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Water voles select and overexploit high-quality habitats, hindering future colonisations: Evidence from drone-based monitoring of dandelion-vole interactions in mountain meadows

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1 **Water voles select and overexploit high-quality habitats, hindering future**
2 **colonisations: Evidence from drone-based monitoring of dandelion-vole**
3 **interactions in mountain meadows**

4
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13
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16 **Author contributions**

17 Adrien Pinot, H el ene Lisse and Virginie Lattard conceived the ideas and designed methodology;
18 H el ene Lisse, Geoffroy Couval and Aur elien Levret collected the data; Marion Buronfosse, Adrien
19 Pinot and Fran ois Gillet analysed the data Marion Buronfosse, Adrien Pinot and Virginie Lattard led
20 the writing of the manuscript. All authors contributed critically to the drafts and gave final approval
21 for publication.

22 **Data availability statement**

23 The data and code used for this study are available at the following link:
24 https://figshare.com/articles/dataset/Dandelion_vole_interaction/24799383/2

25 **Conflict of interest statement**

26 We declare no conflict of interest.

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29

30

31 **Abstract**

32 Like many rodents, the water vole is able to reach high densities in meadows. During
33 outbreaks, voles cause significant changes in plant communities. Although water voles
34 consume a wide variety of plant species, dandelions have a unique position: they are
35 selected by voles year-round and serve as a key resource during winter. Voles harvest all
36 parts of the dandelion and store the roots in almost monospecific food stores. As dandelions
37 are perennial plants that take years to grow, vole activity can significantly affect dandelion
38 populations.

39 Our aim was to estimate the influence of dandelion density on vole space use, particularly
40 habitat selection during natal dispersal. We tested the hypothesis that voles select
41 dandelion-rich plots for settlements. We also measured the variation in dandelion density
42 due to new colonies settlements to assess potential feedback effects. We hypothesized that
43 voles decrease dandelion populations. To achieve that, we used a drone to monitor
44 dandelions and voles over two years. We monitored 52 quadrats, each half an hectare, three
45 times a year. We analysed each image using remote sensing to locate voles and dandelions,
46 and then examined the interactions between their locations over time.

47 We found that dandelion-rich plots were more likely to colonize. In plots with low dandelion
48 density, areas denser than the plot average were also more likely to be colonised. We
49 observed a decrease in the number of dandelions after colony settlement. Finally, we found
50 evidence that existing burrows were more likely to be reused by new voles if dandelions
51 were still present.

52 This study demonstrates that dandelion density is a key criterion in habitat selection for
53 water voles and that vole colonies rapidly deplete this resource after establishment. These
54 findings provide insight into plant-herbivore interactions and offer valuable perspectives for
55 further exploration of the plant hypothesis, particularly with respect to the dynamics of
56 resource availability and its role in cyclic population fluctuations.

57

58 **Key words**

59 dandelion, drone, habitat selection, grasslands, remote sensing, UAV, water vole

60 **Introduction**

61 All species have ecological requirements determined by biotic and abiotic conditions
62 (Hutchinson, 1957). To meet these requirements, animals select and utilise one or more
63 habitats that best meet their needs. The quality of these habitats, defined as the degree to
64 which they meet these requirements, significantly influences the survival and reproductive
65 success of individuals, and thus the individual fitness (Franklin et al., 2000). Consequently,
66 habitat quality selection strategies are expected to have been shaped by evolutionary
67 processes (Morris, 2003). Furthermore, nonrandom spatial distribution due to habitat
68 heterogeneity distribution is expected. This highlights a direct link between habitat selection
69 and the spatial distribution of individuals at the population level.

70

71 Habitat selection is a complex process involving several factors (Hutto, 1985) and can be
72 understood through theoretical frameworks. The ideal free distribution (IFD; Fretwell and
73 Lucas, 1970) theory assumes that individuals assess the food quality of all available habitat
74 patches and preferentially occupy those with higher quality. However, a high congener
75 density can negatively impact the trophic quality of a habitat when food is a limiting
76 resource, leading to a balance of densities according to habitat quality. In contrast, territorial
77 species follow the ideal despotic distribution (IDD; e.g. Fretwell, 1972), where dominant
78 individuals monopolise high-quality resources, forcing certain individuals to select habitats of
79 lower food quality, even while higher-quality patches remain undersaturated. The direct and
80 indirect effects of predation can also restrict access to certain habitats (DeCesar et al., 2014)
81 and influence dispersal capacities (Pulliam 2000), particularly in prey species.

82

83 Rodents face several significant constraints that shape their habitat selection. As prey for
84 many predators, their habitats must provide opportunities for effective predator avoidance
85 (e.g., Crego et al., 2018). Additionally, rodents have low energy efficiency due to their
86 digestive systems (e.g., Zynel and Wunder, 2002) and small body size (McNab 1983),
87 necessitating habitats with high trophic quality (e.g. Cole and Batzli, 1979). This need is
88 particularly crucial during winter, when the lower temperature and the higher fiber content
89 in plants increase the energy demands. Furthermore, their limited dispersal capacity,
90 compounded by the greater risk of predation with distance (Ims and Andreassen, 2000), and
91 their relatively short lifespan, impose further constraints on habitat selection. Consequently,
92 rodents must balance these trade-offs when selecting habitats. The ability to correctly
93 evaluate habitat quality and select the most suitable habitat is likely favored by natural
94 selection.

95

96 Our study focused on whether water voles (*Arvicola amphibius*) assess habitat food quality
97 when selecting territories. This species, widespread in various ecotypes, poses challenges in
98 permanent grasslands at mid altitude (above 750 meters), where population outbreaks -
99 occurring in 5- to 6-year cycles (Saucy, 1994) - can result in densities of more than 500 to 600
100 adults per hectare, sometimes exceeding 1,500 individuals per hectare (our data). These
101 outbreaks lead to significant disturbances in vegetation, as their burrowing activities bring
102 soil to the surface, negatively impacting grassland yields and forage conservation.
103 Understanding the mechanisms of habitat selection is essential to predict species
104 distribution and population dynamics.

105

106 Water voles are ideal subjects for studying habitat selection based on food quality due to
107 their biology and ecological behavior. Highly territorial, they maintain small and stable
108 territories throughout their lifetime (Airoidi, 1976), with colonies identifiable in both space
109 and time (Airoidi and Werra, 1993). Their strong antipredator adaptations, being strictly
110 subterranean (Saucy and Schneider, 1997), allow us to focus on food-related habitat
111 preferences without considering antipredator habitat structure. In mid-altitude regions, their
112 winter survival depends heavily on their ability to store food (Potapov et al., 2004). The
113 dandelion (*Taraxacum officinale*) was identified as a key food resource based on a
114 mutlimethod study including behavioural tests (Lisse and Pinot, 2024, Lisse et al., 2024). The
115 density of dandelion varies on a scale of just a few square meters, indicating a variability in
116 food quality within potential territories on a small scale. Given that water voles have a single
117 dispersal event (Saucy and Schneider, 1997), settlement choices are crucial.

118

119 Our study focused on the ‘functional’ rather than the ‘structural’ aspects of habitat (Gaillard
120 et al. 2010), with the aim of addressing the following questions:

121 -Does colonisation of a new territory depend on its food quality (H1)?

122 -Does the reuse of an old territory depend on its food quality (H2)?

123 -Can a reduction in resources be observed after territory colonisation (H3)?

124

125 **Materials and Methods**

126 **Study model & monitoring scale**

127 We focused on the fossorial form of the water vole (*Arvicola amphibius*), a species
128 commonly found in grasslands under continental climate and in permanent grasslands open

129 fields; water voles exhibit population cycles (Saucy 1988; Giraudoux et al., 1997). During the
130 growth phase, population density can increase from a few individuals per ha to over a
131 hundred within two years (see Pascal and Boujard, 1987 for a nice density curve). However,
132 it is evident that voles are not randomly distributed during peaks, with significant variations
133 in density observed between contiguous field plots of similar habitat.

134

135 Water voles lead an underground lifestyle, with a burrow system that is short (<120m) and
136 centered around a nest (Airoidi, 1976). The burrow territories are relatively stable, covering
137 around fifty square meters and occupied by 1 to 3 adults. (Airoidi, 1976). Voles forage in the
138 burrow by digging underground and release earth onto the surface in the form of mounds.
139 The proportion of these surface mounds (referred to as surface indices) is strongly
140 correlated with population density. This makes surface indices a reliable indicator of vole
141 density (Giraudoux et al. 1995).

142 The longest distance a water vole travels on the surface is during its natal dispersal to
143 establish its own burrow. This occurs when the water vole is between 6 and 8 weeks old and
144 then voles stop moving on the surface (Saucy and Schneiter 1997). Field observations
145 suggest that some young adults may occupy empty burrows (moles, dead voles).

146

147 Given their strong territorial behavior (Airoidi 1976), we hypothesized that water voles
148 follow the IDD model, rather than the IFD model. The study was carried out on the colony
149 scale, a relevant approach, since density is often a poor indicator of habitat quality (Van
150 Horne's, 1983).

151 **Study area & phase of Cycle**

152 This study focused on two regions of France with recurrent vole outbreaks since the 1970s:
153 the Central Massif and the Jura Mountains (Figure 1). In both regions, agricultural
154 specialisation in livestock farming has resulted in a simplified landscape mosaic favorable to
155 vole outbreaks (Giraudoux et al., 1997). The climate is continental in both places. In the
156 Central Massif (CM), the study site was located on the western plateau of Puy Mountain,
157 between 850 and 1200-meters altitude. Locally, agricultural land constitutes 64% of land use
158 that was made up of 95% of permanent grasslands in 2021. Based on public monitoring data
159 for voles (arvicola obs - <https://www.arvicola-obs.fr/>), we were able to select a subarea in
160 the early growth phase of the cycle for positioning the study. This would increase the
161 probability that high-quality territories would be readily available for food-based habitat
162 choices. According to the IDD model, we further anticipated that increasing population
163 density (e.g., during peak periods) would reduce vole selectivity for high-quality habitats.

164 In Jura Mountains, the study site was located between 400 and 900 meters altitude. Locally
165 agricultural land constitutes 56% of land use and was composed of 80% of permanent
166 grasslands in 2021. Dairy farming is the main farming activity in both sites with prestigious
167 cheese production areas.

168 **Sampling Design**

169 On studied areas, 35 plots were monitored in 2020 and 2021 in MC, and 19 in Jura in 2021.
170 The monitoring was carried out using 80 m × 60 m (4800 m²) quadrats, with one quadrat per
171 field plot. The quadrats were placed more than 50 meters from the nearest hedgerow and
172 more than 20 meters from the nearest field plot to mitigate edge effects. The minimum
173 distance between the adjacent quadrats was 100 meters. Plots showing evidence of mole or

174 wild boar activity were excluded to avoid interfering with the detection of surface vole
175 indices. All field plots were mowed (spring) and grazed (fall) each year. In May 2021, the
176 floristic composition of the CM quadrats was dominated by grasses (mainly *Poa trivialis*,
177 *Lolium perenne*, *Dactylis glomerata*, *Trisetum flavescens*, *Holcus lanatus*), with also a high
178 proportion of legumes (17%, mainly *Trifolium repens*) and *Taraxacum officinal* (13%). Plots
179 were selected to represent a wide range of dandelion densities.

180 **Monitoring vole and dandelion using UAV**

181 The quadrats were monitored by drone 3 times a year to map the locations of water voles
182 and dandelions from aerial photographs. In March, our goal was to map voles that had
183 overwintered on the plot. In May, we aimed to map dandelions, focusing on the flowering
184 bloom, which is synchronised by climatic conditions (Tanaka et al. 1988). The density of the
185 dandelions flower was expected to correlate with the biomass of the roots. In October, we
186 aimed to map new areas colonized by voles at the end of the breeding season. For each vole
187 picture, we selected a period with sufficiently bare vegetation to avoid masking surface
188 indices.

189 The flight altitude of the drone was set to achieve a pixel resolution of 1 cm². This resolution
190 enables us to correctly detect dandelion flowers (~ 7 cm² per flower head) while filtering out
191 buttercup flowers (~ 2 cm² per flower), which are also yellow. This also allows good
192 detection of earth mounds. We used an RGB sensor.

193 **Remote sensing**

194 To detect dandelion densities, we classified each pixel in the May image as yellow or not
195 yellow. Yellow pixels were identified as those with an R band > 0.9, a G band > 0.9 and a B
196 band < 0.1. To estimate vole densities, we classified each pixel as brown or non-brown. As

197 the color of the earth changes significantly with humidity, the RGB windows corresponding
198 to brown earth were determined for each image.

199 *Broad-scale index – dataset 1*

200 Dataset 1 summarised information into 2 m × 2 m tiles, resulting in a total of 1200 tiles per
201 quadrat. The tile size was chosen to be much smaller than the vole burrow (Airoldi 1976).
202 We recorded the cover of earth mounds and dandelions in each tile. A tile was considered
203 colonised by a vole if earth mounds covered more than 2.5% of the surface (equivalent to 10
204 mounds of 5 cm radius). The density of dandelion was evaluated by counting the number of
205 flower heads, estimated from the proportion of yellow pixels, assuming that each flower
206 head had an average surface of 7 cm² (diameter 3 cm).

207 We compared the density of dandelion flowers in each tile with the average density of
208 dandelion in quadrats to calculate the dandelion anomaly index. To normalise the
209 distribution of the dandelion anomaly, a fourth root transformation was applied.
210 Subsequently, the transformed values were centered at 0 rather than 1 to facilitate the
211 identification of negative and positive anomalies.

212 *Fine-scale analysis – dataset 2*

213 Dataset 2 was composed of 46 subplots of 20 m×20 m centered on a colony. The 400 m²
214 area was chosen to be substantially larger than the vole territory. Of these subplots, 16 were
215 derived from images taken in the CM in 2021, 15 in the CM in 2022, and 15 in the Jura
216 Mountains in 2022. Using a GIS algorithm, we mapped each earth mound and each
217 dandelion flower within these subplots (more details of remote sensing in SuppInfo1).

218 **Statistical analyzes**

219 All analyzes were performed in the R environment (version 4.2.2). A forward stepwise
220 selection procedure was used to select the model with the lowest Akaike Information
221 Criterion (AIC). All models, except for the point pattern analysis, included the quadrat
222 identifier as a qualitative explanatory variable (Burnham and Anderson, 2002).

223 *H1: New colony settlement*

224 To assess the influence of dandelion density on site selection for new colonies, we analysed
225 the location of new vole colonies by comparing images taken in March and September (in
226 2021 and 2022 in the CM and only in 2022 in the Jura). We used a subset of the data set that
227 included exclusively tiles that were not colonised in March (n = 64537). We defined a binary
228 response variable, where 0 indicated a non-colonised tile and 1 indicated a colonised tile for
229 the September picture. The anomaly of dandelion, the dandelion density in the tile and the
230 dandelion density in the quadrat were used as explanatory variables in a logistic regression
231 to explain tile colonisation probability.

232 *H2: Reuse of old colonies*

233 We investigated the reuse of old colonies by comparing images taken in September 2021
234 and September 2022 (only in Massif central). We used a subset of data set 1 that included
235 only tiles colonised in September 2021 and March 2022 (n = 7851) and defined a binary
236 response variable for colony reuse, where 0 indicated an abandoned tile and 1 indicated a
237 tile that remained colonized in September 2022. The explanatory variables tested in the
238 logistic regression to explain probability of colony reuse were the local dandelion density in
239 the tile in May 2022, the average dandelion density within the quadrat in May 2022 and the
240 dandelion tile anomaly.

241 *H3: Dandelion Density Variation - Broad-Scale Pattern*

242 To assess the effect of vole density on the variation in dandelion density in each tile, we used
243 the logarithmic transformed dandelion population growth rate (DPGR) between May 2021
244 and May 2022 (in the CM only) as the response variable. The DPGR considers the average
245 number of flower heads per plant to account for variations in the flowering stage between

246 2021 and 2022. We used a subset of Data Set 1 that included only tiles that were not
247 colonised in May 2021 ($n = 27852$). The explanatory variable tested in logistic regression
248 was the percentage of surface of the earth mounds in March 2022 (cover of surface indices
249 for vole colonies that have overwintered).

250 *H3: Dandelion density variation – Distance to mounds*

251 The aim of this statistical analysis was to evaluate dandelion depletion as a function of the
252 distance from the mounds. We used point pattern analysis on dataset 2 (20x20m subplots).

253 The distance between the tumuli and the dandelions was calculated using 20 consecutive
254 buffers, ranging logarithmically from 5 cm to 5 m. The number of heads of dandelion flowers
255 within each buffer was counted. To estimate dandelion depletion, we calculated the ratio
256 between the number of flower heads in each buffer and the average number of flower
257 heads in the subplot.

258 We used a generalized additive model (GAM) to predict changes in dandelion density (DD) as
259 a function of the distance to the mounds (DM). The GAM was preferred over the linear
260 model due to the expected non-linear effect of distance. The sub-plot identifier was added
261 as a random effect to account for the dependence among buffers within the same sub-plot
262 for the same year.

263 All hypotheses and models used in the study are summarized in Figure 2.

264 **Results**

265 **Dataset Overview**

266 Surface earth mounds were measured 92 times in March over the years 2021 and 2022. In
267 this month, the surface of the earth mounds within a quadrat was between 0.09% and

268 40.04%. The median was 2.01%, which represents around 615 vole tumuli of 10 cm diameter
269 (SuppInfo 2, Fig. A). Of the 35 quadrats monitored over the two years, 23 showed an
270 increase in soil cover between March 2021 and March 2022, indicating an increase in vole
271 density (SuppInfo 2, Fig. B). The average dandelion cover per quadrat ranged from 0 to 58
272 dandelion flowers per m² (SuppInfo 2, Fig. C). Overall, the abundance of dandelion was
273 higher in 2021 compared to 2022, with a median dandelion growth rate of 0.321 between
274 these two years.

275 **H1: Influence of dandelion density on new colony establishment**

276 There were 64,537 uncolonised tiles in March in the dataset. In September, 11,734 (18.2%)
277 of these tiles had been colonized, while the remaining 52,803 remained uncolonised. The
278 optimal model identified the density of dandelion, the anomaly of dandelion and its
279 interaction as significant factors influencing site selection by voles (Table 1.A).

280 The probability of colonization for a tile was significantly dependent on the average density
281 of dandelion in the quadrat (coefficient = 0.0115 ± 0.0008 , $P < 2e-16$) and the local dandelion
282 anomaly (coefficient = 1.803 ± 0.065 , $P < 2e-16$). However, the interaction between the
283 dandelion anomaly and the average density of dandelion was significantly negative
284 (coefficient = -0.0195 ± 0.0026 , $P = 2.57e-14$).

285 In quadrats with low dandelion density, voles were more attracted to tiles with higher local
286 dandelion density, although the effect of dandelion anomaly decreased in quadrats with
287 high average dandelion density (Figure 3.a). In quadrats with less than four heads of
288 dandelion flowers per m², the probability of colonization increased from 0.01 for tiles
289 without dandelion to 0.13 for tiles with an anomaly of 0.5 (i.e. 5 times the quadrat average).
290 However, in quadrats with high dandelion density (64.2 flower heads per m²), the probability

291 of colonization only changed from 0.08 to 0.14 when the anomaly varied between -0.5 and
292 0.5

293 **H2: Influence of dandelion density on old colony reuse**

294 In our study, 7,851 tiles were colonised in September 2021 and March 2022, but only 2,785
295 of these tiles remained colonised in September 2022 (that is, 35% of the burrows were
296 reused). The model with the lowest AIC included the dandelion density within the tile and its
297 interaction with the average dandelion density when the (fixed) quadrat effect was
298 considered (Table 1.B).

299 According to this model, the probability of reuse for a vole colony was significantly
300 dependent on the density of dandelion within the tile (coefficient = -0.0263 ± 0.0088 , $P =$
301 0.002621). However, the interaction between the tile dandelion density and the average
302 dandelion density was highly significant ($P = 1.12e-06$), indicating that the effect of the local
303 dandelion density strongly depends on the average dandelion density at the quadrat level
304 (Figure 3.b). The effect was positive only in quadrats with high density of dandelion and null
305 when the density was around 28 flowers heads per m^2 .

306

307 **H3: Influence of dandelion density by vole – broad-scale analysis**

308 The best model identified a significant negative effect of the logarithmic transformation of
309 vole density in March (Table 1.C). A significant decrease in dandelion density was observed
310 in areas with higher vole mound densities (coefficient = -0.3074 ± 0.0124 , $P = 2 \cdot 10^{-16}$) (Figure
311 4.a).

312 **H3: Evolution of the dandelion density according to the distance to the mounds - Fine**
313 **pattern analysis**

314 The density of Dandelion was analysed as a function of distance from the mounds. The
315 logarithmic transformation distance to the earth mounds was selected as a strong fixed
316 effect ($P = 2 \cdot 10^{-16}$) in the best model with the colony identifier included as a random effect
317 (Table 1.D). The results indicated that the density of dandelions was lower near the mounds
318 and increased with distance from them (illustrated example in SuppInfo 3). This effect was
319 measurable up to 4 meters around the mounds (Figure 4.b).

320

321 **Discussion**

322 Our study investigated the selection of water vole habitat in relation to the food quality of
323 the territories. We also examined the feedback of vole colonisation (after habitat selection)
324 on the food quality of the territory. To achieve this, we used an unmanned aerial vehicle
325 (UAV, i.e. drone).

326 **Methodological approach: use of drone to investigate plant-vole interactions.**

327 Many scientists have developed methods for detecting animal densities using UAV
328 photography, provided the animals are not cryptic from the air. UAVs have been used to
329 detect wetland birds such as flamingos (Valle 2022), seagulls (Corregidor-Castro et al., 2021),
330 or geese (Aniceto et al., 2018). Regarding rodents, studies have shown that various
331 burrowing species such as marmots (Enkhbat et al., 2023), prairie dogs (Kearney et al.,
332 2023), and ground squirrels (Gedeon et al., 2022) can also be tracked using UAV. Detecting
333 the densities of water voles from earth mounds is therefore not a major novelty, although it

334 is useful for quantifying populations or assessing damage. Numerous studies have also
335 focused on the detection of particular plant species such as endangered dwarf bear poppy
336 (Rominger and Meyer, 2019), cultivated rice (Zheng et al., 2020), or ornamental plants
337 (Bayraktar et al., 2020). The great advantage of UAVs is their ability to survey large areas
338 over time, allowing detailed temporal analyses.

339 Therefore, our study is innovative, as it demonstrates the possibility of detecting two
340 different species and inferring their relationships through the spatial structure of these two
341 species across time.

342 A key point in our approach was the unpredictability of vole settlement locations, making it
343 essential to monitor large areas. Placing the study in the favourable context of population
344 dynamics (i.e., the growth phase) also greatly improved the probability to observe
345 colonisations.

346 Drone photography requires specific environmental conditions that could be difficult to
347 meet. There must be no wind or rain, and the lighting must be at least calibrated. In our
348 case, calm weather conditions free of wind and rain were particularly scarce in mountain
349 climates. Photographing dandelions with drones added further complexity due to their brief
350 and synchronised flowering period (5 to 10 days), which is influenced by meteorological
351 factors (the opening of dandelion flowers is temperature dependent, requiring a minimum
352 of 13°C Tanaka et al., 1988) and elevation. These constraints limited the area we monitored.
353 Additionally, post-processing and interpretation of drone imagery is time consuming and
354 requires substantial data storage capacity. In our case, as the objects we detected (brown
355 spots and yellow dots in a sea of uniform green) were relatively simple, we used simple

356 detection algorithms. However, with more complex objects, it is possible to develop more
357 technical methods such as deep learning.

358 We also believe that this technique could provide useful information for habitat selection in
359 rodents. Some candidate species, such as the common vole, which lives in areas where
360 vegetation is short and whose tunnel mouths can be spotted, seem more affordable than
361 others, such as field mice, tree squirrels, or lemmings, which are more cryptic and live in
362 more complex environments as seen from an aerial photograph.

363

364 **Habitat Selection on Food Availability**

365 In this study, we were interested in how the quality of a habitat type, grassland, is perceived
366 and selected by water voles. To achieve this, we focussed on very low-contrast
367 environments and avoided different habitat types, such as hedges, forests, and wetlands.
368 We concentrated on the species' preferred habitat, where we observed the highest densities
369 (Morilhat et al. 2007). We also avoided variations in grass height between the monitored
370 areas, as this factor is known to modulate the risk of predation for voles (Getz 1985; see, e.g.
371 Jacob 2003). This approach allowed us to establish a quasi-experimental framework with
372 food availability being the only variable in our study. However, our methodology is relatively
373 well-suited to areas where water vole outbreaks occur, typically large open fields of
374 grassland largely devoid of trees.

375 Rodents are well known to have habitat preferences (see, e.g., Bonnet et al., 2013,
376 Heroldova et al., 2021) or to forage in selected patches (see, e.g., Koop 1988). High-quality
377 food has been shown to provide significant benefits for voles at the individual scale (e.g.,
378 Batzli 1986) and to permit high population densities (e.g., Hall et al., 1991) or to prevent

379 winter population crashes (e.g., Johnsen et al., 2017). Furthermore, many studies have
380 shown that voles are able to overgraze in certain cases (e.g., Huitu et al., 2003). Although
381 several studies have focused on the effect of the departure habitat on dispersal (e.g., Lin et
382 al., 2006, Rémy et al., 2011), few have examined the arrival habitat probably because of
383 methodological problems (Glorvigen et al., 2013). However, experimental evidence suggests,
384 consistent with our findings, that voles preferentially settle in habitats with higher food
385 quality, among other selection criteria (Glorvigen et al., 2013).

386 The originality of our study lies in demonstrating that food quality is a strong driver for the
387 selection of water vole habitats in natural settings, probably relegating predation to a
388 secondary role, at least during the growth phase. Water voles have high antipredatory
389 behaviours (see model specie paragraph), suggesting that predation has been a significant
390 force of selection. However, during the growth phase, high-quality habitats are common and
391 probably easy to find. Dispersal distances are also probably short, even to locate good
392 quality habitats, thus eliminating the trade-off between food quality and predation risk.
393 Finally, the degradation of habitat quality upon colonisation may have significant
394 implications for individual replacement and thus on population dynamics.

395

396 **Possible consequences on population dynamics and cycle theory**

397 In this study, we focus primarily on the scale of vole colonies. By monitoring large areas
398 several times, a year over two years, we were able to retrospectively characterise vole
399 territories prior to colonisation. We considered dandelions to be an important component of
400 the trophic quality of the water vole's habitat due to its winter storage behaviour (Lisse et
401 al., 2024). On the territory scale, we observed that dandelion density is a factor of

402 attractiveness. We also measured that once a territory is occupied, dandelion densities
403 decrease, making the territory less likely to be recolonised. The quality of the habitat and,
404 therefore, its attractiveness, can only be restored when the dandelion population
405 regenerates sufficiently, which is suspected to take consequent time.

406 At the plot level, we observed that vole growth rates are higher if the dandelion density is
407 high. Therefore, we expect delayed negative feedback on dandelion densities, making plots
408 less attractive. This process can theoretically be transferred to the landscape scale if
409 dandelions' densities synchronise at high levels during the phase of low vole density.

410 However, changes in the dispersal rate of young voles necessarily impact population
411 structure and genetics. Cerqueira and collaborators (2006) showed that during the decline,
412 voles continue to reproduce but there is a deficit in the number of young individuals.
413 Berthier et al. (2013) observed that dispersal distances are relatively low at the start of the
414 growth phase, highlighting close-to-home colonisation, and increase during the peak. Finally,
415 Giraudoux et al. (1997) observed that outbreaks begin in epicenters and then move in a
416 traveling wave phenomenon. These massive movements in density throughout the
417 landscape can only be explained by extensive dispersal. These three results on the same
418 species model under comparable conditions, obtained at different scales, are all consistent
419 with strong interdependent plant-herbivore relationships mediated by the dispersal of
420 young voles.

421 Four main types of rodent-plant interactions may be responsible for cyclical fluctuations
422 (Soininen & Neby 2023): 1) intrinsic cyclical quality/quantity of plants, 2) reduction in the
423 quantity of available resources through overgrazing, 3) modification of the quality of

424 preferred plants, 4) reduction in quality through a change in diet in favour of elements of
425 lower quality.

426 Our results may be consistent with the second hypothesis as well as with the fourth. This
427 depends on how habitat selection varies with density, which we did not measure in this
428 study. However, to determine whether dandelions are a fundamental parameter of water
429 vole cycles, we need to measure whether vole and dandelion densities covariate throughout
430 an entire cycle.

431 In conclusion, our findings highlight the critical role of dandelion density in the selection of
432 water vole habitats and the subsequent impact on population dynamics. These findings have
433 practical implications for the management of vole outbreaks in agricultural landscapes.
434 Monitoring dandelion densities could serve as an early warning system for potential vole
435 population peaks, enabling timely and targeted interventions to mitigate damage. Future
436 research should explore the integration of these ecological insights into predictive
437 management frameworks, focusing on maintaining balanced trophic dynamics and reducing
438 the risk of cyclical population booms. By doing so, we can develop more sustainable and
439 effective strategies to co-exist with water voles in shared landscapes.

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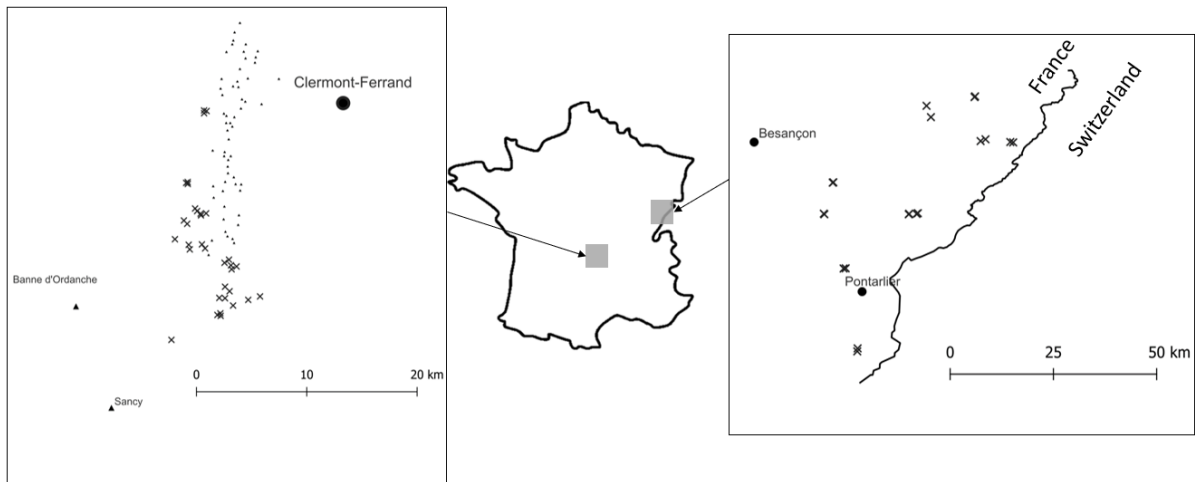
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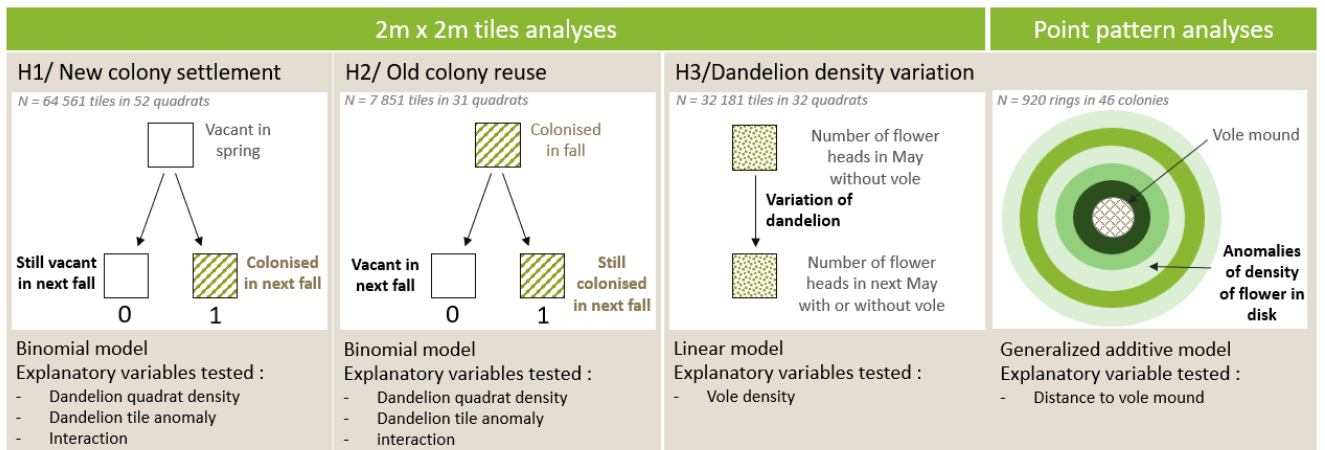
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585 **Figure 1** :Localization of the 35 plots in Massif central (on the left) and the 19 plots in Jura
 586 Mountains (on the right). Plots are materialized with cross.

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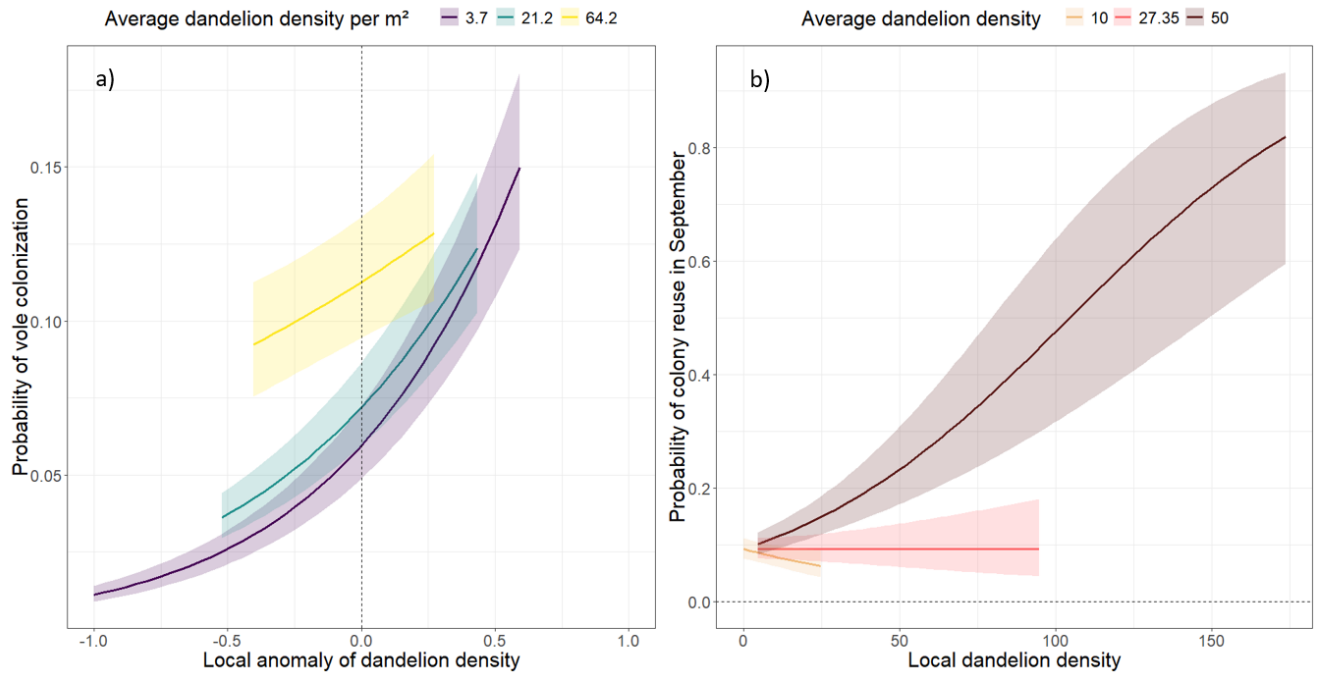


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589 **Figure 2:** Analysis Framework for Vole Colony Dynamics and Dandelion Density Interactions

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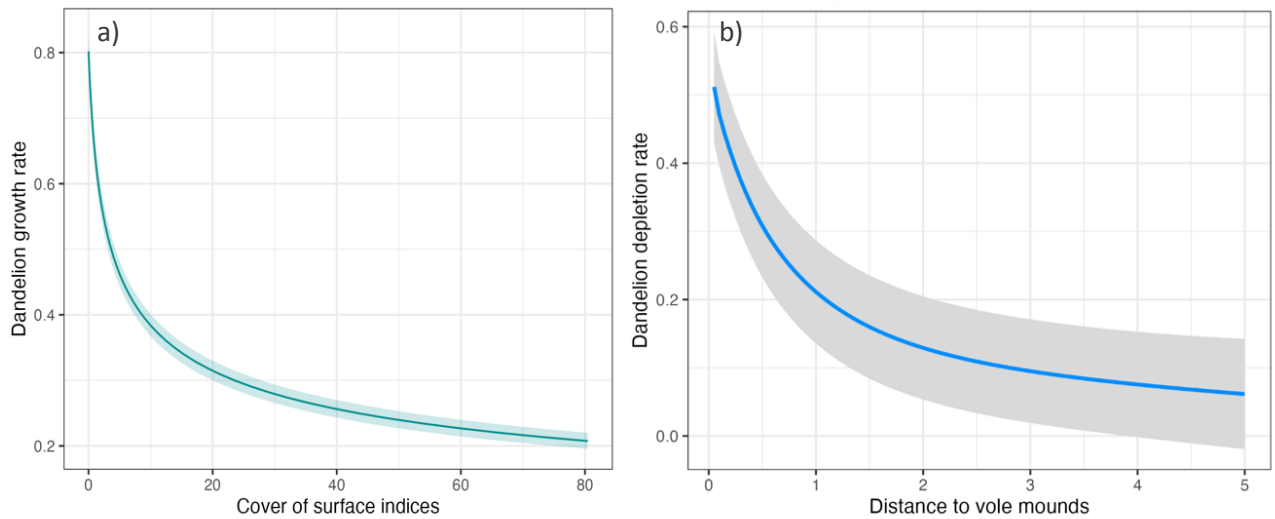


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594 **Figure 3** : Prediction of the probability that a) an empty tile will be colonized by voles based
 595 on dandelion anomaly and b) a vole colony will be reused according to local dandelion
 596 density. Predictions were generated from 1 to 99 percentiles of the observed dandelion
 597 anomaly.

598



599

600 **Figure 4** : a) Prediction of dandelion growth rate between May 2021 and May 2022 based on
 601 the cover of the surface indices of vole density in March 2022. b) Prediction of dandelion
 602 flower-head depletion rate as a function of distance to vole mounds, using generalized
 603 additive models (GAM).

604

605 **Table 1** : Model selection table for the three hypotheses. Col: probability of establishment of
606 a new vole colony, Anom: local dandelion anomaly, D_t : dandelion density in the tile, D_q :
607 average dandelion density in the quadrat, Q: quadrat identifier, Reuse: probability of colony
608 reuse, DGR: dandelion growth rate between 2021 and 2022, Cover: percentage cover of
609 surface indices in March 2022, DD: dandelion depletion rate, DM: distance to the mounds,
610 Subplot: subplot identifier

GLM equation	df	AIC	Δ AIC	Explained variance
A/ Vole colonization				
$Col \sim 1+Q$	52	42060	1248	0.314
$Col \sim Anom+Q$	53	41074	262	0.330
$Col \sim D_t+Q$	53	41812	1000	0.318
$Col \sim D_q+Q$	53	41810	998	0.318
$Col \sim D_t+D_t:D_q+Q$	54	41788	976	0.318
$Col \sim Anom+D_t+Q$	54	41075	263	0.331
$Col \sim Anom+D_q+Q$	54	40868	56	0.334
$Col \sim Anom*D_t+Q$	55	40959	147	0.333
$Col \sim Anom*D_q+Q$	55	40812	0	0.333
B/ Colony reuse				
$Reuse \sim 1+Q$	31	5887.8	56.2	0.429
$Reuse \sim Anom+Q$	32	5887.5	55.9	0.429
$Reuse \sim D_t+Q$	32	5854.8	23.2	0.433
$Reuse \sim D_t+Anom+Q$	33	5856.3	24.7	0.433
$Reuse \sim D_t*Anom+Q$	34	5858.2	26.6	0.433

<i>Reuse</i>~<i>D_t+D_t:D_q+Q</i>	33	5831.6	0	0.435
C/ Effect of vole on dandelion population growth rate (broad-scale analysis)				
<i>log(DGR)</i> ~1+Q	33	94138	611	0.655
<i>log(DGR)</i> ~ <i>Cover</i> +Q	34	93663	136	0.661
<i>log(DGR)</i>~<i>log(Cover+1)</i>+Q	34	93527	0	0.663
D/ Dandelion depletion by vole (fine scale pattern)				
<i>DD</i> ~ <i>Subplot</i>	47.0	-41.3	558	0.477
<i>DD</i> ~ <i>s(DM)</i>	6.5	282.68	882	0.224
<i>DD</i> ~ <i>s(log(DM))</i>	3.5	279.99	879	0.224
<i>DD</i> ~ <i>s(DM)+s(Subplot,bs="re")</i>	51.3	-596.2	3	0.715
<i>DD</i>~<i>s(log(DM))+s(Subplot,bs="re")</i>	50.1	-599.1	0	0.716

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612