Title: Preference and familiarity mediate spatial responses of a large herbivore to experimental manipulation of resource availability

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Abstract

The link between spatio-temporal resource patterns and movement behaviour is a key ecological process, however, limited experimental support has been produced at the home range scale. In this study, we analysed the spatial responses of a resident large herbivore (roe deer *Capreolus capreolus*) during an *in situ* manipulation of a concentrated food resource. Specifically, we experimentally altered feeding site accessibility to roe deer and recorded (for 25 animal-years) individual responses by GPS tracking. We found that, following the loss of their preferred resource, roe deer actively tracked resource dynamics leading to more exploratory movements, and larger, spatially-shifted home ranges. Then, we showed, for the first time experimentally, the importance of site fidelity in the maintenance of large mammal home ranges by demonstrating the return of individuals to their familiar, preferred resource despite the presence of alternate, equally-valuable food resources. This behaviour was modulated at the individual level, where roe deer characterised by a high preference for feeding sites exhibited more pronounced behavioural adjustments during the manipulation. Together, our results establish the connections between movement, space-use, individual preference, and the spatio-temporal pattern of resources in home ranging behaviour.

Introduction

Animals move to change the environmental context they experience[1], including abiotic conditions, the presence of predators and competitors, and the availability of resources. Because foraging efficiency can be linked to individual fitness[2], food acquisition is thought to be a primary driver underlying animal movements[3]. Consequently, space-use represents the geographic realization of optimizing fitness as a function of resource availability and acquisition costs[4].

40 Food resources are usually dynamic in both space and time[5]. In the case of herbivores,
41 animals typically feed on vegetation distributed in patches, which are characterized by important
42 temporal variations in quantity and quality[6]. In this context, strong spatio-temporal gradients in
43 resource availability at either landscape or regional scales appear to drive migration and
44 nomadism tactics[7]. In many herbivore populations, however, individuals show a high year-round
45 fidelity to a spatially-localized home range. It has been suggested that the foraging benefits of site
46 familiarity, where resources are constant or predictable, are responsible for the formation of a
47 stable home range (see [8] for a review). While the home range has traditionally been perceived as
48 a relatively static space-use tactic, recent evidence suggests that animals have sub-seasonal home
49 ranges[9] i.e., focus their movements into particular areas in response to seasonal variation in local
50 resource availability. For example, sub-seasonal home ranges are a ubiquitous behavioural tactic
51 across a wide ecological gradient in roe deer (*Capreolus capreolus*)[10].
52 The link between movement behaviour and resource dynamics is less clear when
53 observing home ranging behaviour than migration or nomadism[3] because of the difficulty to
54 quantify spatio-temporal variability in resource heterogeneity at small spatial scales[10]. In this
55 study, we address this issue by experimentally manipulating the spatio-temporal patterns of food
56 availability within home ranges. *In situ* food manipulation experiments have a long history in the
57 study of population dynamics, with a primary focus on understanding the numerical response to
58 food supplementation[11], and of animal communities[12]. Although these field experiments have
59 provided fundamental insights in animal ecology, they have seldom been combined with the
60 emerging technological capabilities of animal tracking[13] to investigate the implications of food
61 availability on individual movements and space-use at larger spatial scales. In a rare example of
62 field experiment in large herbivores, white-tailed deer (*Odocoileus virginianus*) shifted their
63 core-area i.e., familiar areas of use, in response to novel food supplementation[14]. In turn, great tits

64 (*Parus major*) showed personality-dependent variability in responses to an alteration of resource
65 distribution[15].

66 Our research builds upon these two studies by investigating the spatial responses of a
67 large herbivore, roe deer, to an experimental *in situ* manipulation of a high-quality, concentrated
68 food resource in relation to both individual resource preferences and site familiarity. Roe deer, as
69 solitary browsers with limited fat reserves[16], exhibit a tight association between movement and
70 resource dynamics[17] with a strong plasticity to adapt its resource acquisition at different spatio-
71 temporal scales[18–20]. In contrast to group-living ungulates, their foraging decisions are expected
72 to be clearly expressed at the level of individuals.

73 We tagged roe deer in the Eastern Italian Alps with GPS units and followed their
74 movements during transitory alterations of food availability at supplemental feeding sites (FS)
75 i.e., discrete resource patches with an identifiable resource value distinguishable from the
76 vegetation matrix[4,5]. The six-week experiment consisted of three two-week phases – pre-closure,
77 closure and post-closure. During the closure phase, we physically restricted the accessibility of
78 food at the most attended feeding site of each individual (hereafter referred to as Manipulated, M,
79 and considered as most familiar; Fig. 1). Throughout the experiment, roe deer had access to two
80 alternative resources within the broader landscape: alternate feeding sites (A), whose food
81 provisioning was held constant, and natural vegetation (V). The experiment was conducted
82 during winter, when food scarcity limits roe deer foraging performance, and individuals are most
83 inclined to adjust their spatial behaviour to continue meeting their energy requirements[21]. The
84 experiment therefore mimics – on free-ranging animals – the variation in the availability of
85 concentrated, high-reward resources akin to watering holes for savannah ungulates[22] and feral
86 horses (*Equus ferus*)[23], or fruit trees for hornbills (C*eratogymna atrata* and *C. cylindricus*)[24] and
87 frugivorous primates[25,26].

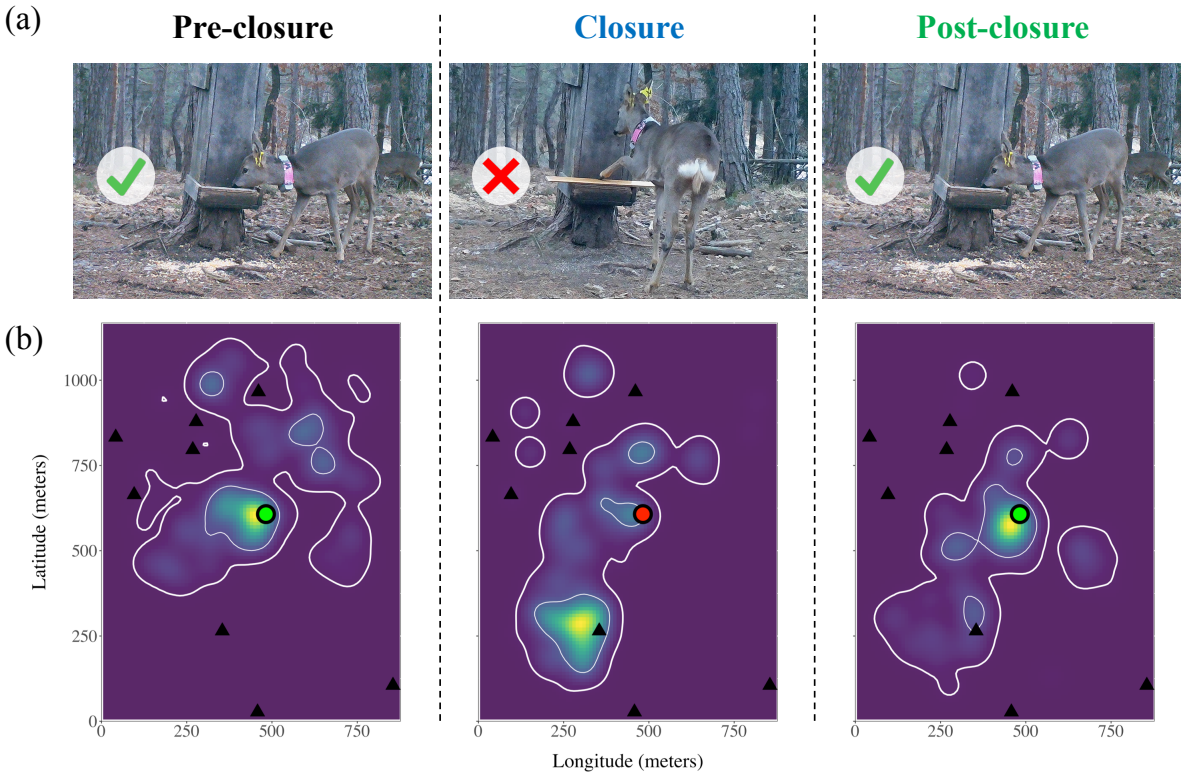

Figure 1.

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 manipulated, familiar FS (M) when food accessibility was prevented (P1.4a) and compensated for this loss by using alternate, accessible FS (A; 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[27], we predicted

101 that they would respond less markedly to the experiment than females (P2.1). We also predicted
102 the responsiveness of roe deer to be positively influenced by the individual's prior preference for
103 FS (P2.2).

104 If the spatial patterns of roe deer home ranges result from the benefits of site
105 familiarity[28,29], animals should strive to use familiar areas and resources when accessible (H3;
106 Table 1). Accordingly, we predicted that when initial conditions of food accessibility are re-
107 established after perturbation, the initial space-use patterns would be restored (P3.1), following a
108 return to high use of the familiar FS (M; P3.2).

109

110 Table 1. Hypotheses and corresponding predictions.

Hypotheses	Predictions
H1: roe deer alter their space-use patterns and movement behaviour to track the dynamics in resource availability.	*The closure of the manipulated, familiar feeding site (M) 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 M - P1.4b: a compensation by using alternate, accessible feeding sites (A)
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 manipulated, familiar feeding site (M) leads to…* - P3.1: the return of space-use to pre-closure patterns - P3.2: the return of resource use to pre-closure patterns

111

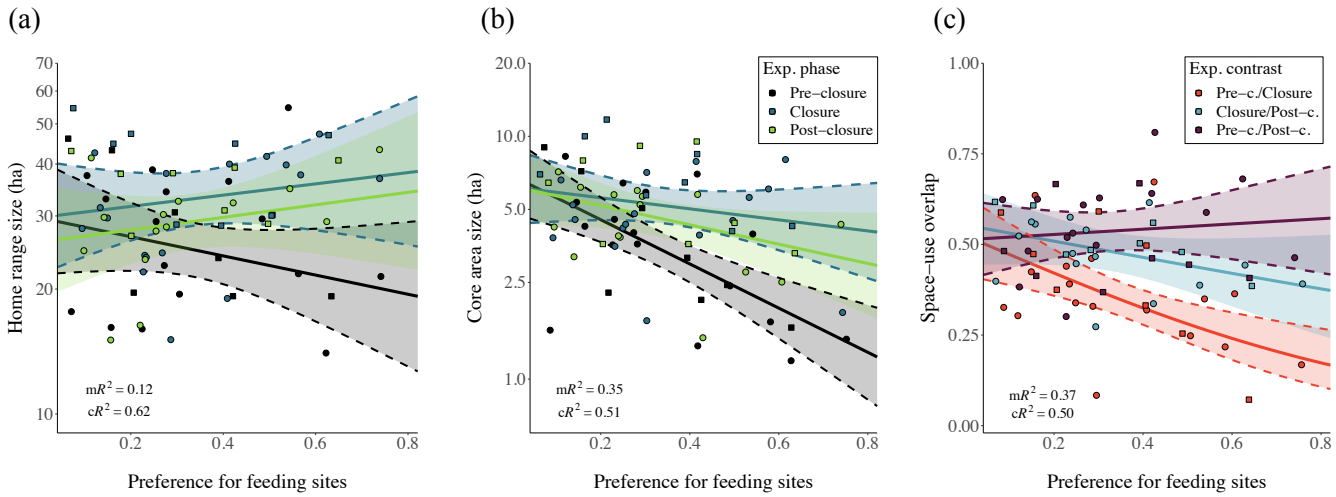

Figure 2.

Results

Space-use and movement responses to alteration of resource availability

Roe deer space-use changed significantly during the experiment: the size of both home ranges (95% UD isopleth; Fig. 2a; Supplementary S4: Table S1) and core areas (50% isopleth; Fig. 2b; Supplementary S4: Table S2) increased significantly during the experimental closure (P1.1). On average, home range 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} tended to have smaller home ranges during the pre-closure, smaller core areas overall, and stronger increases in both home range and core area sizes following the experimental closure (Fig. 2a-b; Supplementary S4: Tables S1, S2; P2.2). There was no significant effect of sex or interactions

between sex and experimental phase on home range size (Supplementary S4: Table S3; P2.1), but a marginally significant interaction between sex and experimental phase on core area size (Supplementary S4: Table S4), 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. 2c): 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. 2c; P2.2), with higher h_{FS} being associated to larger space-use shifts following closure (Supplementary S4: Table S5). However, there was no apparent influence of sex in the observed space-use patterns (Supplementary S4: Table S6; 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 important 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 (Supplementary S5: Fig. S1, right-hand panels, Table S1; P2.1), and individuals associated with high h_{FS} values (Supplementary S5: Fig. S1, top panels, Table S1; 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} (Supplementary S5: Fig. S2, top-right panel, Tables S2, S3; 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 resource use (Fig. 3; Supplementary S6: Table S1). On average, the proportion of use of the manipulated 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 alternate FS (A) – 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 A and V declined to 9% and 72%, respectively. The shifts in resource use were very consistent among animal-years for M and A but were more variable for V (Fig. 3, 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 A (Fig. 3, bottom panels; Supplementary S6: Table S1). 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 A during closure (P2.2). This compensation for A during closure was stronger for females (Supplementary S6: Fig. S1, Table S1; P2.1). However, sex did not influence the use of M or V (Supplementary S6: Table S2; 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, A and V, respectively).

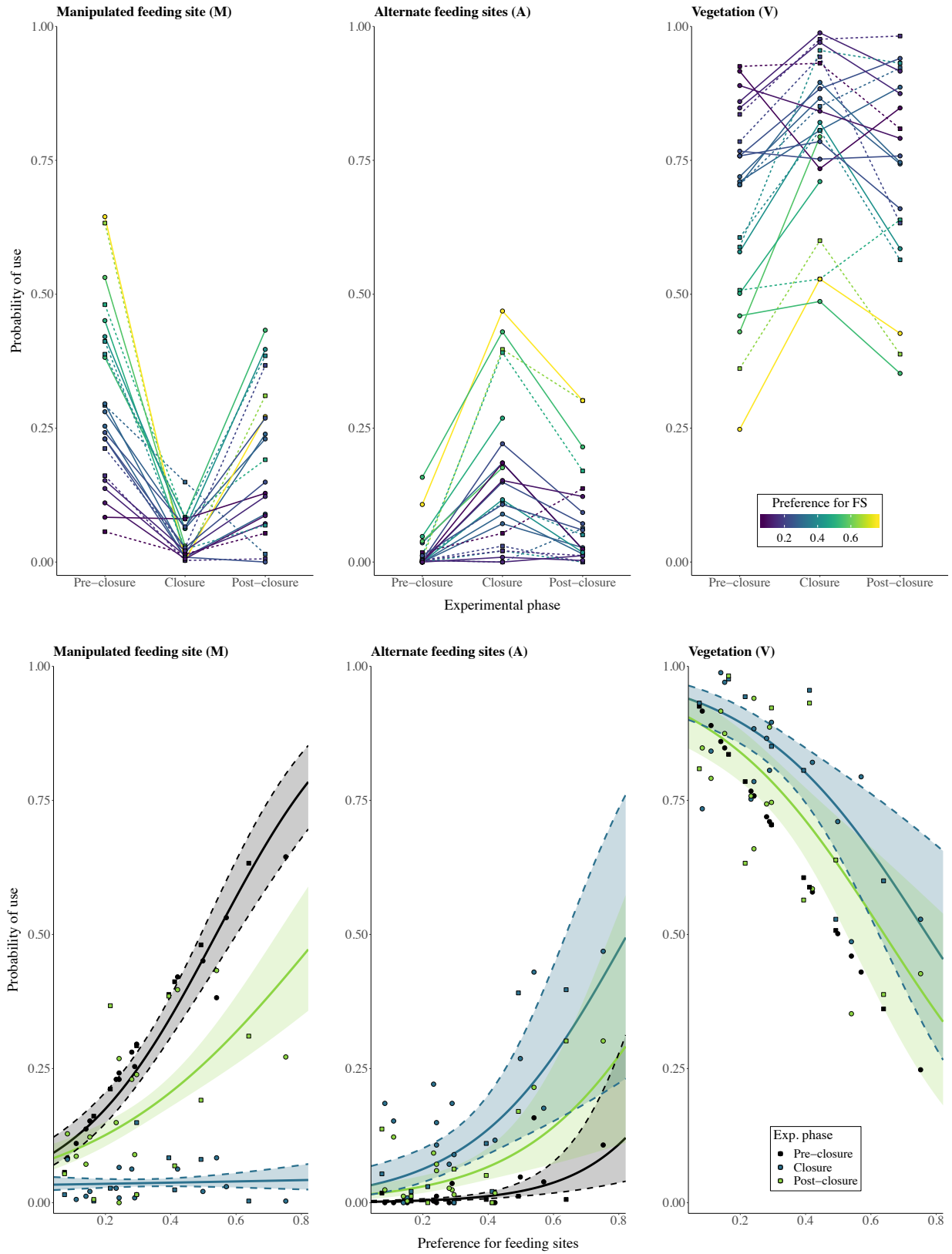
Manipulated feeding site (M)
Alternate feeding sites (A)
Vegetation (V)
Probability of use
1.00
0.75
0.50
0.25
0.00
Pre−closure
Closure
Post−closure
Experimental phase
Preference for FS
0.2
0.4
0.6
Preference for feeding sites
Exp. phase
Pre−closure
Closure
Post−closure

Figure 3.

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 resident large herbivore. Specifically, we show that roe deer track resource dynamics (Fig. 3; H1), which leads to changes in their space-use (Fig. 2) and underpinning movements (Supplementary S5: Figs S1, S2), and that individual traits, especially resource preference, mediate these behavioural adjustments (H2). In addition, 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.

The experimental alterations of food availability led to larger, spatially-shifted home ranges (Fig. 3), and more explorative movements by roe deer (Supplementary S5: Figs S1, S2), thereby directly establishing the connections between movement, space-use and the spatio-temporal patterns of resources.

In a previous observational study, elk were shown to alternate between two movement modes: a low speed and high sinuosity mode thought to be within-patch area-restricted search, and a high speed and low sinuosity mode between resource patches[38]. In our experimental study, we can directly link these movement modes to changing resources: the exploratory movements of roe deer (high velocity and low sinuosity) observed during the closure phase (P1.3) suggested that the animals were motivated to find alternate resource patches when their familiar feeding site (FS) became inaccessible, thereby increasing (P1.1), but mainly shifting (P1.2), their home range. While changes in home range size and location following resource manipulation have been found

200 in studies of lizards[39], birds[15] and voles[40], to date, there have been few experimental
201 investigations of the connections between space-use and the spatio-temporal distribution of
202 resources in large mammals.

203 In an earlier study, white-tailed deer shifted their home range core towards the vicinity of
204 newly deployed FS[14]. Our study builds upon these results by demonstrating multiple, successive
205 responses to resource manipulation, linking measured changes in underlying fine-scale movement
206 behaviour of individuals to resulting patterns of space-use that indicate dynamic resource
207 tracking behaviour by roe deer (H1). Although roe deer increased their use of the vegetation
208 matrix during the closure phase, individuals compensated the loss of their manipulated FS (M), to
209 a large degree, by shifts in their movements and space-use towards alternate FS (A; Figs 3;
210 P1.4a-b). Consequently, individuals maintained a high overall use of FS throughout the
211 experiment.

212 While resource tracking behaviour may be expected under the optimal foraging theory,
213 other individual- and population-based factors, such as social fences due to territoriality or
214 density-dependent resource competition, can constrain the movement responses of individuals to
215 changes in the spatial distribution of resources[41]. The marked responses shown here are likely the
216 result of two non-mutually exclusive conditions. First, with the exception of adult males during
217 spring and summer[42], roe deer do not generally defend territories, and consequently their spatial
218 distribution can approximate that of an ideal free distribution[43]. In fact, territorial tenure[27] may
219 explain the marginally different response of males (P2.1), specifically their tendency to have
220 larger core areas (Supplementary S4: Table S4), more explorative movements (Supplementary
221 S5: Tables S1, S2) and lower resource compensation than females following closure
222 (Supplementary S6: Table S1, Fig. S1). Second, while intra- and inter-specific competition in

223 herbivores is largely linked to resource depletion[6], this density-dependent constraint of food
224 availability was prevented by providing *ad libitum* forage at the FS.
225
226 This study demonstrates that inter-individual variation in preference for FS strongly
227 mediated the responses of roe deer movement patterns, space-use and resource use to changes in
228 the spatio-temporal distribution of resources (H2). During the closure phase, the changes in all
229 measured variables were of larger magnitude for individuals associated with a high FS preference
230 (P2.1). The influence of FS preference was particularly striking in the shifts of space-use (Fig.
231 2c) and in the compensating use of alternate FS following the loss of the familiar resource (Fig.
232 3). The observed inter-individual differences in FS preference (Supplementary S3: Table S1) may
233 be linked to either the environment the individuals were exposed to, or a property of the
234 individuals themselves. In our experimental setting, all roe deer had access to at least one FS
235 provided with *ad libitum* food where use was not prevented by inter-individual competition[17].
236 Hence, we could quantitatively approximate FS preference as the relative use of FS over natural
237 vegetation. Preference for FS was derived from the relative use of FS, and so our definition
238 implies a conditionality on both the physiological state of the individual and on the relative
239 nutritional value of the provisioned food (corn) over natural vegetation in a given season. In
240 addition, the dynamics in the quality and quantity of natural browse – either spatial (e.g., between
241 home ranges) and/or temporal (e.g., between years) – could lead to temporal variations in FS
242 preference. Indeed, FS preference was higher in 2017 than in 2018 for all roe deer manipulated in
243 these consecutive years (Supplementary S3: Table S1). Preference can therefore be considered a
244 dynamic variable[30] that we evaluated at the individual level over a short period of relative
245 stability (pre-closure phase in each winter). We considered the temporal extent of our experiment
246 (*ca* 6 weeks) short enough to consider FS preference for each animal-year to be relatively

247 constant, because in this time period the physiological conditions and vegetation nutritional value
248 would not vary substantially or consistently.

249 Animals attending FS benefit from exploiting a forage-rich location but may risk elevated
250 intra- and inter-specific contacts, anthropogenic disturbance, and an increased susceptibility to
251 predation by humans. In roe deer, individual behavioural profile (e.g., body temperature at
252 capture) correlates with the use of risky but profitable habitats such as open areas, suggesting that
253 variations in personality could lead to individual differences in habitat use[44]. By analogy, FS
254 preference could be associated to bold or risk-taking personalities. Interestingly, preference for
255 FS tended to correlate with individual body temperature at capture (Pearson's r = - 0.37 p-value =
256 0.084; Supplementary S8), with bolder individuals (lower temperature) using FS more intensely.
257 Personality may not only lead individuals to use resources to a different extent, but also condition
258 their tendency to track spatio-temporal resource dynamics[45]. For instance, risk-taking
259 personalities tend to be associated with explorations of novel environments[46], as shown
260 experimentally in great tits following the loss of a familiar foraging area[15].
261

262 During the post-closure phase of the experiment, roe deer increased their use of familiar
263 FS (M), whose food accessibility had been restored after a transitory restriction (Fig. 3, left-hand
264 panels; P3.1), and home ranges shifted back to pre-closure patterns, as suggested by the high
265 spatial overlap between temporally-disjointed pre- and post-closure space-use (Fig. 2c; P3.2).
266 The restoration of these pre-manipulation patterns supports the hypothesis that site familiarity
267 provides inherent benefits to animals maintaining a home range (H3)[47]. These results are coherent
268 with published literature demonstrating that ungulates tend to select for previously visited
269 locations i.e., site familiarity[48,49].

Unlike most observational studies, our experimental approach allowed us to contrast two concentrated resources (M and A) of equal nutritional value but of distinct familiarity, and hence to separate the effects of resource tracking from those of familiarity. Resource tracking can explain roe deer use of alternate FS (A) to compensate the inaccessibility of the familiar, manipulated FS (M) during closure. However, the systematic return of roe deer to M during the post-closure phase, while both alternative resources were accessible, cannot be explained by resource tracking alone. Our experiment therefore suggests that roe deer were actively selecting for familiar areas and that site familiarity has an inherent value.

In observational studies of animal movement, a spurious familiarity effect can occur when an important factor influencing animal behaviour is not considered, and the re-visitation of particular locations is interpreted as an evidence for site familiarity selection[50]. However, this confounding effect is unlikely to affect the results of this experiment. First, corn was delivered *ad libitum* across all FS (M or A) i.e., homogeneous foraging value. Second, the FS were located in comparable environments and especially in relation to cover, a factor that largely influences roe deer movements and space-use[51,52]. Third, and most importantly, the specific identities of M and A varied interchangeably between individuals. Hence, we conclude that the return to pre-closure patterns of foraging behaviour and space-use are unlikely to be result of variations in the characteristics of specific FS, but rather of an inherent familiarity effect. In roe deer, site familiarity could allow a more profitable exploitation of natural forage, as seen in bison (*Bison bison)*[49] or reduce intraspecific competition for such resource (see [28] for a theoretical argument). Alternatively, the attraction to familiar areas could be related to a predator (natural or human) avoidance tactic[53].

Our results imply that when resource patterns are changing, individual behavioural decisions probably reflect a trade-off between the advantages of site familiarity and resource

294 tracking. Species with little fat reserves need a constant, high-nutritional intake, and may hence
295 be required to rapidly adjust their movements away from their most familiar areas to track spatio-
296 temporal resource dynamics, as seen in roe deer during the closure phase of this experiment or in
297 great tits[15]. It would be interesting to investigate whether capital breeding species, with greater
298 capacity to buffer transitory shortages of food availability, are more reluctant to abandon familiar
299 locations.
300
301 Ultimately, site familiarity is the manifestation of an animal's ability to acquire spatial
302 information, in particular by means of spatial memory[8]. Large herbivores are capable of
303 memorizing the location and profitability of resources[49]. In this study, it is likely that the
304 variations in roe deer responses to resource changes that are not explained by preference may be
305 the result of individual prior experience and knowledge of the status and distribution of
306 concentrated resources. An interesting avenue for further studies will be to evaluate the role of
307 these cognitive processes on individual foraging decisions.
308
309 **Methods**
310 *Study area*
311 Roe deer is the primary large herbivore in the study area (7-8 individuals km^{-2}), located in
312 the north-eastern Italian Alps (Argentario range, Autonomous Province of Trento). The area is
313 characterized by a continental climate (mean temperature of January: 1.0 °C; July: 21.0 °C; mean
314 annual rainfall: 966 m) with occasional snow cover, and is largely forested (80%). It
315 encompasses four hunting reserves in which selective hunting occurs between September and
316 December (see Supplementary S1 for further details).

317 Supplemental feeding management of roe deer is conducted year-round at > 50 distinct
318 feeding sites (FS; Supplementary S2: Fig. S1). FS are typically shaped as wooden hopper
319 dispensers that provide a continuous supply of corn accessible through a tray (Fig. 1a). They are
320 managed by private hunters for roe deer but are also attended sporadically by red deer (*Cervus*
321 *elaphus*).
322
323 *Experimental design*
324 We took advantage of roe deer use of a focal, identifiable resource – the FS – to design an
325 *in situ* experimental manipulation of resource availability. We created three successive
326 experimental phases of the availability of this resource – pre-closure, closure and post-closure –
327 by physically managing the accessibility of food at the FS. During the closure phase, access to
328 forage at FS was transitorily restricted by placing wooden boards obstructing the tray; these were
329 then removed again in the post-closure phase (Fig. 1).
330 The experiment was conducted between January and April, when roe deer use of
331 supplemental feeding is the most intense[17], for three consecutive winters (2017, 2018 and 2019).
332 We implemented the experiment on 18 individuals, including five recaptures and two
333 deployments spanning two winters, leading to a total of 25 animal-years (21 adults: 15 females, 6
334 males; 4 yearlings: 2 females, 2 males; sample size n=4, 11 and 10 in 2017, 2018 and 2019
335 respectively; see Supplementary S2 for details). The animal-year was our sampling unit, on the
336 assumption that the same individual may respond independently to manipulations in different
337 years. Roe deer were captured using baited box traps (n=16) or net drives (n=3), and were fitted
338 with GPS-GSM radio collars programmed to acquire hourly GPS locations for a year, after which
339 they were released via a drop-off mechanism. Captures and marking were performed complying
340 with ethical and welfare rules, under authorization of the Wildlife Committee of the Autonomous

341 Province of Trento (Resolution of the Provincial Government n. 602, under approval of the
342 Wildlife Committee of 20/09/2011, and successive integration approved on the 23/04/2015).
343 Radio-collared roe deer moved an average of 61.2 m per hour. This value of the average hourly
344 movement distance *(l)* was subsequently utilized in the analyses described below.

345 For all captured animals, we assumed a post-capture response in ranging behaviour. We
346 therefore considered the first re-visitation of the capture location as the sign of resettlement in the
347 original range and we used this time as onset of the experimental pre-closure phase. Although not
348 all the individuals were manipulated at the same time, we avoided interference between capture
349 operations and FS manipulations, and between co-occurring different manipulation phases (i.e.,
350 ensuring that co-occurring manipulations occurred in separate areas).

351 During the *pre-closure phase*, we assessed the use of FS by radio-collared roe deer. We
352 identified the "manipulated" FS (M) for each individual as the site with the largest number of
353 locations within a radius *l* during this initial phase, and considered it as the FS to which an
354 individual is most familiar. During the *closure phase*, corn was made inaccessible at M for a
355 duration of about 15 days, depending on personnel availabilities (min=14.0 days, max=18.1,
356 mean=15.5). M was then re-opened, thereby initiating the *post-closure phase*. During both pre-
357 and post-closure phases, corn was available *ad libitum* at M. All "alternate" (A) managed FS –
358 i.e., that were provisioned at least once in the month prior to the experiment – had corn available
359 *ad libitum* throughout the duration of the experiment.

360

361 *Data preparation*

362 To ensure meaningful comparisons between animal-years, we homogenized the durations
363 of each experimental phase to the minimum length of the closure phase in our sample (i.e., 14
364 days). Specifically, we truncated the movement data by removing initial excess positions for the

365 pre-closure and closure phases, and terminal excess positions for the post-closure phase. GPS
366 acquisition success was extremely high (99.57 % during the experiment) and we did not
367 interpolate missing fixes in the collected data.

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

377

378 *Preference for feeding sites*

379 We calculated each individual's preference for FS (h_{FS}) as the relative use of FS over
380 natural vegetation during the pre-closure phase (i.e., the proportion of GPS fixes classified as
381 either M or A). Because preference is considered to be temporally dynamic[30], we chose to
382 evaluate h_{FS} for each year separately in case individuals were manipulated in two separate
383 winters. This reasoning allowed to account for the influence of individual condition and of the
384 relative quality and quantity of vegetation resources on h_{FS}. We included h_{FS} in all space-use,
385 movement, and resource use analyses described below.

386 The variability of h_{FS} across animal-years was maximal when FS attendance was defined
387 as a GPS location within a distance equal to the population mean hourly step length l i.e., 61.2 m

388 from the FS (interquartile range=0.278, mean=0.343; Supplementary S3: Table S1). Accordingly,
389 the results described below are based on this definition (see Supplementary S7 for a sensitivity
390 analysis). At this scale, h_{FS} did not differ consistently between sex (mean for females=0.346;
391 mean for males=0.336; t-test: p-value=0.901).
392
393 *Analysis*
394 We analysed how the experimental manipulation, and its interaction with both preference
395 for FS and sex, affected roe deer space-use, movement behaviour, and resource use.
396 *Space-use:* We assessed the changes of home range and core area sizes (P1.1), and of
397 space-use overlap (P1.2, P3.1) between experimental phases. We calculated utilization
398 distributions (UD)[31] for each animal-year and experimental phase using a Gaussian kernel density
399 estimation. After visual inspection, we chose to compute the UDs at a spatial resolution of 10 m
400 and with a fixed bandwidth set to half the average hourly movement distance (i.e., $l/2$=30.6 m).
401 For home range and core area sizes, we calculated the area (in hectares) corresponding to
402 the 95% and 50% UD contours, respectively, during each experimental phase (*Phase*; three
403 levels; reference level: *Pre-closure*). We then analysed the log-transformed areas using a linear
404 mixed-effect model (LMM) with five fixed effects: *Phase*, h_{FS}, *Sex* (categorical predictor;
405 reference level: *Female*), and two interaction terms (*Phase:*h_{FS} and *Phase:Sex*). We included
406 animal-year (*ind*) as random effect (intercept). In all analyses, interaction terms were dropped
407 when statistically non-significant (p-value>0.05).
408 For space-use patterns, we estimated the overlaps for three pairs of UDs – pre- and post-
409 closure, pre-closure and closure, and closure and post-closure (*Contrast*; three levels; reference
410 level: Pre-/Closure) – using the volume of intersection statistic (VI)[32]. VI ranges from 0 (no

411 overlap) to 1 (complete overlap). We analysed the logit-transformed overlaps using an LMM
412 with *Contrast*, h_{FS}, *Sex*, *Contrast:*h_{FS} and *Contrast:Sex* as fixed effects, and *ind* as random
413 intercept.

414 *Movement behaviour*: We investigated the movement responses of roe deer to the
415 experiment (P1.3) by analysing the changes in hourly step length (Euclidean distance between
416 two successive relocations) and turning angle θ_t (angle between two successive movement
417 steps). Turning angles range between $-\pi$ and π, and were symmetric around 0. We analysed the
418 log-transformed step length, s_t, and the logit-transformed absolute turning angle, $\varphi_t =$
419 $log\left(\frac{|\theta_t|}{1-|\theta_t|}\right)$ using LMMs with *Phase*, h_{FS}, *Sex*, *Phase:*h_{FS} and *Phase:Sex* as fixed effects, and
420 *ind* as random intercept. Because step length was characterized by strong serial autocorrelation at
421 short temporal lags and at circadian periodicities (a common pattern in animal movement
422 trajectories[33]), we also included step length measured at lags 1, 2 and 24 h (i.e., $s_{t-1}, s_{t-2}, s_{t-24}$)
423 as fixed effects to reduce the autocorrelation of the model residuals.

424 *Resource use*: To test whether the experiment led to a transitory change in resource use
425 (P1.4a-b, P3.2), we fitted separate mixed-effect logistic regression models to the three single-
426 state presence/absence time series ($u_{M,t}$, $u_{A,t}$ and $u_{V,t}$) using *Phase*, h_{FS}, *Sex*, *Phase:*h_{FS} and
427 *Phase:Sex* as fixed effects, and *ind* as random intercept. The pre-closure level for *Phase* was
428 dropped for u_V to avoid circularity ($h_{FS} = 1 - \bar{u}_{V,t_{Pre-closure}}$). We also included the response
429 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
430 the autocorrelation of the model residuals. However, for the sake of conciseness and clarity, we
431 omit these response lags when visualizing resource use predictions. Because the model results
432 were consistent regardless of the inclusion of the response lags (Supplementary S6: Tables S1,
433 S3), this decision had no impact on the interpretation. Two animal-years were excluded from the

analyses of resource use due to the absence of suitable A-state: F4-2017 did not seem to have visited any alternate FS (A) prior to the experiment; and F16-2016 had two distinct, highly-used FS during pre-closure, but only the second most visited FS could be manipulated (due to stakeholder acceptance). While the use of A was more variable when including these two outliers, the general patterns remained unchanged (Supplementary S6: Tables S1, S4).

Software: All analyses were conducted in the R environment[34]. We used the packages adehabitatLT and adehabitatHR[35] for the spatial analyses, fitted all mixed-effect models via Maximum Likelihood with the package lme4[36], and obtained the coefficients of determination using MuMin[37].

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Figure Legends

Figure 1. Schematic representation of the experiment. (a) The manipulation consists of a transitory alteration of resource accessibility at a manipulated (M) feeding site. (b) The experiment is expected to lead to spatial responses in the monitored roe deer, and in particular in a shift of use from M (green/red dot, change of colour denoting the alteration of accessibility) towards alternative resources – alternate feeding sites (A; black triangles) or the natural 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).

Figure 2. Changes in roe deer space-use patterns – home range size (y-axis, panel a), core area size (y-axis, panel b) and space-use overlap (y-axis, panel c) – as a function of preference for feeding sites (x-axis) and experimental phase (colour; panels a and b) and phase contrast (colour; panel c). Observations are represented as dots (females) and squares (males) with a slight jitter, and model predictions as solid lines (95% confidence intervals: ribbons). Parameter estimates and associated significance can be found in Supplementary S4: Tables S1, S2 and S5.

Figure 3. Roe deer shifts in resource use during the experiment – manipulated feeding site (M, left), alternate feeding sites (A, centre) and vegetation (V, right). Top panel: mean proportional use (dots and lines) as a function of the experiment phase (x-axis) and preference for feeding sites (colour scale). Bottom panel: predictions of the resource use models ($u_{M,t}$, $u_{A,t}$ and $u_{V,t}$; estimate: solid lines; 95% confidence interval: ribbon) and mean relative use (females: dots; males: squares) as a function of the experiment phase (colour) and preference for feeding sites (x-axis). The model predictions do not consider resource lags at 1, 2 and 24 h nor the influence of *Sex* (although selected in the final model for $u_{A,t}$) for clarity and conciseness. Parameter estimates and associated significance can be found in Supplementary S6: Table S1.