Title: Movement and space-use responses of a large herbivore to experimental alteration of resource availability

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Abstract

Resource acquisition is a key factor governing patterns of animal movement. While the link between spatio-temporal resource patterns and movement behaviour has been widely documented for migration, our understanding of home ranging behaviour in relation to resource dynamics has been limited by challenges of quantifying resource heterogeneity at fine spatio-temporal scales. In this study, we addressed this issue by analysing the movement responses of a resident large herbivore in response to an *in situ* manipulation of a high-quality, concentrated food resource. Specifically, we fitted roe deer (*Capreolus capreolus*) with GPS collars in the Eastern Italian Alps and recorded their fine-scale movement responses to an alteration of feeding site accessibility, for a total of 25 animal-years. The experiment involved identifying, for each animal, a familiar feeding site, whose accessibility was transitorily restricted (i.e., closed) while maintaining the availability of forage at alternative feeding sites. First, we tested whether individuals altered their spatial behaviour to track dynamical changes in resource availability. Experimental closure led to larger, spatially-shifted home ranges, resulting from more exploratory movements. Individual roe deer compensated the loss of their familiar feeding site by using alternative ones, and by doing so maintained their overall use of these concentrated resources. Our results demonstrate that roe deer actively track resource dynamics, and rapidly adjust their space-use and movement behaviour in response to changes in resource availability. Second, we showed that individual resource preferences mediate these behavioural adjustments: individuals characterized by a high preference for feeding sites exhibited larger space-use shifts and stronger changes in resource use in response to the resource manipulation. In contrast, sex had relatively minor influence on the observed patterns. Third, we investigated the role of site familiarity in roe deer foraging decisions. We found that space-use and resource use during the

post-closure period were restored to pre-closure patterns, thereby providing evidence for the inherent benefits of site familiarity to animals maintaining a home range. Together, our results establish the connections between movement, space-use, individual preference, and the spatio-temporal pattern of resources in deer home ranging behaviour.

Key-words: *Capreolus capreolus*; concentrated resource; familiarity; home range; *in situ* experiment; resource preference; roe deer; supplemental feeding site.

Introduction

Animals move to change the environmental context they experience (Van Moorter, Rolandsen, Basille, & Gaillard, 2016), including abiotic conditions, the presence of predators and competitors, and the availability of resources. Because foraging efficiency can be linked to individual fitness (Stephens & Krebs, 1986), food acquisition is thought to be a primary driver underlying animal movements (e.g., Mueller & Fagan, 2008). Consequently, space-use represents the geographic realization of optimizing fitness as a function of resource availability and acquisition costs (Mitchell & Powell, 2004).

Food resources are usually dynamic in both space and time (Wiens, 1976). In the case of herbivores, animals typically feed on resources distributed in patches, which are characterized by important temporal variations in quantity and quality (Owen-Smith, Fryxell, & Merrill, 2010). In this context, Mueller et al. (2011) have shown that strong spatio-temporal gradients in resource availability at either landscape or regional scales appear to drive migration and nomadism tactics. In many herbivore populations, however, individuals show a high year-round fidelity to a 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

research builds upon these two studies by investigating the spatial responses of a large herbivore, roe deer, to an experimental *in situ* manipulation of a high-quality, concentrated food resource in relation to both individual resource preferences and site familiarity.

Observational studies have suggested that, as browsers with limited fat reserves (Andersen, Gaillard, Linnell, & Duncan, 2000), roe deer exhibit a tight association between movement and resource dynamics (Ossi et al. 2017) with a strong plasticity to adapt its resource acquisition at different spatio-temporal scales (De Groeve et al., 2019; Morellet et al., 2013; Peters et al., 2017). In contrast to group-living ungulates, the foraging decisions of roe deer are expected to be clearly expressed at the level of individuals. The experiment was conducted during winter, when food scarcity limits roe deer foraging performance, and individuals are most inclined to adjust their spatial behaviour to continue meeting their energy requirements (Ossi, Gaillard, Hebblewhite, & Cagnacci, 2015).

We tagged roe deer in the Eastern Italian Alps with GPS units and followed their movements during transitory alterations of food availability at supplemental feeding sites (FS), i.e. discrete resource patches with an identifiable resource value distinguishable from the vegetation matrix (Mitchell & Powell, 2004; Wiens, 1976). The experiment therefore mimics – on free-ranging animals – the variation in the availability of concentrated, high-reward resources akin to watering holes for savannah ungulates (Owen-Smith, 2004) and feral horses (*Equus ferus*; Rozen-Rechels et al. 2015), or fruit trees for hornbills (C*eratogymna atrata* and *C. cylindricus*; Holbrook et al. 2002), forest chimpanzees (*Pan troglodytes*; Normand et al. 2009) and other frugivorous primates.

In large herbivores, and roe deer in particular, our initial hypothesis states that individuals alter their movement behaviours and consequently space-use patterns to track dynamics in

resource availability (H1; Table 1). We predicted that the loss of a key foraging resource should lead to larger (P1.1), and spatially-shifted (P1.2) home ranges, resulting from more explorative movements (P1.3). Furthermore, we predicted that roe deer reduced the intensity of use of the familiar FS when food accessibility was prevented (P1.4a) and compensated for this loss by using other accessible FS (P1.4b).

We further hypothesized that the behavioural adjustments to changes in resource availability would vary between individuals (H2; Table 1). In particular, because roe deer males have been shown to maintain a high year-round fidelity to their summer territory (Linnell & Andersen, 1998), we predicted that they would respond less markedly to the experiment than females (P2.1). We also predicted the responsiveness of roe deer to be positively influenced by the individual's prior preference for FS (P2.2).

If the spatial patterns of roe deer home ranges result from the foraging benefits of site familiarity (Riotte-lambert, Benhamou, & Chamaillé-Jammes, 2015; Van Moorter et al., 2009), animals should strive to use familiar areas and resources when accessible (H3; Table 1). Accordingly, we predicted that when initial conditions of food accessibility are re-established after perturbation, the initial space-use patterns would be restored (P3.1), following a return to high use of the familiar FS (P3.2).

Materials and methods

Study area

Roe deer is the primary large herbivore in the study area (7-8 individuals km^{-2}), located in the north-eastern Italian Alps (Argentario range, Autonomous Province of Trento). The area is 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

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*

To ensure meaningful comparisons between animal-years, we homogenized the durations of each experimental phase to the minimum length of the closure phase (i.e., 14 days). Specifically, we truncated the movement data by removing initial excess positions for the pre-closure and closure phases, and terminal excess positions for the post-closure phase. GPS acquisition success was extremely high (99.57 % during the experiment) and we did not interpolate missing fixes in the collected data.

The analyses of space-use and movement behaviour were based on spatially-explicit, raw movement trajectories. The analyses of resource use relied on spatially-implicit, state time series derived from the underlying movement data. To this end, we created an initial time series, for each animal, by intersecting the relocations with three spatial domains: vegetation (the matrix; V), main FS (M) and other FS (O). We converted FS locations (M and O) into areas by buffering them. To investigate the sensitivity of buffer choice we considered six buffer sizes: l (i.e., 61.2 m) multiplied by 0.5, 1, 1.5, 2, 3 and 4. We associated all locations falling outside M and O to the state V. The three-state time series was then converted into three single-state presence/absence time series.

Preference for feeding sites

We calculated each individual's preference for FS (h_{FS}) as the relative use of FS over natural vegetation during the pre-closure phase (i.e., the proportion of GPS fixes classified as either M or O). Because preference is considered to be temporally dynamic (Beyer et al., 2010), we chose to evaluate h_{FS} for each year separately in case individuals were manipulated in two separate years. This reasoning allowed for the influence of individual condition and of the

relative quality and quantity of vegetation resources on h_{FS}. We included h_{FS} in all space-use, movement, and resource use analyses described below.

The variability of h_{FS} across animal-years was maximal when FS attendance was defined as a GPS location within a 61.2 m distance (i.e., the population mean hourly step length) from the FS (interquartile range=0.278, mean=0.343; Appendix S3: Table S3.1). Accordingly, the results described below are based on this definition (see Appendix S7 for sensitivity analysis). At this scale, h_{FS} did not differ consistently between sex (mean for females=0.346; mean for males=0.336; t-test: p-value=0.901).

Analysis

We analysed how the experimental manipulation, and its interaction with both preference for FS and sex, affected roe deer space-use, movement behaviour, and resource use.

Space-use: We assessed the changes of home range and core area sizes (P1.1), and of space-use overlap (P1.2, P3.1) between experimental phases. We calculated utilization distributions, (UD; *sensu* Worton 1989) for each animal-year and experimental phase using a Gaussian kernel density estimation. After visual inspection, we chose to compute the UDs at a spatial resolution of 10 m and with a fixed bandwidth, set to half the average hourly movement distance (i.e. $l/2$=30.6 m).

For home range and core area sizes, we calculated the area (in hectares) corresponding to the 95% and 50% UD contours, respectively, for each experimental phase (*Phase*; three levels; reference level: *Pre-closure*). We then analysed the log-transformed areas using a linear mixed-effect model (LMM) with five fixed effects: *Phase*, h_{FS}, *Sex* (categorical predictor; reference level: *Female*), and two interaction terms (*Phase:*h_{FS} and *Phase:Sex*). We included animal-year

(*ind*) as random effect (intercept). In all analyses, interaction terms were dropped when statistically non-significant (p-value>0.05).

For space-use patterns, we estimated the overlaps for three pairs of UDs – pre- and post-closure, pre-closure and closure, and closure and post-closure (*Contrast*; three levels; reference level: Pre-/Closure) – using the volume of intersection statistic (VI; Fieberg and Kochany 2005). VI ranges between 0 (no overlap) and 1 (complete overlap). We then analysed the logit-transformed overlaps using an LMM with *Contrast*, h_{FS}, *Sex*, *Contrast:*h_{FS} and *Contrast:Sex* as fixed effects, and *ind* as random intercept.

Movement behaviour: We investigated the movement responses of roe deer to the experiment (P1.3) by analysing the changes in hourly step length (Euclidean distance between two successive relocations) and turning angle θ_t (angle between two successive movement steps). Turning angles range between $-\pi$ and π, and were symmetric around 0. We analysed the log-transformed step length, s_t, and the logit-transformed absolute turning angle, $\varphi_t = log\left(\frac{|\theta_t|}{1-|\theta_t|}\right)$ using LMMs with *Phase*, h_{FS}, *Sex*, *Phase:*h_{FS} and *Phase:Sex* as fixed effects, and *ind* as random intercept. Because step length was characterized by strong serial autocorrelation at short lags and at circadian periodicities (a common pattern in movement trajectories; Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010), we also included step length measured at 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 model residuals.

Resource use: To test whether the experiment led to a transitory change in resource use (P1.4a-b, P3.2), we fitted separate mixed-effect logistic regression models to the three single-state presence/absence time series ($u_{M,t}$, $u_{O,t}$ and $u_{V,t}$) using *Phase*, h_{FS}, *Sex*, *Phase:*h_{FS} and *Phase:Sex* as fixed effects, and *ind* as random intercept. The pre-closure level for *Phase* was

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,

and settled to 29.40 ha (σ=9.27) during post-closure. Core area size followed a similar trend with averages of 4.23 ha (σ=2.34), 5.85 ha (σ=2.33) and 4.98 ha (σ=2.09), respectively.

Home range and core area sizes were influenced by individual preference for FS (h_{FS}) and there was an interaction between h_{FS} and experimental phase: individuals with a high h_{FS} had smaller home ranges during the pre-closure and, overall, smaller core areas than those with lower h_{FS}, but stronger increases following the experimental closure (Fig. 2; Table 2; Appendix S4: Table S4.1; P2.2). There was no significant effect of sex or interactions between sex and experimental phase on home range size (Appendix S4: Table S4.2; P2.1), but a marginally significant interaction between sex and experimental phase on core area size (Appendix S4: Table S4.3) with responses to closure tending to be slightly larger for males. Overall, the models quantifying the changes in observed home range and core area sizes accounted for a high proportion of the total variance (conditional coefficient of determination, cR^2: 0.62 and 0.51, respectively).

Alongside home range size, the spatial pattern of roe deer home ranges shifted dramatically following the experimental closure (Fig. 3): the degree of space-use overlap between pre-closure and closure phases was significantly lower (mean=0.370, CI=0.301-0.405; P1.2) than the overlap between the temporally-separated pre- and post-closure phases (mean=0.535, CI=0.475-0.594; P3.1). Space-use overlap was significantly affected by h_{FS} (Fig. 3; Table 3; P2.2), with higher h_{FS} being associated to larger space-use shifts. However, there was no apparent influence of sex in the space-use patterns (Appendix S4: Table S4.4; P2.1). The model predicting space-use overlap accounted for an important proportion of the variance (cR^2=0.50).

Underpinning these changes in home range size and space-use patterns were significant changes in roe deer movement behaviour during the experiment. Average hourly step length during the pre-closure phase was 60.32 m (σ=85.79); during closure it increased to 74.26 m (σ=108.11); and during post-closure it decreased to 68.18 m (σ=96.61, P1.3). In general, males (Appendix S5: Fig. S5.1, right-hand panels, Table S5.1; P2.1), and individuals associated with high h_{FS} values (Appendix S5: Fig. S5.1, top panels, Table S5.1; P2.2) were characterized by stronger increases in step length during the closure phase. In addition, roe deer movements were more persistent during the closure phase, as shown by a significant decrease in the mean absolute turning angle for males with a high h_{FS} (Appendix S5: Fig. S5.2, top-right panel, Tables S5.2, 5.3; P1.3, P2.1, P2.2).

Resource use responses to alteration of availability

The spatio-temporal dynamics of resources availability during the experiment led to important shifts in FS resource use (Fig. 4; Table 4). On average, the proportion of use of the main FS (M) dropped from 31% during the pre-closure phase to 4% during closure (P1.4a), and then rebounded to 19% in the post-closure phase (P3.2). This decrease in the use of M during the closure phase was partially compensated by elevated use of the other FS (O) – which increased from 3% to 16% following closure (P1.4b), and an increase of the use of vegetation (V) from 66% to 80% following closure. During the post closure, use of O and V declined to 9% and 72%, respectively. The shifts in resource use were very consistent among animal-years for M and O but were more variable for V (Fig. 4, top panels).

Roe deer preference for FS significantly influenced how animals used the three resource types and, in particular, interacted with experimental phase for M and O (Fig. 4, bottom panels;

Table 4). Roe deer characterized by a high h_{FS} had significantly higher use of M during pre-closure (by definition) and post-closure, as well as consistently lower use of V. High h_{FS} animals were associated with stronger decreases in use of M and larger increases in the use of O during closure (P2.2). This compensation for O during closure was stronger for females (Table 4; Appendix S6: Fig. S6.1; P2.1). However, sex did not influence the use of M or V (Appendix S6: Table S6.1; P2.1). Overall, the fitted models accounted for a high proportion of the variance in resource use (cR^2: 0.35, 0.21 and 0.31 for M, O and V, respectively).

Discussion

The results of this field resource manipulation experiment provide direct evidence for the tight coupling between the spatio-temporal distribution of resources and consequently spatially-restricted movements of a large herbivore. Specifically, we show that roe deer track resource dynamics (Fig. 4; H1), which leads to changes in their space-use (Figs. 2, 3) and underpinning movements (Appendix S5: Figs S5.1, S5.2), and that individual traits, especially resource preference, mediate these behavioural adjustments (H2). In additional, we show that roe deer exhibit a high attraction to familiar locations, a process which leads to site fidelity (H3). As far as we are aware, this is the first experimental demonstration of these interdependencies in a large mammalian herbivore.

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

The experimental alterations of food availability led to larger (Fig. 2), spatially-shifted home ranges (Fig. 3), and more explorative movements by roe deer (Appendix S5: Figs S5.1,

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.

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*

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*

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

of alternative FS. An interesting avenue for further studies will be to evaluate the role of these cognitive processes on individual foraging decisions.

Acknowledgements

N. Ranc was supported by Harvard University Graduate Fellowship and Fondazione Edmund Mach International Doctoral Programme Fellowship. F. Cagnacci was supported by the Sarah and Daniel Hrdy Fellowship 2015-2016 at Harvard University OEB during part of the development of this ms. We are grateful to all the people involved in the roe deer captures and data collection, and especially M.B. Almeida, P. Bonanni, A. Corradini, J. De Groeve, G. Lilli, S. Mumme, S. Nicoloso, D. Righetti, M. Rocca, M. Salvatori, M. Sanchez and P. Semenzato. We thank J.W. Cain, B. Ölveczky, N. Pierce, all the members of the Cagnacci lab and of the Moorcroft lab, and the graduate students of the Harvard Statistics Consulting Service for their valuable suggestions. We also thank the Wildlife and Forestry Service of the Autonomous Province of Trento and the Trentino Hunting Association (ACT) for their support. Finally, we express our gratitude to the hunters of Albiano, Civezzano, Fornace and Trento Nord without whose help this study could not be conducted.

Author's contributions

NR, FC and PM conceived the ideas and designed the methodology; FC supervised the field study; NR, FO, WH and TS collected the data; NR analysed the data with support from WH and TS; NR led the writing of the manuscript, together with FC and PM. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

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

References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, *31*(1), 140–160. doi: 10.1111/j.2007.0906-7590.05236.x

Andersen, R., Gaillard, J.-M., Linnell, J. D. C., & Duncan, P. (2000). Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology*, *69*, 672–682. doi: 10.1046/j.1365-2656.2000.00425.x

Bartón, K. (2018). *MuMIn: Multi-model inference. R Package version 1.42.1. http//CRANR-project.org/package=MuMIn*.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi: 10.18637/jss.v067.i01

Benhamou, S. (2014). Of scales and stationarity in animal movements. *Ecology Letters*, *17*(3), 261–272. doi: 10.1111/ele.12225

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2245–2254. doi: 10.1098/rstb.2010.0083

Bongi, P., Ciuti, S., Grignolio, S., Del Frate, M., Simi, S., Gandelli, D., & Apollonio, M. (2008). Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. *Journal of Zoology*, *276*(3), 242–251. doi: 10.1111/j.1469-

7998.2008.00481.x

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., … Morellet, N. (2015). Interindividual variability in habitat use: Evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, *26*(1), 105–114. doi: 10.1093/beheco/aru169

Brown, J. H., & Munger, J. C. (1985). Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, *66*(5), 1545–1563. doi: 10.2307/1938017

Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2157–2162. doi: 10.1098/rstb.2010.0107

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516–519. doi: 10.1016/j.ecolmodel.2006.03.017

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 4065–4076. doi: 10.1098/rstb.2010.0176

Couriot, O., Hewison, A. J. M., Saïd, S., Cagnacci, F., & Chamaillé, S. (2018). Truly sedentary ? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia*, *187*(1), 47–60. doi: 10.1007/s00442-018-4131-5

Dalziel, B. D., Morales, J. M., & Fryxell, J. M. (2008). Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. *The American Naturalist*, *172*(2), 248–258. doi: 10.1086/589448

De Groeve, J., Cagnacci, F., Ranc, N., Bonnot, N. C., Gehr, B., Heurich, M., … Van De Weghe, N. (2019). Individual Movement - Sequence Analysis Method (IM-SAM): characterizing spatio-temporal patterns of animal habitat use across landscapes. *International Journal of Geographical Information Science*, *0*(0), 1–22. doi: 10.1080/13658816.2019.1594822

Eifler, D. A. (1996). Experimental manipulation of spacing patterns in the widely foraging lizard Cnemidophorus uniparens. *Herpetologica*, *52*(4), 477–486.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*, 1316–1329. doi: 10.1111/ele.12165

Fieberg, J., & Kochany, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management*, *69*(4), 1346–1359. doi: 10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S., & Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2233–2244. doi: 10.1098/rstb.2010.0079

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., … Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *PNAS*, *105*(49), 19114–19119. doi: 10.1073/pnas.0801737105

Holbrook, K. M., Smith, T. B., & Hardesty, B. D. (2002). Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography*, *25*(6), 745–749. doi: 10.1034/j.1600-0587.2002.250610.x

Ims, R. A. (1987). Responses in spatial organization and behaviour to manipulations of the food

resouce in the vole Clethrionomys rufocanus. *Journal of Animal Ecology*, *56*, 585–596. doi: 10.2307/5070

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65–71. doi: 10.2307/1937156

Kilpatrick, H. J., & Stober, W. A. (2002). Effects of temporary bait sites on movements of suburban white-tailed deer. *Wildlife Society Bulletin*, *30*(3), 760–766.

Krebs, J. R. (1971). Territory and breeding density in the great tit, Parus Major L. *Ecology*, *52*(1), 2–22. doi: 10.2307/1934734

Liberg, O., Johansson, A., Andersen, R., & Linnell, J. D. C. (1998). Mating system, mating tactics and the function of male territory in roe deer. In R. Andersen, P. Duncan, & J. D. C. Linnell (Eds.), *The European roe deer: the biology of success* (pp. 221–256). Oslo, Norway: Scandinavian University Press.

Linnell, J. D. C., & Andersen, R. (1998). Territorial fidelity and tenure in roe deer bucks. *Acta Theriologica*, *43*(1), 67–75. doi: 10.4098/AT.arch.98-5

McNamara, J. M., & Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology*, *68*(5), 1515–1519. doi: 10.2307/1939235

Merkle, J. A., Fortin, D., & Morales, J. M. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters*, *17*, 924–931. doi: 10.1111/ele.12294

Mitchell, M. S., & Powell, R. A. (2004). A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, *177*(1–2), 209–232. doi: 10.1016/j.ecolmodel.2004.01.015

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., … Mysterud, A.

(2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*(6), 1326–1339. doi: 10.1111/1365-2656.12105

Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments behaviors to population distributions. *Oikos*, *117*, 654–664. doi: 10.1111/j.0030-1299.2008.16291.x

Mueller, T., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., … Fagan, W. F. (2011). How landscape dynamics link individual- to population-level movement patterns: A multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, *20*(5), 683–694. doi: 10.1111/j.1466-8238.2010.00638.x

Mysterud, A., Loe, L. E., Zimmermann, B., Bischof, R., Veiberg, V., & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos*, *120*, 1817–1825. doi: 10.1111/j.1600-0706.2011.19439.x

Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (Pan troglodytes verus) remember the location of numerous fruit trees. *Animal Cognition*, *12*(6), 797–807. doi: 10.1007/s10071-009-0239-7

Ossi, F., Gaillard, J. M., Hebblewhite, M., & Cagnacci, F. (2015). Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. *European Journal of Wildlife Research*, *61*(1), 111–124. doi: 10.1007/s10344-014-0879-z

Ossi, F., Gaillard, J. M., Hebblewhite, M., Morellet, N., Ranc, N., Sandfort, R., … Cagnacci, F. (2017). Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. *Ecosphere*, *8*(1). doi: 10.1002/ecs2.1629

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: The

behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2267–2278. doi: 10.1098/rstb.2010.0095

Owen-Smith, Norman. (2004). Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, *19*, 761–771. doi: 10.1007/s10980-005-0247-2

Peters, W., Hebblewhite, M., Mysterud, A., Spitz, D., Focardi, S., Urbano, F., … Cagnacci, F. (2017). Migration in geographic and ecological space by a large herbivore. *Ecological Monographs*, *87*(2), 297–320. doi: 10.1002/ecm.1250

Piper, W. H. (2011). Making habitat selection more "familiar": a review. *Behavioral Ecology and Sociobiology*, *65*(7), 1329–1351. doi: 10.1007/s00265-011-1195-1

R Development Core Team. (2016). *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org.*

Riotte-lambert, L., Benhamou, S., & Chamaillé-Jammes, S. (2015). How memory-based movement leads to nonterritorial spatial segregation. *The American Naturalist*, *185*(4), E103-116. doi: 10.1086/680009

Rozen-Rechels, D., van Beest, F. M., Richard, E., Uzal, A., Medill, S. A., & Mcloughlin, P. D. (2015). Density-dependent, central-place foraging in a grazing herbivore: Competition and tradeoffs in time allocation near water. *Oikos*, *124*(9), 1142–1150. doi: 10.1111/oik.02207

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, *20*(1), 3–18. doi: 10.1111/ele.12708

Stamps, J. (1995). Motor learning and the value of familiar space. *The American Naturalist*, *146*(1), 41–58. doi: 10.1086/285786

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, New Jersey, USA: Princeton University Press.

Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology*, *65*(6), 715–724. doi: 10.2307/5670

Van Moorter, B., Rolandsen, C. M., Basille, M., & Gaillard, J. M. (2016). Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology*, *85*(1), 21–31. doi: 10.1111/1365-2656.12394

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., & Gaillard, J.-M. (2009). Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, *118*(5), 641–652. doi: 10.1111/j.1600-0706.2008.17003.x

Van Moorter, B., Visscher, D., Herfindal, I., Basille, M., & Mysterud, A. (2013). Inferring behavioural mechanisms in habitat selection studies getting the null-hypothesis right for functional and familiarity responses. *Ecography*, *36*(3), 323–330. doi: 10.1111/j.1600-0587.2012.07291.x

van Overveld, T., & Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (Parus major). *Biology Letters*, *6*, 187–190. doi: 10.1098/rsbl.2009.0764

Walhström, L. K., & Kjellander, P. (1995). Ideal free distribution and natal dispersal in female roe deer. *Oecologia*, *103*(3), 302–308. doi: 10.1007/BF00328618

Wiens, J. A. (1976). Population responses to patchy environments. *Annual Review of Ecology and Systematics*, *7*(1976), 81–120. doi: 10.1146/annurev.es.07.110176.000501

Worton, B. J. (1989). Kernel methods for estimating the utilization cistribution in home-range

studies. *Ecology*, *70*(1), 164–168. doi: 10.2307/1938423

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

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

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

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

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

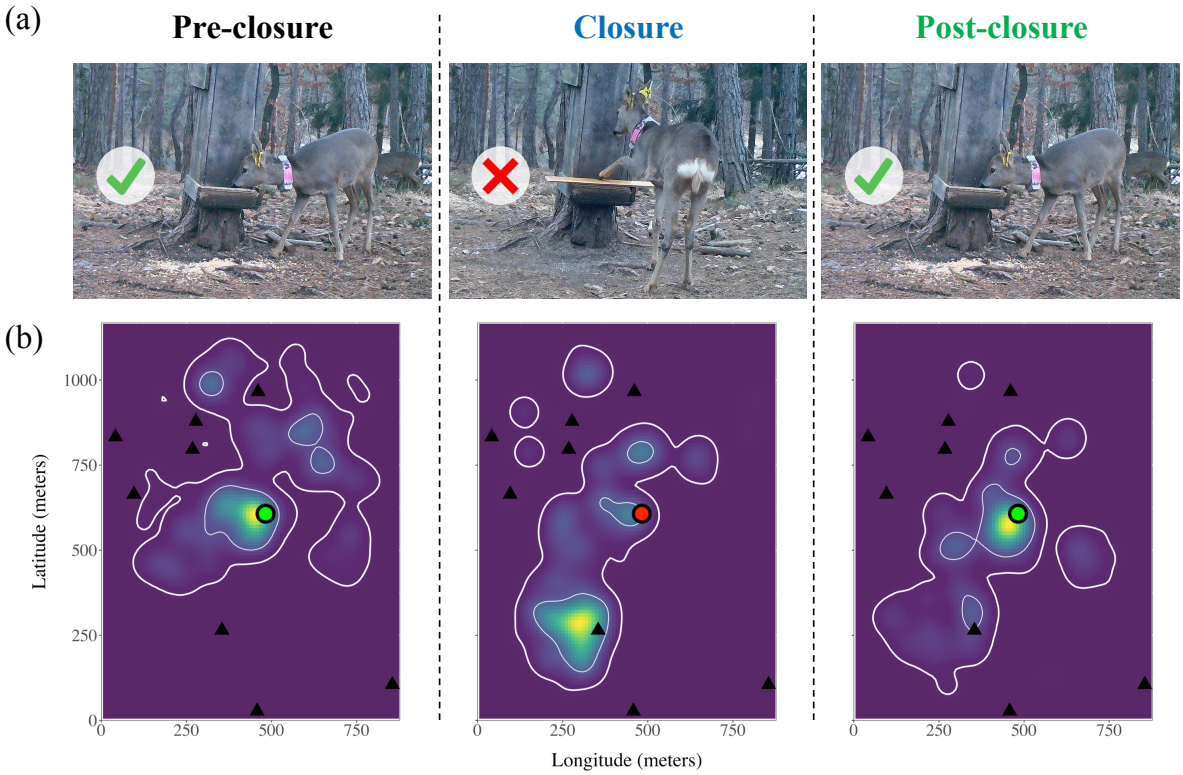
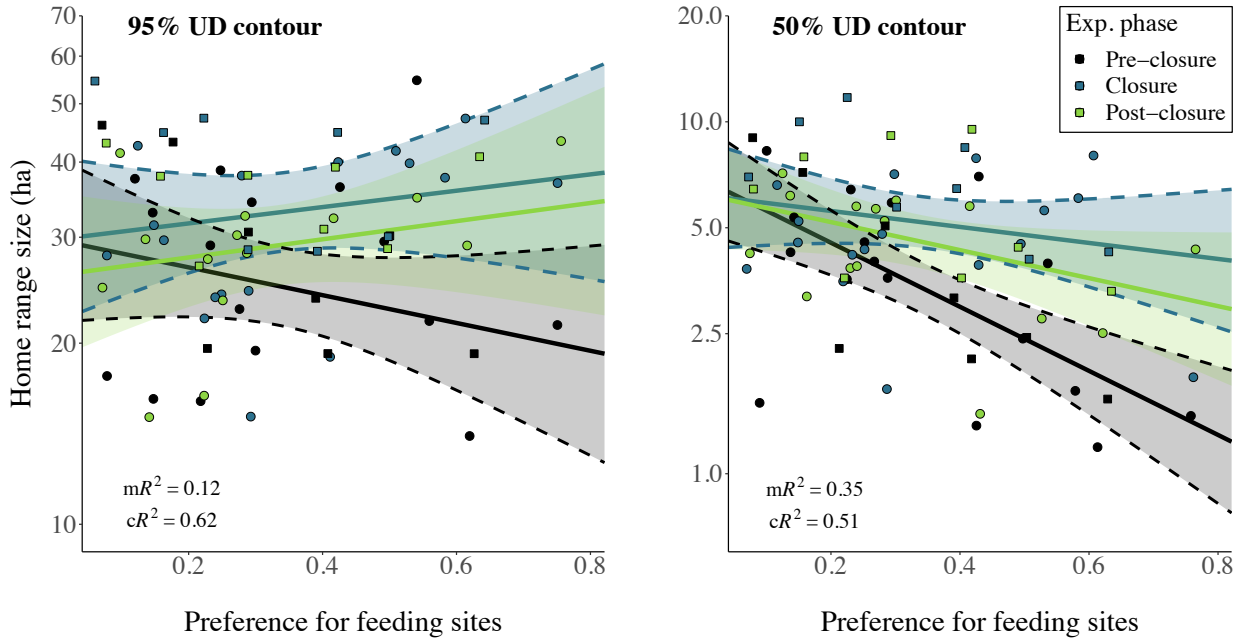


Figure 1. Schematic representation of the experiment. (a) The manipulation consists of a transitory alteration of resource accessibility at a main (M) feeding site. (b) In response to the experiment, roe deer are expected to shift from M (green/red dot, change of colour denoting the alteration of accessibility) 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).



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).

679

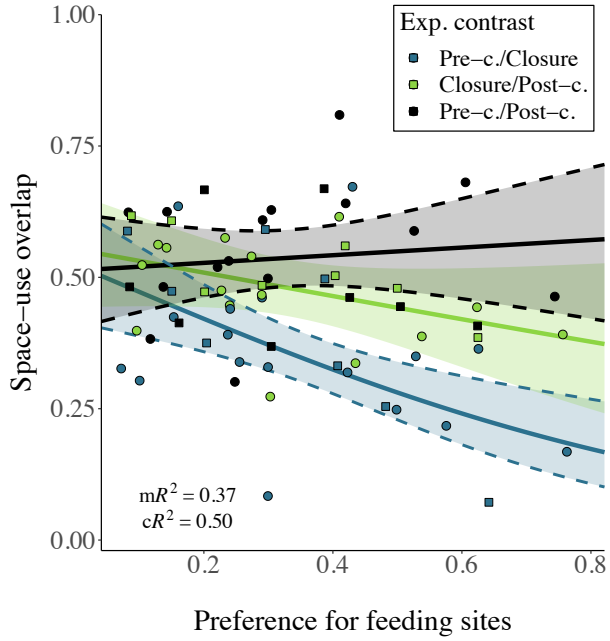
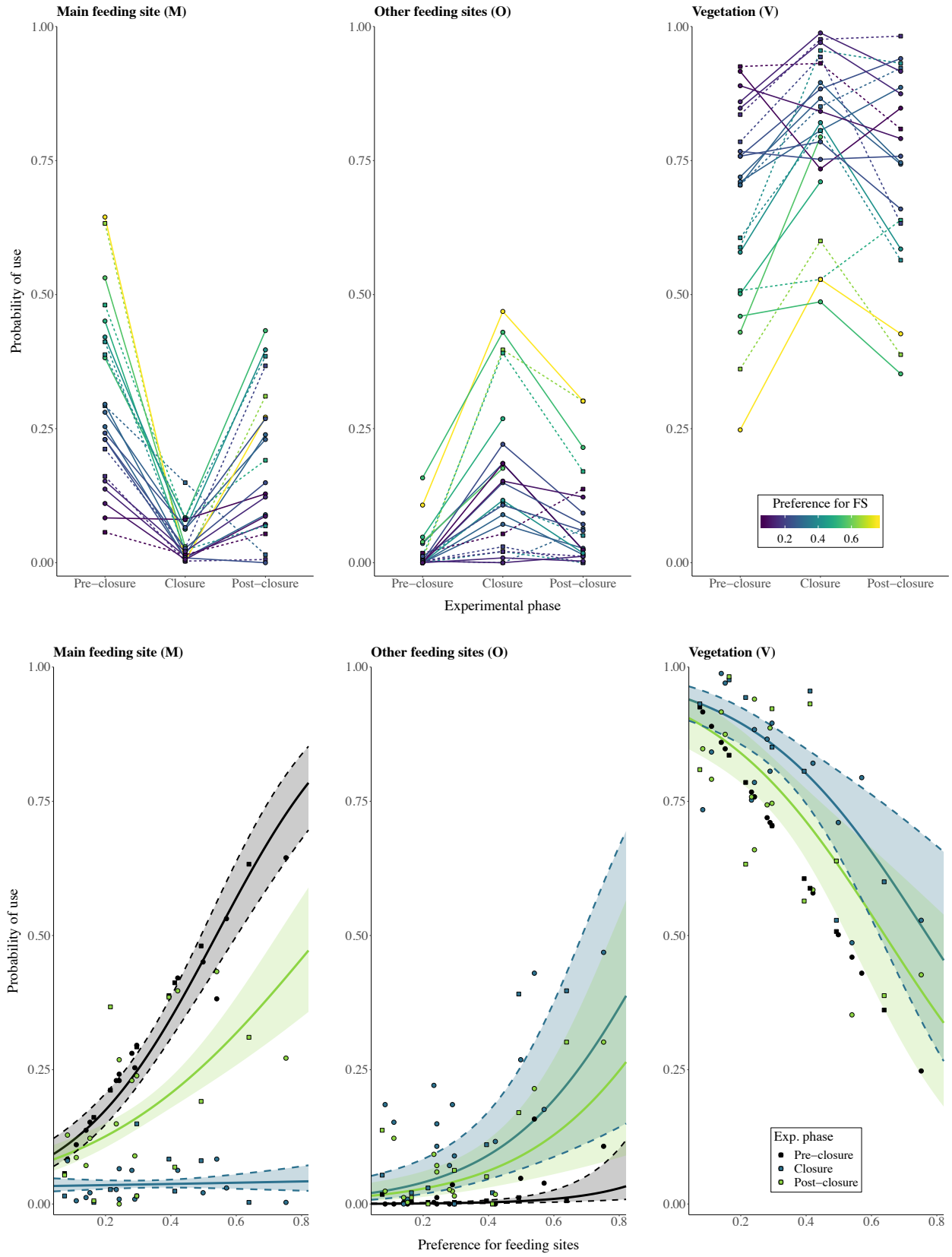


Figure 3. Roe deer space-use overlap (y-axis) as a function of preference for feeding sites (x-axis) and experimental phase contrast. Observations are represented as dots (females) and squares (males) and model predictions as solid lines (95% confidence intervals: ribbons).


Main feeding site (M)
Other feeding sites (O)
Vegetation (V)
Probability of use
1.00
0.75
0.50
0.25
0.00
Pre−closure
Closure
Post−closure
Experimental phase
Preference for FS
0.2
0.4
0.6
Preference for feeding sites
Exp. phase
Pre−closure
Closure
Post−closure

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 $u_{O,t}$).