with lme4 (Bates,

257   Mächler, Bolker, & Walker, 2015), and obtained the coefficients of determination using MuMin

258   (Bartón, 2018).

259

260   **Results**

261   *Space-use and movement responses to alteration of resource availability*

262   Roe deer space-use changed significantly during the experiment: the size of both home

263   ranges (95% UD isopleth; Appendix S4: Table S4.1) and core areas (50% isopleth; Table 2)

264   increased significantly during the experimental closure (Fig. 2; P1.1). On average, home range

265   size increased from 27.99 ha (σ=11.02) during pre-closure to 34.97 ha (σ=10.17) during closure,

266   and settled to 29.40 ha (σ=9.27) during post-closure. Core area size followed a similar trend with

267   averages of 4.23 ha (σ=2.34), 5.85 ha (σ=2.33) and 4.98 ha (σ=2.09), respectively.

268   Home range and core area sizes were influenced by individual preference for FS (h_{FS})

269   and there was an interaction between h_{FS} and experimental phase: individuals with a high h_{FS}

270   had smaller home ranges during the pre-closure and, overall, smaller core areas than those with

271   lower h_{FS}, but stronger increases following the experimental closure (Fig. 2; Table 2; Appendix

272   S4: Table S4.1; P2.2). There was no significant effect of sex or interactions between sex and

273   experimental phase on home range size (Appendix S4: Table S4.2; P2.1), but a marginally

274   significant interaction between sex and experimental phase on core area size (Appendix S4:

275   Table S4.3) with responses to closure tending to be slightly larger for males. Overall, the models

276   quantifying the changes in observed home range and core area sizes accounted for a high

277   proportion of the total variance (conditional coefficient of determination, cR^2: 0.62 and 0.51,

278   respectively).

279   Alongside home range size, the spatial pattern of roe deer home ranges shifted

280   dramatically following the experimental closure (Fig. 3): the degree of space-use overlap

281   between pre-closure and closure phases was significantly lower (mean=0.370, CI=0.301-0.405;

282   P1.2) than the overlap between the temporally-separated pre- and post-closure phases

283   (mean=0.535, CI=0.475-0.594; P3.1). Space-use overlap was significantly affected by h_{FS} (Fig.

284   3; Table 3; P2.2), with higher h_{FS} being associated to larger space-use shifts. However, there was

285   no apparent influence of sex in the space-use patterns (Appendix S4: Table S4.4; P2.1). The

286   model predicting space-use overlap accounted for an important proportion of the variance

287   (cR^2=0.50).

13

288   Underpinning these changes in home range size and space-use patterns were significant

289   changes in roe deer movement behaviour during the experiment. Average hourly step length

290   during the pre-closure phase was 60.32 m (σ=85.79); during closure it increased to 74.26 m

291   (σ=108.11); and during post-closure it decreased to 68.18 m (σ=96.61, P1.3). In general, males

292   (Appendix S5: Fig. S5.1, right-hand panels, Table S5.1; P2.1), and individuals associated with

293   high h_{FS} values (Appendix S5: Fig. S5.1, top panels, Table S5.1; P2.2) were characterized by

294   stronger increases in step length during the closure phase. In addition, roe deer movements were

295   more persistent during the closure phase, as shown by a significant decrease in the mean absolute

296   turning angle for males with a high h_{FS} (Appendix S5: Fig. S5.2, top-right panel, Tables S5.2,

297   5.3; P1.3, P2.1, P2.2).

298

299   *Resource use responses to alteration of availability*

300   The spatio-temporal dynamics of resources availability during the experiment led to

301   important shifts in FS resource use (Fig. 4; Table 4). On average, the proportion of use of the

302   main FS (M) dropped from 31% during the pre-closure phase to 4% during closure (P1.4a), and

303   then rebounded to 19% in the post-closure phase (P3.2). This decrease in the use of M during the

304   closure phase was partially compensated by elevated use of the other FS (O) – which increased

305   from 3% to 16% following closure (P1.4b), and an increase of the use of vegetation (V) from

306   66% to 80% following closure. During the post closure, use of O and V declined to 9% and 72%,

307   respectively. The shifts in resource use were very consistent among animal-years for M and O

308   but were more variable for V (Fig. 4, top panels).

309   Roe deer preference for FS significantly influenced how animals used the three resource

310   types and, in particular, interacted with experimental phase for M and O (Fig. 4, bottom panels;

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311   Table 4). Roe deer characterized by a high h_{FS} had significantly higher use of M during pre-

312   closure (by definition) and post-closure, as well as consistently lower use of V. High h_{FS} animals

313   were associated with stronger decreases in use of M and larger increases in the use of O during

314   closure (P2.2). This compensation for O during closure was stronger for females (Table 4;

315   Appendix S6: Fig. S6.1; P2.1). However, sex did not influence the use of M or V (Appendix S6:

316   Table S6.1; P2.1). Overall, the fitted models accounted for a high proportion of the variance in

317   resource use (cR^2: 0.35, 0.21 and 0.31 for M, O and V, respectively).

318

319   **Discussion**

320   The results of this field resource manipulation experiment provide direct evidence for the

321   tight coupling between the spatio-temporal distribution of resources and consequently spatially-

322   restricted movements of a large herbivore. Specifically, we show that roe deer track resource

323   dynamics (Fig. 4; H1), which leads to changes in their space-use (Figs. 2, 3) and underpinning

324   movements (Appendix S5: Figs S5.1, S5.2), and that individual traits, especially resource

325   preference, mediate these behavioural adjustments (H2). In additional, we show that roe deer

326   exhibit a high attraction to familiar locations, a process which leads to site fidelity (H3). As far

327   as we are aware, this is the first experimental demonstration of these interdependencies in a large

328   mammalian herbivore.

329

330   *Roe deer alter space-use and movement behaviour to track resources*

331   The experimental alterations of food availability led to larger (Fig. 2), spatially-shifted

332   home ranges (Fig. 3), and more explorative movements by roe deer (Appendix S5: Figs S5.1,

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333   S5.2), thereby directly establishing the connections between movement, space-use and the

334   spatio-temporal patterns of resources.

335   In a previous observational study, Fryxell et al. (2008) showed that elk alternated

336   between two movement modes: a low speed and high sinuosity mode thought to be within-patch

337   area-restricted search, and a high speed and low sinuosity mode between resource patches. In our

338   experimental study, we can directly link these movement modes to changing resources: the

339   exploratory movements of roe deer (high velocity and low sinuosity) observed during the closure

340   phase (P1.3) suggested that the animals were motivated to find alternative resource patches when

341   their familiar feeding site (FS) became inaccessible, thereby increasing (P1.1), but mainly

342   shifting, their home range (P1.2). While changes in home range size and location following

343   resource manipulation have been found in studies of lizards (Eifler 1996), birds (van Overveld

344   and Matthysen 2010) and voles (Ims 1987), to date, there have been few experimental

345   investigations of the connections between space-use and the spatio-temporal distribution of

346   resources in large herbivores.

347   In an earlier study, Kilpatrick and Stober (2002) showed that white-tailed deer shifted

348   their home range core towards the vicinity of newly deployed FS. Our study builds upon these

349   results by demonstrating multiple, successive responses to resource manipulation, linking

350   measured changes in underlying fine-scale movement behaviour of individuals to resulting

351   patterns of space-use that indicate dynamic resource tracking behaviour by roe deer (H1).

352   Although roe deer increased their use of the vegetation matrix during the closure phase,

353   individuals compensated the loss of their main FS (M), to a large degree, by shifts in their

354   movements and space-use towards alternative FS (O; Figs 4; P1.4a-b). Consequently, individuals

355   maintained a high overall use of FS throughout the experiment.

16

356   While resource tracking behaviour may be expected under the optimal foraging theory,

357   other individual- and population-based factors, such as social fences due to territoriality or

358   density-dependent resource competition, can constrain the movement responses of individuals to

359   changes in the spatial distribution of resources (e.g., Mysterud et al. 2011). The marked

360   responses shown here are likely to be explained by three factors. First, with the exception of

361   adult males during spring and summer (Liberg, Johansson, Andersen, & Linnell, 1998), roe deer

362   do not generally defend territories, and consequently their spatial distribution can approximate

363   that of an ideal free distribution (Walhström & Kjellander, 1995). Territorial tenure (Linnell &

364   Andersen, 1998) may explain the marginally different response of males (P2.1), specifically their

365   tendency to have larger core areas (Appendix S4: Table S4.3), more explorative movements

366   (Appendix S5: Table S5.1, S5.2) and lower resource compensation than females following

367   closure (Table 4; Appendix S6: Fig. S6.1). In fact, except for one individual (M11) showing high

368   spatial instability during its two-year monitoring, the space-use patterns of males tended to be

369   less influenced by the experimental closure than females.

370   Second, the rapidity and magnitude of the observed responses are likely linked to the

371   inability of roe deer to buffer transitory shortages of food availability: as income breeders with

372   little fat reserves, roe deer need a constant, high-nutritional intake (Andersen et al., 2000). Third,

373   while intra- and inter-specific competition in herbivores is largely linked to resource depletion

374   (Owen-Smith et al., 2010), this density-dependent constraint of food availability was prevented

375   by providing *ad libitum* forage at the FS.

376

377   *Resource tracking is mediated by individual preference*

17

378   This study moves beyond the findings of Kilpatrick and Stober (2002) by demonstrating

379   that inter-individual variation in preference for FS strongly mediated the responses of roe deer

380   movement patterns, space-use and resource use to changes in the spatio-temporal distribution of

381   resources (H2). During the closure phase, the changes in all measured variables were of larger

382   magnitude for individuals associated with a high FS preference (P2.1). The influence of FS

383   preference was particularly striking in the shifts of space-use (Fig. 3) and in the compensating

384   use of alternative FS following loss of the familiar resource (Fig. 4).

385   In this study, FS preference varied across individuals (Appendix S3: Table S3.1). These

386   inter-individual differences may be linked to either the environment the individuals were

387   exposed to, or a property of the individuals themselves. In our experimental setting, all roe deer

388   had access to at least one FS provided with *ad libitum* food where use was not prevented by

389   inter-individual competition (Ossi et al. 2017; Ossi et al. in prep). Hence, we could quantitatively

390   approximate FS preference as the relative use of FS over natural vegetation. Preference for FS

391   was derived from the relative use of FS, and so our definition implies a conditionality on both the

392   physiological state of the individual and on the relative nutritional value of the provisioned food

393   (corn) over natural vegetation in a given season. For example, the body condition at the onset of

394   winter is likely to vary between years. In addition, the dynamics in the quality and quantity of

395   natural browse – either spatial (e.g., between home ranges) and/or temporal (e.g., between years)

396   – could lead to variations in FS preference. Indeed, FS preference was higher in 2017 than in

397   2018 for all roe deer manipulated in these consecutive years (Appendix S3: Table S3.1).

398   Preference can therefore be considered a dynamic variable (Beyer et al., 2010) that we evaluated

399   at the individual level over a short period of relative stability (pre-closure phase in each winter).

400   We considered the temporal extent of our experiment (*ca* 6 weeks) short enough to consider FS

401   preference for each animal-year to be relatively constant, because in this time period the

402   physiological conditions and vegetation nutritional value would not vary substantially or

403   consistently.

404   Individuals attending a FS benefit from exploiting a forage-rich location, but risk elevated

405   intra- and inter-specific contacts (Ossi et al. in prep), high anthropogenic disturbance, and an

406   increased susceptibility to predation by humans. Because FS are associated with such risks,

407   individuals in poorer condition may be more willing to trade on predation risk to access a forage-

408   rich patch (McNamara & Houston, 1987). Alternatively, FS preference could be linked to

409   differences in personality. In roe deer, Bonnot et al. (2015) investigated the association between

410   individual behavioural profile (e.g., body temperature at capture) and the use of risky but

411   profitable habitats (open areas), and suggested that variations in personality could lead to

412   individual differences in habitat use. Similarly, FS preference could be associated to bold or risk-

413   taking personalities. Interestingly, preference for FS tended to correlate with individual body

414   temperature at capture (Pearson's r = - 0.37 p-value = 0.084; Appendix S8), with bolder

415   individuals (lower temperature) using FS more intensely.

416   The underlying drivers of preference listed above may not only lead individuals to use

417   resources to a different extent, but also condition their tendency to track spatio-temporal resource

418   dynamics (Spiegel, Leu, Bull, & Sih, 2017). For instance, risk-taking personalities tend to be

419   associated with explorations of novel environments (Cote, Clobert, Brodin, Fogarty, & Sih,

420   2010), as shown experimentally in great tits following the loss of a familiar foraging area (van

421   Overveld & Matthysen, 2010).

422

423   *The role of site familiarity*

19

424   During the post-closure phase of the experiment, roe deer increased their use of familiar

425   FS (M), whose food accessibility had been restored after a transitory restriction (Fig. 4, left-hand

426   panels; P3.1), and home ranges shifted back to pre-closure patterns, as suggested by the high

427   overlap between temporally-disjointed pre- and post-closure space-use (Fig. 3; P3.2). The

428   restoration of these pre-manipulation patterns supports the hypothesis that site familiarity

429   provides inherent benefits to animals maintaining a home range (H3; Piper 2011). These results

430   are coherent with published literature demonstrating that ungulates tend to select for previously

431   visited locations i.e., site familiarity (e.g., Dalziel, Morales, & Fryxell, 2008; Merkle, Fortin, &

432   Morales, 2014).

433   Unlike most observational studies, our experimental approach allowed us to contrast two

434   alternative, concentrated resources (M and O) of equal nutritional value but of distinct

435   familiarity, and hence to separate the effects of resource tracking from those of familiarity.

436   Resource tracking can explain roe deer use of other FS (O) to compensate the inaccessibility of

437   the familiar, main FS (M) during closure; however, the systematic return of roe deer to M during

438   the post-closure phase, while both alternative resources were accessible, cannot be explained by

439   resource tracking alone. Our experiment suggests that roe deer were actively selecting for

440   familiar areas and that site familiarity has an inherent value.

441   In observational studies of animal movement, a spurious familiarity effect (*sensu* Van

442   Moorter et al. 2013) can occur when an important factor influencing animal behaviour is not

443   considered, and the re-visitation of particular locations is interpreted as an evidence for site

444   familiarity selection. However, this confounding effect is unlikely to affect the results of this

445   experiment. First, corn was delivered *ad libitum* across all FS (M or O) i.e., homogeneous

446   foraging value. Second, the FS were located in comparable environments with close proximity to

447   cover, a factor that largely influence roe deer movements and space-use (e.g., Tufto et al. 1996,

448   Bongi et al. 2008). Third, and most importantly, the specific identities of M and O varied

449   interchangeably between individuals. Hence, we conclude that the return to pre-closure patterns

450   of foraging behaviour and space-use are unlikely to be result of variations in the characteristics

451   of specific FS, but rather of an inherent familiarity effect. In roe deer, site familiarity could allow

452   a more profitable exploitation of natural forage, as seen in bison (*Bison bison*; Merkle et al.,

453   2014) or reduce intraspecific competition for such resource (see Riotte-lambert et al. 2015 for a

454   theoretical argument). Alternatively, the attraction to familiar areas could be related to a predator

455   (natural or human) avoidance tactic (Gehr et al., in prep; Stamps, 1995).

456   Our results imply that when resource patterns are changing, individual behavioural

457   decisions probably reflect a trade-off between the advantages of site familiarity and resource

458   tracking. In some cases, finding an alternative resource patch of high nutritional value may cause

459   an individual not to return to familiar sites (e.g., Ims 1987, Eifler 1996, van Overveld and

460   Matthysen 2010), as seen in this study during the closure phase. The relative influence of

461   resource tracking and site familiarity likely depends on species traits and ecology. For example,

462   it is possible that the greater capacity of capital breeding species to buffer temporal dynamics in

463   resource compared to income breeders such as roe deer alters the trade-off between tracking

464   resources and site fidelity.

465   Ultimately, site familiarity is the manifestation of an animal's ability to acquire spatial

466   information, in particular by means of spatial memory (Fagan et al., 2013). Large herbivores are

467   capable of memorizing resource location (e.g., Merkle et al., 2014). In this study, it is likely that

468   the variations in roe deer responses to resource changes that are not explained by preference for

469   FS may be the result of individual prior experience and knowledge of the status and distribution

21

470   of alternative FS. An interesting avenue for further studies will be to evaluate the role of these

471   cognitive processes on individual foraging decisions.

472

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486

487   **Author's contributions**

488   NR, FC and PM conceived the ideas and designed the methodology; FC supervised the

489   field study; NR, FO, WH and TS collected the data; NR analysed the data with support from WH

490   and TS; NR led the writing of the manuscript, together with FC and PM. All authors contributed

491   critically to the drafts and gave final approval for publication.

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493 **Data availability statement**

494 Data will be made available from the Dryad Digital Repository upon acceptance.

495

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655

656 **Tables**

657 Table 1. Hypotheses and corresponding predictions.

Hypotheses	Predictions
H1: roe deer alter their space-use patterns and movement behaviour to track dynamics in resource availability.	*The closure of the familiar feeding site (FS) leads to…* - P1.1: an increase in HR size - P1.2: a spatial shift in space-use - P1.3: more explorative movements - P1.4a: a reduced use of the familiar FS - P1.4b: a compensation by using other, alternative FS
H2: these behavioural adjustments are mediated by sex and FS preference.	- P2.1: males respond less markedly to the experimental transitions - P2.2: individuals with a high preference for FS respond more markedly to the experimental transitions
H3: roe deer strive to use familiar resources when accessible.	*The re-opening of the familiar FS leads to…* - P3.1: the return of space-use to pre-closure patterns - P3.2: the return of resource use to pre-closure patterns

658

659   Table 2. Summary of the final model for core area size (50% UD).

	Estimate	Std. Error	df	t value	p-value
(Intercept)	1.930	0.181	65.921	10.684	<0.001***
PhaseClosure	-0.106	0.223	48.722	-0.478	0.635
PhasePost-closure	-0.101	0.224	48.970	-0.450	0.655
h_{FS}	-2.096	0.464	65.921	-4.514	<0.001***
PhaseClosure:h_{FS}	1.572	0.572	48.722	2.747	0.008**
PhasePost-closure:h_{FS}	1.179	0.591	49.914	1.997	0.051(*)

	Std. Dev		R^2	
Random effect	0.209	Marginal	0.351	
Residual	0.373	Conditional	0.506	

660

661   Table 3. Summary of the final model for space-use overlap.

	Estimate	Std. Error	df	t value	p-value
(Intercept)	0.096	0.225	66.109	0.428	0.670
ContrastClosure/Post-c.	0.119	0.286	47.785	0.414	0.680
ContrastPre-c./Post-c.	-0.045	0.286	47.785	-0.156	0.877
h_{FS}	-2.073	0.578	66.109	-3.590	0.001**
ContrastClosure/Post-c.:h_{FS}	1.179	0.753	49.192	1.565	0.124
ContrastPre-c./Post-c.:h_{FS}	2.366	0.753	49.192	3.141	0.003**

	Std. Dev			R^2
Random effect	0.238		Marginal	0.372
Residual	0.476		Conditional	0.498

662

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33

664   Table 4. Summary of the final models for the use of the main feeding site ($u_{M,t}$), other feeding

665   sites ($u_{O,t}$) and vegetation ($u_{V,t}$).

Main feeding site (M)				
	Estimate	Std. Error	z value	p-value
(Intercept)	-3.325	0.112	-29.804	<0.001***
PhaseClosure	-0.645	0.172	-3.740	<0.001***
PhasePost-closure	-0.102	0.126	-0.809	0.418
h_{FS}	1.723	0.288	5.990	<0.001***
PhaseClosure:h_{FS}	-1.657	0.459	-3.606	<0.001***
PhasePost-closure:h_{FS}	-0.473	0.325	-1.456	0.145
$u_{M,t-1}$	3.155	0.065	48.555	<0.001***
$u_{M,t-2}$	0.900	0.068	13.286	<0.001***
$u_{M,t-24}$	0.739	0.062	11.917	<0.001***
	Std. Dev			R^2
Random effect	0.161		Marginal	0.346
Residual	1.000		Conditional	0.349

Other feeding sites (O)				
	Estimate	Std. Error	z value	p-value
(Intercept)	-6.032	0.379	-15.913	<0.001***
PhaseClosure	2.191	0.297	7.38	<0.001***
PhasePost-closure	1.663	0.308	5.395	<0.001***
h_{FS}	3.869	0.829	4.668	<0.001***

	Estimate	Std. Error	z value	p-value
Sex	-0.917	0.372	-2.464	0.014*
PhaseClosure:h_{FS}	-1.726	0.571	-3.022	0.003**
PhasePost-closure:h_{FS}	-1.831	0.594	-3.081	0.002**
PhaseClosure:SexM	0.529	0.292	1.815	0.069(*)
PhasePost-closure:SexM	0.855	0.302	2.835	0.005**
$u_{O,t-1}$	2.993	0.081	36.935	<0.001***
$u_{O,t-2}$	1.175	0.086	13.611	<0.001***
$u_{O,t-24}$	0.394	0.087	4.521	<0.001***

	Std. Dev			R^2
Random effect	0.551		Marginal	0.188
Residual	1.000		Conditional	0.208

Vegetation (V)				
	Estimate	Std. Error	z value	p-value
(Intercept)	-0.496	0.187	-2.655	0.008**
PhasePost-closure	-0.252	0.055	-4.593	<0.001***
h_{FS}	-1.870	0.443	-4.223	<0.001***
$u_{V,t-1}$	2.597	0.061	42.240	<0.001***
$u_{V,t-2}$	0.853	0.064	13.327	<0.001***
$u_{V,t-24}$	0.382	0.061	6.256	<0.001***

	Std. Dev			R^2
Random effect	0.361		Marginal	0.298
Residual	1.000		Conditional	0.314

35

(a) Pre-closure   Closure   Post-closure

(b)
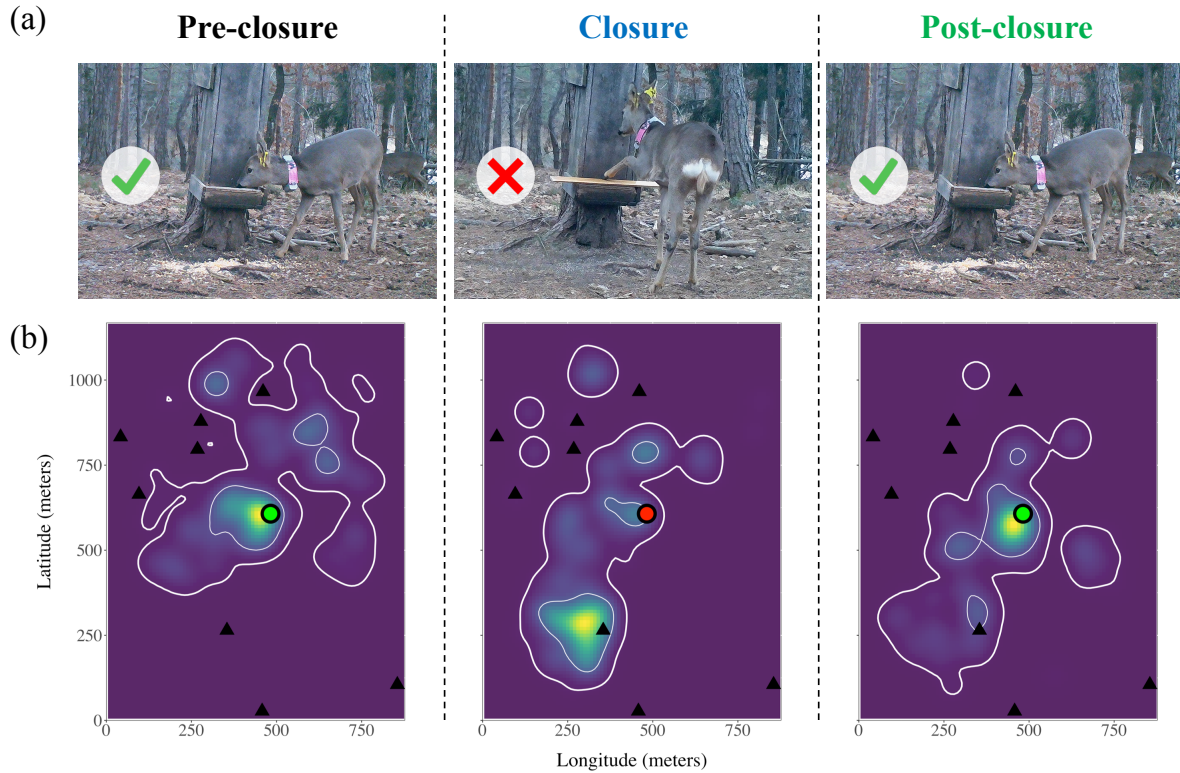
Figure 1. Schematic representation of the experiment. (a) The manipulation consists of a transitory alteration of resource accessibility at a main (M) feeding site. (b) In response to the experiment, roe deer are expected to shift from M (green/red dot, change of colour denoting the alteration of accessibility) towards alternative resources – other feeding sites (O; black triangles) or the vegetation (V; underlying matrix). In particular, this can lead to spatio-temporal dynamics in space-use (utilization distribution: colour gradient; 95% and 50% contour lines: thick and thin white lines, respectively; data from roe deer F5-2018).
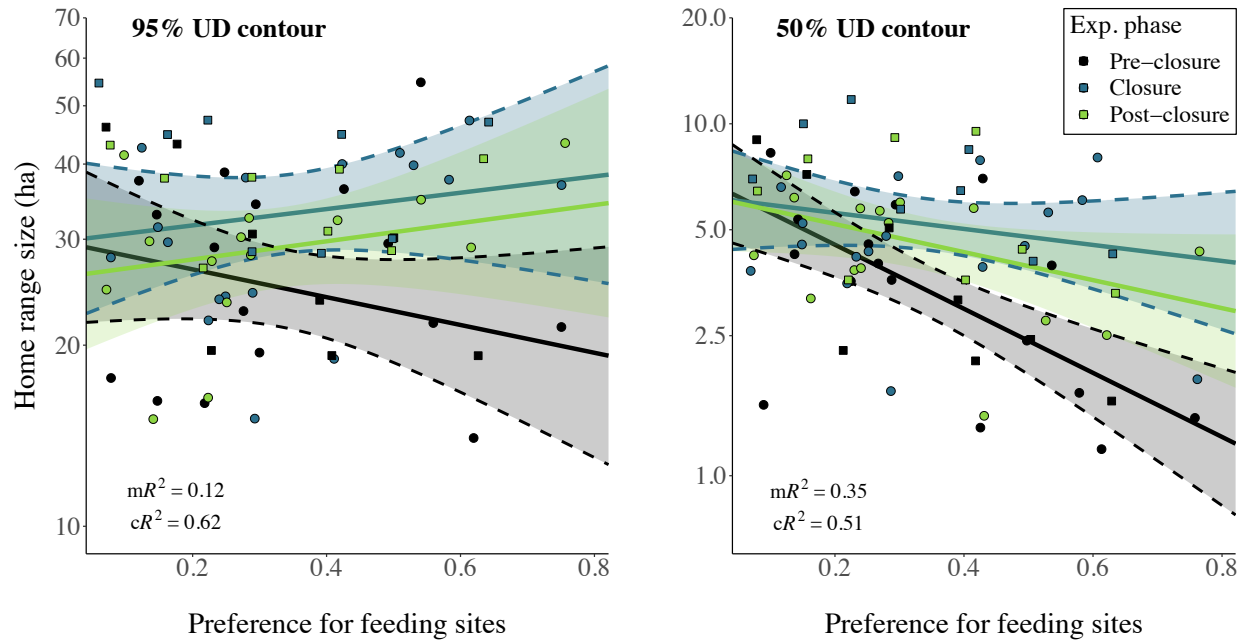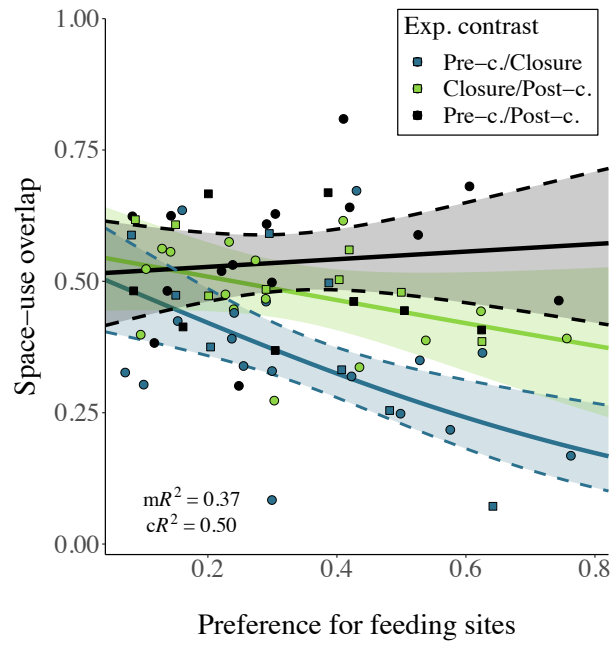
95% UD contour

$mR^2 = 0.12$
$cR^2 = 0.62$

50% UD contour

Exp. phase
- Pre–closure
- Closure
- Post–closure

$mR^2 = 0.35$
$cR^2 = 0.51$

Preference for feeding sites

Preference for feeding sites

674

675 Figure 2. Roe deer home range (y-axis, left panel) and core area (y-axis, right panel) sizes as a

676 function of preference for feeding sites (x-axis) and experimental phase. Observations are

677 represented as dots (females) and squares (males), (points are jittered slightly), and model

678 predictions as solid lines (95% confidence intervals: ribbons).

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681

682 Figure 3. Roe deer space-use overlap (y-axis) as a function of preference for feeding sites (x-axis)

683 and experimental phase contrast. Observations are represented as dots (females) and squares

684 (males) and model predictions as solid lines (95% confidence intervals: ribbons).

685
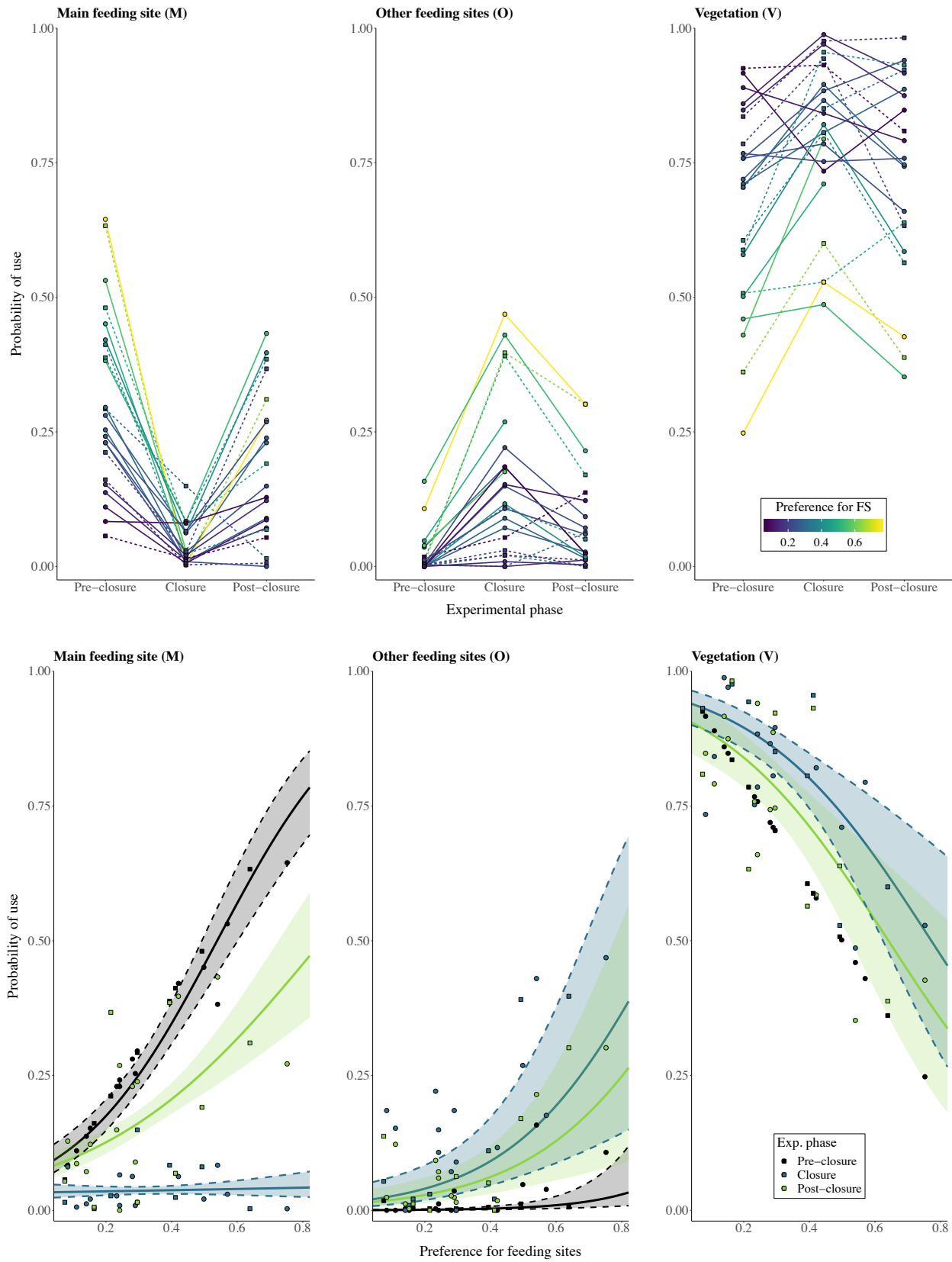
686   Figure 4. Roe deer shifts in resource use during the experiment – main feeding site (M, left), other

687   feeding sites (O, centre) and vegetation (V, right). Top panel: mean proportional use (dots and

688   lines) as a function of the experiment phase (x-axis) and preference for feeding sites (colour scale).

689   Bottom panel: model predictions for $u_{M,t}$, $u_{O,t}$ and $u_{V,t}$ (estimate: solid lines; 95% confidence

690   interval: ribbon) and mean relative use (females: dots; males: squares) as a function of the

691   experiment phase (colour) and preference for feeding sites (x-axis). The model predictions do not

692   consider resource lags at 1, 2 and 24h nor the influence of *Sex* (although selected in the final model

693   for $u_{O,t}$).