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## The use of military bunkers by the European badger and red fox in Western Europe

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# 1 The use of military bunkers by the European badger and red fox in Western Europe

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6 **Running Title:** New homes for badgers and foxes

## 7 Abstract

8 Intensification of agriculture and land consolidation policy induced the removal of most  
9 natural features from farmland, reducing the habitat of many wild species. Abandoned WWII  
10 bunkers, unaffected by land consolidation, are a potential shelter for wildlife and could be  
11 used as burrows by carnivores such as European badgers and red foxes.

12 We explored 182 abandoned bunkers in a farmland area in eastern France in summer 2016.  
13 Bunkers were located in crops, forests, or groves. Over a three-month period, signs of  
14 presence, the number and type of burrows inside the bunkers and in their immediate vicinity  
15 were noted. Environmental variables were obtained using GIS, and binomial models were  
16 created to reveal parameters influencing bunker use by badgers and foxes. The degree of  
17 bunkers burrowing was used as a co-variable. Twenty-one groves without bunkers were also  
18 studied in order to estimate the added value of bunkers in groves.

19 Badger and fox tracks were found on 34% of the sites, and burrows on 24% of them with  
20 similar rates for badgers and foxes. Animals used partially buried bunkers more than  
21 underground or overground bunkers. The sizes of annual crops and urban areas around the  
22 bunker were positively correlated with bunker use. The presence of a bunker in groves was  
23 positively correlated with the presence of burrows in groves.

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24 As bunkers were widely used by badgers and foxes, they may improve conservation in  
25 intensive farming landscapes. We recommend the management of these ruins to facilitate the  
26 sustainable installation of a variety of species.

27 *Keywords:* refuges, artificial habitat, military fortifications, farmlands, burrows

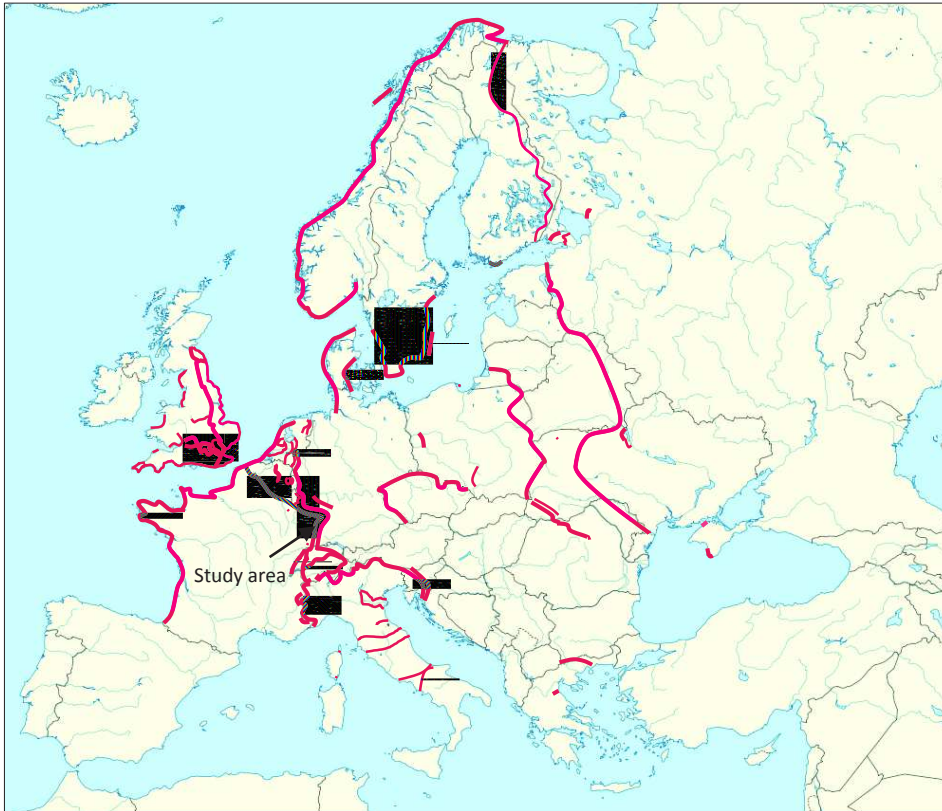
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## 30 Introduction

31 A huge number of military fortifications were built before and during the Second World  
32 War, often located close to border areas like the Maginot Line or the Atlantic Wall. These  
33 concrete bunkers (English), Blockhäuser (German) or casemates (French) are often located  
34 underground, either by design or due to burying over time. They have a small number of  
35 rooms, and the largest constructions have a well to collect water (van der Well & van Beveren  
36 2016). Entrances to the larger defence bunkers are hard to reach, either due to ditches or  
37 because they are completely underground. The entrances of bunkers used as storage units or  
38 as garrisons (blockhouses) are larger and easier to reach. At the end of the war, these  
39 structures were often abandoned. They are currently in a good state of conservation but are  
40 less accessible. This is particularly true on farmland, where bunkers have been covered by  
41 successive ploughing. As they were built in defensive or support lines, bunkers are widely  
42 dispersed, covering large areas of land (Mermy et al. 2011). In Europe, they are found from  
43 the Stalin Line in the East to the Atlantic Wall and the GHQ line in the West. There is no  
44 precise inventory of these structures, but the number present along the different defensive  
45 lines represented in **Figure 1** could be estimated between 120 000 and 200 000. Although the  
46 majority of bunkers were constructed before and during WW2, some were built after the end

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47 of the war. For example, 700 000 bunkers were built in Albania in the second half of the 20<sup>th</sup>  
48 century (Bajrovic & Satter 2014; Ayers & Parangoni 2015). On a local scale, bunkers are  
49 clustered in small defensive lines located near strategic locations.  
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58 **Figure 1:** Location of defensive lines in Europe (according to Kaufmann & Jurga 1999).  
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67 Bunkers can improve the quality of life and the survival of birds such as the common starling  
68 (*Sturnus vulgaris* ; Evans, Ardia, & Flux, 2009) or the barn swallow (*Hirundo rustica* ; Zduniak,  
69 Czechowski, & Jedro, 2011). However, bunkers do not generally appear to be an optimal  
70 habitat. This is illustrated by an Albanian island where chiropterans were rare despite an  
71 abundance of bunkers; however, the rarity of this species on the island may also be explained  
72 by the remoteness of the island and the good habitat quality on the mainland (Théou & Bego  
73 2013). To our knowledge, only one study has focused on the presence of carnivores in  
74 bunkers (Crossland & Schöne 2007).

75       Urbanisation and the intensification of agriculture in developed countries led to the  
76 creation of landscapes that are solely dedicated to agricultural production. Current intensive  
77 agriculture landscapes are characterized by large monospecific farm plots (Foley et al. 2005;  
78 Tschardt et al. 2005), where pesticide use is common. The habitat quality and biodiversity  
79 of these environments are usually low (Benton et al. 2003; Maxwell et al. 2016). During the  
80 second half of the 20<sup>th</sup> century, land consolidation policy led to the removal of natural  
81 habitats such as wetlands or copses (Bonfanti et al. 1997; Butet & Leroux 2001; Robinson &  
82 Sutherland 2002). This continuing agricultural intensification mainly has a negative impact on  
83 biodiversity (Poschlod et al. 2005; Desjeux et al. 2014 ; Benton et al., 2003). However, bunkers  
84 found in these areas can play a role in preserving semi-natural elements in their vicinity such  
85 as hedges, pathway verges and groves, which can all be used by a variety of species in  
86 including mesopredators (Dondina et al. 2016), or can even be used by animal species as  
87 alternative habitats.

88       The red fox (*Vulpes vulpes*) and the European badger (*Meles meles*) are probably the most  
89 common fossorial carnivores in Western European farmlands (Hoffmann & Sillero-Zubiri  
90 2016; Kranz et al. 2016). In stable ecosystems, these mesopredators regulate agricultural

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91 pests which have a huge impact on the productivity of agricultural areas or entail damage to  
92 food stocked in warehouses and silos (König 2013). They also limit the dispersion of invasive  
93 species, as illustrated by the reduction in the populations of American mink (*Neovison vison*)  
94 by the red fox in Fennoscandia (Ritchie et al. 2012). Scavenging by foxes is considered as an  
95 ecosystemic service by providing sanitary services (Sekercioglu 2006; DeVault et al. 2011). The  
96 European badger provides services such as the dissemination of seeds and their resurfacing  
97 from the soil seed bank, and abandons burrows that will then be used by other mammal  
98 species (Kurek et al. 2013).

99 Burrow use is very different in these two species, which both use a number of burrows  
100 that are spread across their territory. The red fox mainly has small burrows with one or two  
101 entrances. The badger has a variety of burrows (called “setts”) that vary in size and function.  
102 The main sett is large with up to hundred entrances and can be very old, sometimes having  
103 been used by several generations of badgers (Roper et al. 1991). There is one main sett per  
104 group territory, where breeding occurs. Annexe and subsidiary setts have fewer entrances  
105 and are located near the main burrow. Outlier setts are located on the edge of the territory  
106 and have just one or two entrances (Roper 1992). While the main sett is used for breeding,  
107 thermoregulation and avoiding predators, the benefits provided by outlier burrows remain  
108 unclear. They could play a role in regulating ectoparasite load, reducing the incidence of  
109 breeding suppression and minimizing the costs of travelling through the territory (Davison et  
110 al. 2008).

111 We hypothesized that bunkers are used as outlier burrows by both of these fossorial  
112 species but that entrances located at an accessible height are necessary for this to occur.

113 The objectives of this study were (1) to quantify the proportion of bunkers used by  
114 European badgers and by red foxes, (2) to identify how these species use them, and (3) to  
115 understand the factors associated with this use.

## 116 **Materials and methods**

### 117 **Protocol**

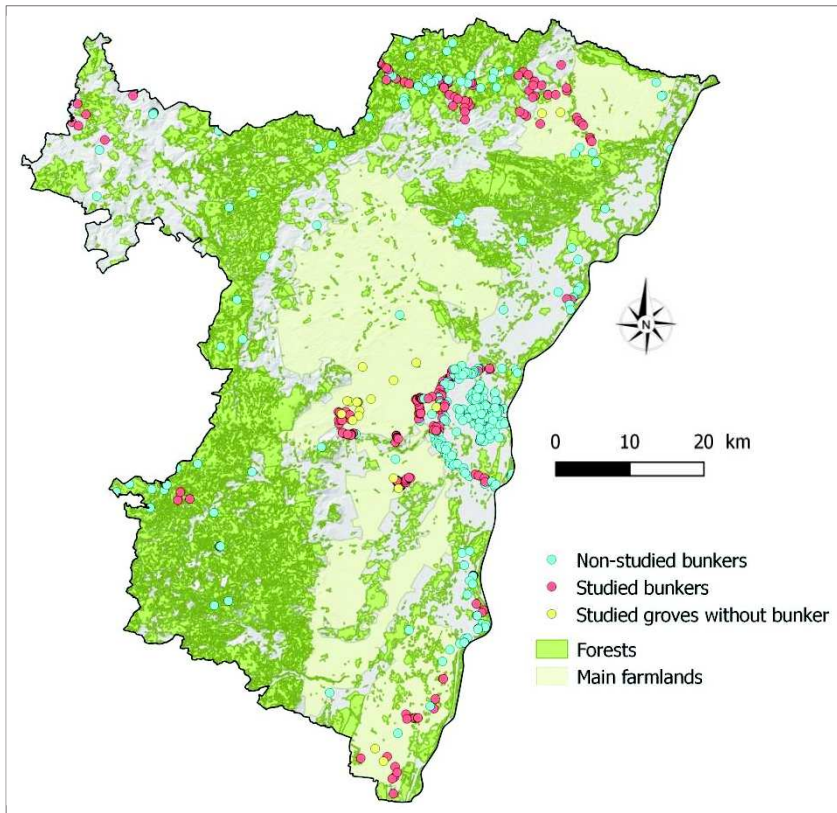
#### 118 *Studied area and bunkers*

119 The military bunkers studied are located on the German defensive line of Strasbourg and  
120 at the eastern extremity of the Maginot Line, located in the Bas-Rhin (Alsace, Grand Est,  
121 France). The annual average temperature of Bas-Rhin is 10.4 °C. Annual precipitation is about  
122 700 mm/y with an average altitude of 150 m. Bunkers are scattered throughout the territory,  
123 with the majority located on farmland that is mainly composed of corn and wheat crops with  
124 rare groves. In this study, a *grove* was defined as a small group of trees (>3 m high) with a size  
125 between 0.01 and 1 ha, with or without an understorey. If the area exceeded 1ha, the  
126 landscape type was considered to be *forest*. Six hundred and fourteen fortifications have  
127 been found and geolocated in this region, but this list is non-exhaustive and the overall  
128 number could be far higher (Mermy et al. 2011). Indeed, new bunkers are regularly found  
129 through archaeological excavations.

130 Not all the bunkers were studied; those located within towns and cities were excluded  
131 from the present study. The remaining bunkers (N=120) were randomly sampled to obtain a  
132 representation of all the bunkers in the studied area. In addition to the 120 selected bunkers,  
133 a further 62 bunkers were found during inspections. The analyses therefore concern a total of  
134 182 bunkers (**Figure 2**). Twenty-one groves without bunkers and surrounded by crops were  
135 also studied over the same period in order to compare their attractiveness with that of groves



136 with bunkers. Groves within one km of selected bunkers were randomly selected to ensure  
137 the same environmental type.



138  
139 **Figure 2:** Location of the 182 bunkers and the 21 groves without bunkers

140 *Local variables*

141 Up to ten bunkers were inspected during daytime by groups of two to four field assistants  
142 trained to identify signs of use by animals. Geographically close bunkers were inspected  
143 during a randomly chosen day between June and August 2016. Any footprints and evidence of  
144 the presence of badgers and foxes (fur, prey leftovers, faeces, burrows, freshly dug earth or  
145 footprints) were identified within a 10 to 20 m range around and inside the bunkers. The  
146 freshness of this evidence was assessed to evaluate the recentness of bunker use (latrine,  
147 faeces and food, newly dug and humid ground). Badger and fox burrows were differentiated  
148 by multiple signs including the number, shape and size of the entrances, odour, and presence  
149 of in-proximity latrines and footprints (Marton et al. 2016). Any unidentified bunkers which

150 were found by chance were also inspected. Geolocation was carried out using GPS (Bushnell  
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2  
3 151 Backtrack D-Tour). Freshness of evidence and the actual use of burrows were confirmed with  
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5 152 a second visit to each bunker one month after the initial visit. The relative position of each  
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7 153 burrow (inside or outside the bunker) was noted, as well as the type of badger sett (“central  
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9 154 sett” including main, annexe and subsidiary burrows if they had three or more entrances and  
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12 155 “outlier sett” if they had one or two entrances). The landscape type in which bunkers were  
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14  
15 156 found was also written down for each of them (*Forest, Grove* or *Crops*). We evaluated the  
16  
17  
18 157 accessibility of each bunker as follows:

- 21 158 • *Underground*: the bunker was entirely or almost entirely buried and all the entrances  
22  
23  
24 159 created by humans were underground. Only the roof was visible. No animal could reach  
25  
26  
27 160 it without digging;
- 28  
29 161 • *Partially buried*: the bunker was partially buried and had one or more entrances created  
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31  
32 162 by humans where carnivorous species of the studied area could enter, but humans  
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35 163 could not gain access without crawling;
- 36  
37 164 • *Overground*: the bunker had at least one large human-made entrance that allowed easy  
38  
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40 165 access to both carnivores and humans.

#### 43 166 *Landscape analysis*

45 167 GIS was used to map landscape elements within an 800 m radius of each bunker. This  
46  
47  
48 168 corresponds to an average badger home range in western Europe, and represents a smaller  
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51 169 home range than the red fox (Meia & Weber 1995; Balestrieri et al. 2016). The distance to the  
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54 170 nearest landscape element of each type was computed, and the size of each landscape  
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56 171 element type was calculated within each 800 m radial buffer. Landscape elements types were  
57  
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59 172 as follows: watercourses, ponds and lakes, groves, hardwood forests, scrublands, mixed

173 forests, plantations, resinous forests, riparian forests, meadows, vineyards, urban area and  
174 annual crops (CIGAL© data (CIGAL 2013), accuracy 1/10 000). The average distance between  
175 bunkers of a same small defensive line was measured, as well as the size of all the groves.

## 176 Analysis

### 177 Method

178 Four dependent variables were used: (1) the use or non-use of the bunker/grove (use was  
179 considered to occur if any evidence of badger or fox presence was observed), (2) the  
180 presence of a burrow inside a bunker or in its immediate vicinity, (3) the presence of currently  
181 occupied burrows (also called burrow in use) indicated by fresh evidence of their use, and (4)  
182 the type of badger sett (central/outlier). These dependent variables were used for bunkers  
183 and for groves without bunkers.

### 184 Statistics

185 Generalized linear binomial models (GLM $\beta$ ) were used to explain the variations of dependent  
186 variables of bunkers, using the following variables as co-variables:

- 187 • The percentage of each landscape element type in each 800m radial buffer;
- 188 • The nearest distance to each landscape element type;
- 189 • The accessibility of each bunker (*underground, partially buried, overground*).

190 The three first dependent variables were also used to compare groves with and without a  
191 bunker. To explain their variations, GLM $\beta$  were also used with the following variables as co-  
192 variables:

- 193 • The size of the grove;
- 194 • The absence/presence of a bunker in the grove;
- 195 • The species (fox, badger or both of these species).

196 Collinear variables were identified and removed using a stepwise procedure based on the  
 197 Variance Inflation Factor (VIF), associated with ACP and Spearman tests. Models were  
 198 selected using AIC backward elimination/forward selection. Modalities of variables were  
 199 compared with a Tuckey-HSD post-hoc test. Statistics were performed with R software  
 200 (v3.3.0) and GIS analysis using QGIS (v2.18.3). The significance threshold was set to  $p < 0.05$ .

## 201 Results

### 202 *Characteristics of bunkers*

203 Nineteen bunkers were located in groves (10.44%), 57 in forests (31.32%) and 106 on  
 204 crops (58.24%). Accessibility type was more balanced, with 39 underground bunkers  
 205 (21.43%), 60 partially buried bunkers (32.97%) and 83 overground bunkers (45.60%)(**Table 1**).  
 206 Only five underground bunkers were located in groves and in forests. The small defensive  
 207 lines in the studied area were composed of an average 9.4 bunkers ( $\pm 2.3$  SE,  $N=15$ ), with an  
 208 average inter-distance of 389 metres ( $\pm 64.64$  SE).

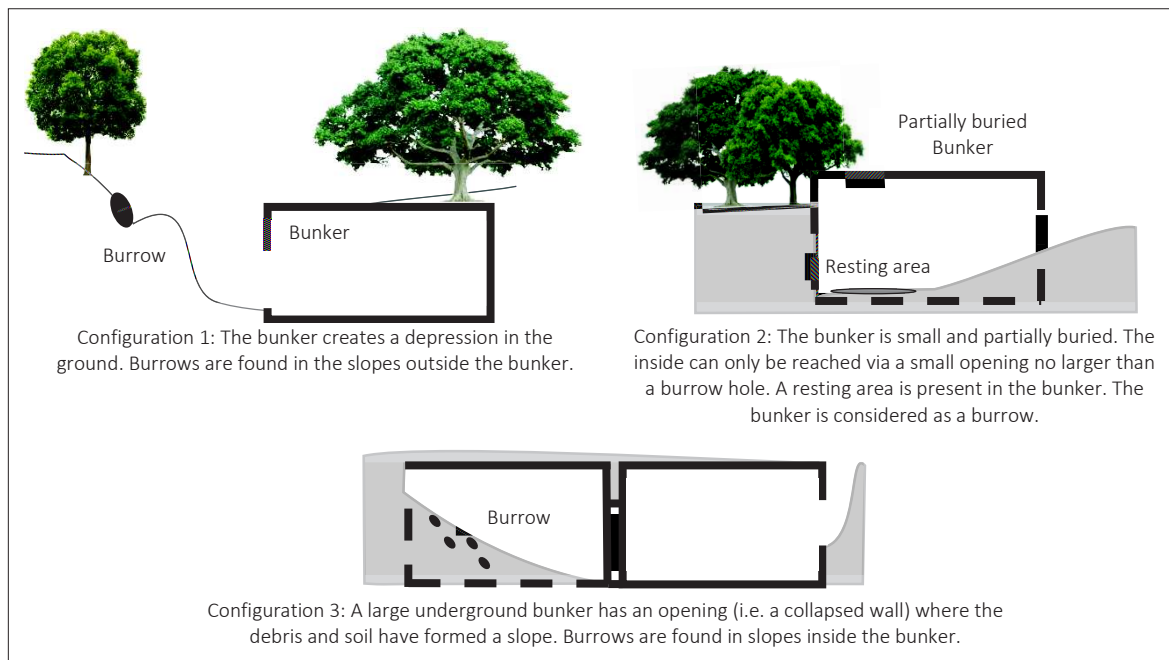
209 **Table 1:** *Number of studied bunkers per accessibility type and main surrounding*  
 210 *landscape.*

Surroundings	Underground	Partially buried	Overground	Total
Crop	34	26	46	106
Grove	2	11	6	19
Forest	3	23	31	57
Total	39	60	83	182

### 212 *Use of bunkers*

213 Evidence of badger or fox presence was found in 61 of the 182 studied bunkers  
 214 (33.52%). Each species used a significantly similar number of bunkers ( $W = 21214$ ,  $p=0.357$ ).  
 215 Burrows were found on 43 sites (23.63%), 30 (69.77%) of which were still occupied at the  
 216 time of the study. We found 18 (41.86%) burrows inside the bunkers and 25 (58.14%) outside.

217 Twenty-seven badger setts were found inside or in the vicinity of bunkers, of which 20 (74%)  
 218 were outlier burrows and seven (26%) were central burrows. Five of these seven central  
 219 burrows were found outside the bunkers. "Resting areas" composed of hay and badger/fox  
 220 fur were found inside nine small partially buried bunkers. The latter were considered as  
 221 outlier burrows in the analyses but with no assigned species. We identified three different  
 222 burrow configurations in relation to the bunkers, as illustrated in **Figure 3**.



**Figure 3:** *The three different configurations of burrows observed in this study.*

233 On eight sites (4.4%), bunkers were used by humans (house, wood/tractor storage, waste  
 234 disposal site). In two bunkers, several underfed amphibians were found with a number of  
 235 dead animals of different species trapped in underground rooms that could only be reached  
 236 using a ladder.

237 *Landscape analysis*

238 Selection of collinear variables resulted in 14 collinear groups. The 14 main  
 239 explanatory variables were extracted (**Table 2**). Data for both species were pooled to obtain  
 240 sufficient data for landscape analysis.

241 **Table 2:** List of used environmental variables

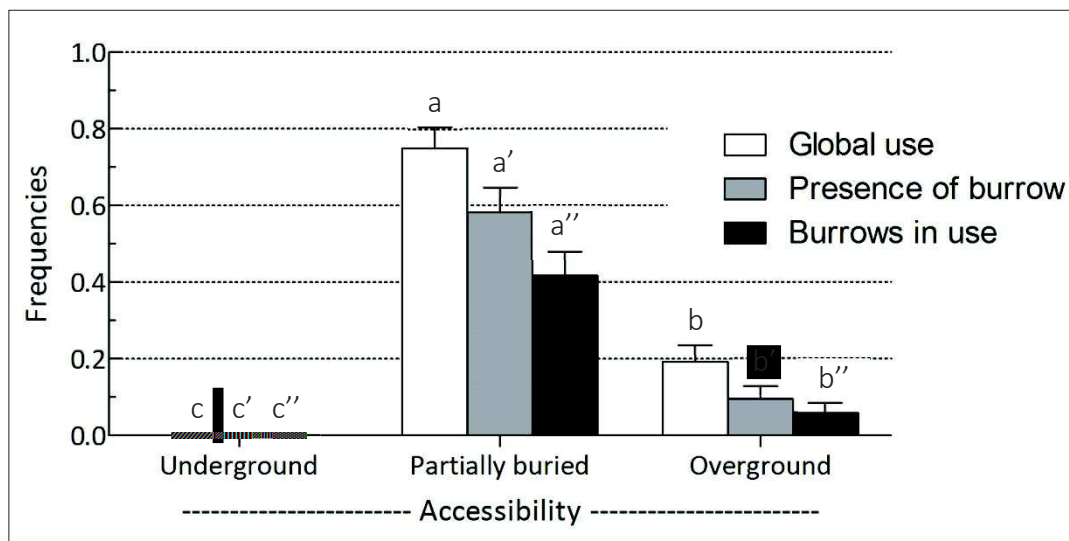
Distance to:	Watercourses, Ponds and lakes, Scrublands, Vineyards
Size of:	Groves, watercourses, annual crops, ponds and lakes, scrublands, mixed forests, meadows, urban area, orchards, vineyards

242 The use of bunkers and the use of groves without bunkers were both positively  
 243 correlated to the annual crop size in the surrounding buffers (least significant values:  $Z=2.831$ ;  
 244  $p<0.01$ ). Both types of use were also negatively correlated to the distance to annual crops by  
 245 a significant negative correlation between the annual crop size and distance to annual crops  
 246 ( $\rho=-0.905$ ;  $p<0.01$ ).

247 The presence of burrows and the number of burrows in use were positively correlated  
 248 to annual crop size (least significant values:  $Z=3.044$ ;  $p<0.01$ ) and to the size of urban area  
 249 (least significant values:  $Z=3.148$ ;  $p<0.01$ ).

250 *The effect of accessibility*

251 The accessibility of bunkers had a significant effect on use ( $\chi^2=72.074$ ,  $df=2$ ,  $p<0.01$ ), on  
 252 the presence of burrows ( $\chi^2=54.877$ ,  $df=2$ ,  $p<0.01$ ) and on the number of burrows in use  
 253 ( $\chi^2=35.037$ ,  $df=2$ ,  $p<0.01$ ) (Figure 4).



254

255 **Figure 4:** *Effects of the accessibility of bunkers on their use by animals (global use shown in*  
256 *white, presence of burrows in grey, and presence of burrows in use in black), for each of the*  
257 *three accessibility categories. Error bars are standard errors.*

258  
259 *Comparison of groves with and without a bunker.*

260 Use of groves was not correlated to the presence of a bunker ( $\chi^2=0.523$ ,  $df=1$ ,  $p=0.469$ ).  
261 There were more burrows ( $\chi^2=10.354$ ,  $df=1$ ,  $p<0.01$ ) and more burrows in use ( $\chi^2=5.107$ ,  $df=1$ ,  
262  $p=0.02$ ) when a bunker was present. The area of the groves had no effect on grove use, on  
263 the presence of burrows and on the number of burrows in use (most significant values:  $Z=-$   
264  $0.361$ ;  $p=0.718$ ). Among the eleven species-determined burrows found in groves, seven were  
265 badger setts and two were fox burrows.

## 266 Discussion

### 267 *Bunkers as habitat*

268 Bunkers form a network of habitats which provide resources for wildlife. The presence of  
269 burrows in over one third of the studied bunkers and a relatively high occupation rate suggest  
270 that badgers and foxes have had to adapt to a man-made habitat due to the reduction in their  
271 natural environment. These are not the only carnivorous species using bunkers; wildcats (*Felis*  
272 *silvestris*) are also known to inhabit a large number of bunkers (Crossland & Schöne 2007).  
273 Camera traps could be a more appropriate tool to study this type of discrete species in forest  
274 bunkers (Anile et al. 2009; Velli et al. 2015). This technique could also allow a more precise  
275 quantification of bunker use and an evaluation of the effect of human disturbance.

276 The abundance of badgers in the studied area may be lower than that of foxes, as  
277 badgers were less observed than foxes in non-exhaustive naturalist local surveys (Data 2008-

2017; 2 185 observations of badgers vs 3 036 observations of foxes (1.39 times more) in the  
4 755 km<sup>2</sup> of the studied area; Odonat, 2017). If these figures are correct, the observation of  
equal use of bunkers by each species in this study thus suggests that badgers are particularly  
attracted by these remaining habitats in highly changed landscapes. These animals also have a  
greater network of burrows than foxes, with setts that are composed of different types of  
chamber. Most of the badger burrows found were outlier setts, characterized by few  
entrances and usually a nest chamber. A similar configuration was found in partially buried  
bunkers. They were regularly used by badgers and foxes. As nesting sites were found inside  
these partially buried bunkers, we considered the latter to be burrows.

Partially buried bunkers provide shelter. However, entirely buried bunkers were never  
used by the studied species, indicating that visible human-made openings are needed to  
make them accessible to these animals. This observation suggests that badgers and foxes do  
not dig to reach the underground rooms, even when the bunker roof is visible. Partially buried  
bunkers could be habitat opportunities requiring an initial physical effort to gain access, yet  
they are not particularly sought after by these species. Foxes and badgers can also use  
bunkers that are highly accessible and can be easily entered by humans, but the quality of  
these shelters seems lower than that provided by partially buried bunkers. This difference in  
quality could be explained by the larger size of inner rooms, the luminosity and human  
disturbances, all of which are greater when bunkers are not buried (Aaris-Sørensen 1987).  
When burrows were found inside or in the vicinity of these highly accessible bunkers, it was  
always in cases where the structures created a ground depression outside the bunker or  
when a large amount of dirt was found inside. In both cases, a dirt slope was present, in which  
burrows had been dug.



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301 A higher number of burrows and burrows in use were found in areas with larger  
302 annual crops and greater urbanisation. The destruction of natural habitats for the benefit of  
303 crops and urban area may force badgers and foxes to live in bunkers, which are preserved  
304 from overly intense human action (Remonti et al. 2006). Bunkers may represent safe areas  
305 where foxes and badgers could rest, feed and reproduce, i.e. a source of refuge on farmland.  
306 The importance of refuge habitats has already been raised for other carnivores, such as the  
307 polecat in the Mediterranean landscape (Rondinini et al. 2006). They also provide resources  
308 for other species such as birds, plants, spiders, insects and other mammals (Sheperd &  
309 Swihart 1995; Zollner 2000; Benton et al. 2003; Duelli & Obrist 2003; Grashof-Bokdam & van  
310 Langevelde 2005; Billeter et al. 2008; Wretenberg et al. 2010; Redon (de) et al. 2015).

311 Wildlife obtains different services from bunkers and groves without bunkers when  
312 they use them as refuge habitats. Indeed, the presence of a bunker in a grove increased the  
313 probability of finding a burrow and a burrow in use there. A major difference between these  
314 two landscape elements was the presence of slopes created by ground depression around  
315 bunkers.

#### 316 *Distribution of bunkers in the studied area*

317 Few bunkers were found in groves. These were mainly small bunkers used for storage and  
318 were hidden from the enemy when constructed in wooded areas. However, as other storage  
319 bunkers were found on crops, we presume that land consolidation strategy has ensured the  
320 maintenance of groves. Administratively speaking, if the presence of a bunker made a piece  
321 of land “uncultivable” on the land registry plan, the piece of land remained registered as such  
322 and the bunker and grove were both preserved in their natural state. If not, the piece of land  
323 became cultivable and farmers were free to plant crops around the bunker. Moreover, the  
324 use of land for crops has led to the burial of bunkers, as shown by the high number of

1  
2 325 underground bunkers found on farmland. As carnivores do not dig to reach buried bunkers,  
3 326 these structures have lost their habitat potentiality.

4  
5 327 As bunkers were built around strategic points in small defensive lines, they form a  
6  
7 328 network of potential shelters for wildlife. The distance between the successive bunkers of one  
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9 329 small defensive line allows badgers to have three or four outlier burrows in their territory,  
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11  
12 330 whilst foxes have even more.

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14  
15 331 *Towards an ecological management of bunkers*

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18 332 Although bunkers are widely used by carnivores, they are often unhealthy structures,  
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20  
21 333 with stagnant water containing high numbers of mosquitoes and animal carcasses. Hygienic  
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23  
24 334 conditions are usually poor, and it is unlikely that animals can live in these places for long  
25  
26 335 periods of time. The frequent presence of frogs trapped in bunker chambers that are only  
27  
28  
29 336 reachable by a ladder merits attention and should be notified to the competent authorities to  
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31  
32 337 ensure that the concerned bunkers are made safe, especially when they represent a danger  
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34 338 for children in urban areas.

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36  
37 339 Some trees were found close to the bunkers, even in middle of large crops fields. They  
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39  
40 340 did not provide enough cover to form a grove but provided roosting areas for avian  
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42 341 mesopredators. Furthermore, preserved groves located on farmland can be used by these  
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45 342 species, including corvids, hawks, buzzards and owls. There was no evidence of badgers or  
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47 343 foxes around bunkers that did not have visible human-made openings, suggesting that access  
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49  
50 344 was insufficient.

51  
52 345 These results show that bunkers are currently used by wildlife, but some have lost  
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54  
55 346 their habitat potentiality. This situation can be changed and improved by the management of  
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57  
58 347 bunkers which would be advantageous not only for badger and foxes but also for a variety of  
59  
60 348 other species. First, the accessibility of bunkers with large apertures should be reduced by  
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349 leaving only small holes such as those used by carnivores and bats (Nowicki et al. 2008).  
1  
2 350 Indeed, even when entirely surrounded by scrubland, bunkers with large human-made  
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4  
5 351 openings are attractive to people who sometimes put these spaces to surprising use, such as  
6  
7  
8 352 the exhibition of thousands of hubcaps we found in one bunker. The surroundings of bunkers  
9  
10 353 located on cropland should be included on the land registry plan to ensure their  
11  
12  
13 354 management. A ground depression should be created around underground bunkers to  
14  
15 355 excavate them and create slopes that can be used by wildlife to create burrows and settle  
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17  
18 356 (Macdonald et al. 2004). Burrows were found inside or in the vicinity of 35 of the 99 bunkers  
19  
20  
21 357 that had a slope (35.4%). This means that if all the studied bunkers (182) were managed with  
22  
23 358 a slope, 64 potential burrows could be expected, and hundreds could be observed if all the  
24  
25  
26 359 bunkers in the study area (at least 614) managed in the same way. The planting of trees  
27  
28 360 would create small groves around the bunkers to provide benefits for avian predators. Finally,  
29  
30  
31 361 certain interesting bunkers located close to urban areas could be video-equipped as an  
32  
33  
34 362 awareness-raising project to educate people about wildlife.

### 363 **Conclusion**

364 Bunkers are widely used as shelters by red foxes and European badgers. However, a  
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42 365 high proportion of these military structures, especially on farmland, are in poor condition for  
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45 366 their use as a habitat. The present study provides the necessary information to significantly  
46  
47 367 improve the habitat potentiality of bunkers for the two most representative fossorial  
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50 368 carnivore species living on Western European farmlands. Knowing the high number of  
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52  
53 369 bunkers concerned and their relatively equal distribution in the studied area, their  
54  
55 370 management could help to slow the inexorable deterioration and homogenisation of the  
56  
57 371 agricultural landscape.

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### 376 **Author Contributions**

377 All authors approve this version of the manuscript. They agree to be accountable for  
378 the aspects of the work that they conducted, and will ensure that any questions related to the  
379 accuracy or integrity of any part of their work are appropriately investigated and resolved. JJ  
380 conceived the idea and design methodology; JJ, DW, NG and LG collected the data; JJ and LG  
381 carried out data analysis; JJ, YH and FB organised the writing of the manuscript. All authors  
382 played an active part in the drafting of the manuscript and gave their final approval for  
383 publication.

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### 389 **Bibliography**

- 390 Aaris-Sørensen, J. (1987). Past and present distribution of badgers *Meles meles* in the  
391 Copenhagen area. *Biol. Conserv.*, 41, 159–165.
- 392 AFP. (2014). Forgotten war site now a bat cave [WWW Document]. *IOL*. URL  
393 <http://www.iol.co.za/news/forgotten-war-site-now-a-bat-cave-1672065>
- 394 Anile, S.T., Bizzarri, L.O. & Ragni, B.E. (2009). Camera trapping the European wildcat (*Felis*  
395 *silvestris silvestris*) in Sicily (southern Italy): Preliminary results. *Hystrix Ital. J. Mammal.*,  
396 20, 55–60.
- 397 Ayers, B. & Parangoni, I. (2015). Industrial heritage in albania: an assessment. *Ind. Archaeol.*  
398 *Rev.*, 37, 111–122.

- 399 Bajrovic, I. & Satter, J. (2014). Albania: from bunkers to ballots. *J. Democr.*, 25, 142–153.
- 1  
2 400 Balestrieri, A., Cardarelli, E., Pandini, M., Remonti, L., Saino, N. & Prigioni, C. (2016). Spatial  
3 401 organisation of European badger (*Meles meles*) in northern Italy as assessed by camera-  
4 402 trapping. *Eur. J. Wildl. Res.*, 62, 219–226.
- 5  
6 403 Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat  
7 404 heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- 8  
9 405 Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J.,  
10 406 Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H.,  
11 407 Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F.,  
12 408 Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M.,  
13 409 Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans,  
14 410 M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. & Edwards, P.J. (2008).  
15 411 Indicators for biodiversity in agricultural landscapes: A pan-European study. *J. Appl. Ecol.*,  
16 412 45, 141–150.
- 17  
18 413 Bonfanti, P., Fregonese, A. & Sigura, M. (1997). Landscape analysis in areas affected by land  
19 414 consolidation. *Landsc. Urban Plan.*, 37, 91–98.
- 20  
21 415 Butet, A. & Leroux, A.B.A. (2001). Effects of agriculture development on vole dynamics and  
22 416 conservation of Montagu’s harrier in western French wetlands. *Biol. Conserv.*, 100, 289–  
23 417 295.
- 24  
25 418 Ciechanowski, M. & Sachanowicz, K. (2014). Fat Dormouse *Glis glis* (Rodentia: Gliridae) in  
26 419 Albania: Synopsis of Distributional Records with Notes on Habitat Use. *Acta Zool. Bulg.*,  
27 420 66, 39–42.
- 28  
29 421 CIGAL. (2013). Données faune Alsace [WWW Document]. *Coopération pour l’information*  
30 422 *géographique en Alsace*. URL <https://www.cigalsace.org/portail/>
- 31  
32 423 Crossland, D. & Schöne, S. (2007). From Wehrmacht to Wildcats: World War II Bunkers Turn  
33 424 Into Wildlife Haven [WWW Document]. *SPIEGEL ONLINE*. URL  
34 425 <http://www.spiegel.de/international/germany/from-wehrmacht-to-wildcats-world-war-ii-bunkers-turn-into-wildlife-haven-a-507880.html>
- 35  
36 426  
37 427 Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics,  
38 428 patterns of use and management implications. *J. Zool.*, 275, 190–200.
- 39  
40 429 Desjeux, Y., Dupraz, P., Kuhlman, T., Paracchini, M.L., Michels, R., Maignan, E. & Reinhard, S.  
41 430 (2014). Evaluating the impact of rural development measures on nature value indicators  
42 431 at different spatial levels: Application to France and the Netherlands. *Ecol. Indic.*, 59, 41–  
43 432 61.
- 44  
45 433 DeVault, T.L., Olson, Z.H., Beasley, J.C. & Rhodes, O.E. (2011). Mesopredators dominate  
46 434 competition for carrion in an agricultural landscape. *Basic Appl. Ecol.*, 12, 268–274.
- 47  
48 435 Dondina, O., Kataoka, L., Orioli, V. & Bani, L. (2016). How to manage hedgerows as effective  
49 436 ecological corridors for mammals: A two-species approach. *Agric. Ecosyst. Environ.*, 231,  
50 437 283–290.
- 51  
52 438 Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: the  
53 439 contribution of seminatural habitat islands. *Basic Appl. Ecol.*, 4, 129–138.
- 54  
55  
56  
57  
58  
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63  
64  
65

- 440 Evans, L.E., Ardia, D.R. & Flux, J.E.C. (2009). Breeding synchrony through social stimulation in a  
1 441 spatially segregated population of European starlings. *Anim. Behav.*, 78, 671–675.  
2
- 3 442 Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe,  
4 443 M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J.,  
5 444 Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global  
6 445 consequences of land use. *Science (80-. )*, 309, 570–4.  
7
- 8  
9 446 Grashof-Bokdam, C.J. & van Langevelde, F. (2005). Green veining: Landscape determinants of  
10 447 biodiversity in European agricultural landscapes. *Landsc. Ecol.*, 20, 417–439.  
11
- 12 448 Hoffmann, M. & Sillero-Zubiri, C. (2016). *Vulpes vulpes*, Red Fox. *IUCN Red List Threat. Species*  
13 449 *2016*, e.T23062A4, 1–10.  
14
- 15 450 Kaufmann, J. & Jurga, R. (1999). *Fortress Europe: European Fortifications Of World War II*. 1st  
16 451 edn. First Da Capo Press.  
17
- 18 452 König, C. (2013). Les ravageurs, menace pour nos céréales, 1–24.  
19
- 20 453 Kranz, A., Abramov, A.V., Herrero, J. & Maran, T. (2016). *Meles meles*. *IUCN Red List Threat.*  
21 454 *Species 2016*, 8235, e.T29673A45203002.  
22
- 23 455 Kurek, P., Kapusta, P. & Holeksa, J. (2013). Burrowing by badgers (*Meles meles*) and foxes  
24 456 (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest.  
25 457 *Ecol. Res.*, 29, 1–11.  
26
- 27  
28 458 Macdonald, D.W., Newman, C., Dean, J., Buesching, C.D. & Johnson, P.J. (2004). The  
29 459 distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field  
30 observations contradict the sett dispersion hypothesis. *Oikos*, 106, 295–307.  
31
- 32 461 Marton, M., Markolt, F., Szabo, L., Kozak, L., Lanszki, J., Patko, L. & Heltai, M. (2016). Den site  
33 462 selection of the European badger, *Meles meles* and the red fox, *Vulpes vulpes* in  
34 463 Hungary. *FOLIA Zool.*, 65, 72–79.  
35
- 36  
37 464 Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and  
38 465 bulldozers. *Nature*, 536, 146–145.  
39
- 40 466 Meia, J.-S. & Weber, J.-M. (1995). Home ranges and movements of red foxes in central  
41 467 Europe: stability despite environmental changes. *Can. J. Zool.*, 73, 1960–1966.  
42
- 43 468 Mermy, D.C., Guignat, H.S., Zammit, R., Heckenmeyer, E. & Lizée, M. (2011). *Inventaire*  
44 469 *départemental des cavités souterraines hors mines du Bas-Rhin*.  
45
- 46  
47 470 Nowicki, F., Dadu, L., Carsignol, J., Bretaud, J.-F. & Bielsa, S. (2008). Rapport bibliographique :  
48 471 Routes et chiroptères Etat des connaissances. *Les Rapp.*, 1–253.  
49
- 50 472 Odonat : Office des données naturalistes du Grand-Est. (2017). Atlas des espèces d'Alsace  
51 473 [WWW Document]. [www.faune-alsace.org](http://www.faune-alsace.org). URL [http://www.faune-alsace.org/index.php?m\\_id=620](http://www.faune-alsace.org/index.php?m_id=620)  
52 474 [alsace.org/index.php?m\\_id=620](http://www.faune-alsace.org/index.php?m_id=620)  
53
- 54 475 Poschlod, P., Bakker, J.P. & Kahmen, S. (2005). Changing land use and its impact on  
55 476 biodiversity. *Basic Appl. Ecol.*, 6, 93–98.  
56
- 57  
58 477 Redon (de), L., Le Viol, I., Jiguet, F., Machon, N., Scher, O. & Kerbiriou, C. (2015). Road  
59 478 network in an agrarian landscape: Potential habitat, corridor or barrier for small  
60 479 mammals? *Acta Oecologica*, 62, 58–65.  
61  
62  
63  
64  
65

- 480 Remonti, L., Balestrieri, A. & Prigioni, C. (2006). Factors determining badger *Meles meles* sett  
1 481 location in agricultural ecosystems of NW Italy. *Folia Zool.*, 55.1, 19–27.  
2
- 3 482 Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012).  
4 483 Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.*, 27, 265–  
5 484 71.  
6
- 7 485 Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity  
8 486 in Great Britain. *J. Appl. Ecol.*, 39, 157–176.  
9
- 10 487 Rondinini, C., Ercoli, V. & Boitani, L. (2006). Habitat use and preference by polecats ( *Mustela*  
11 488 *putorius* L.) in a Mediterranean agricultural landscape. *J. Zool.*, 269, 213–219.  
12
- 13 489 Roper, T.J. (1992). The structure and function of badger setts. *J. Zool.*, 227, 691–694.  
14
- 15 490 Roper, T.J., Tait, A.I., Fee, D. & Christian, S.F. (1991). Internal structure and contents of three  
16 491 badger ( *Meles meles* ) setts. *J. Zool.*, 225, 115–124.  
17
- 18 492 Sachanowicz, K. & Zub, K. (2002). Numbers of hibernating *Barbastella barbastellus* (Schreber,  
19 493 1774) (Chiroptera, Vespertilionidae) and thermal conditions in military bunkers. *Mamm.*  
20 494 *Biol. - Zeitschrift für Säugetierkd.*, 67, 179–184.  
21
- 22 495 Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*,  
23 496 21, 464–71.  
24
- 25 497 Sheperd, B.F. & Swihart, R.K. (1995). Spatial dynamics of fox squirrels ( *Sciurus niger* ) in  
26 498 fragmented landscapes. *Can. J. Zool.*, 73, 2098–2105.  
27
- 28 499 Théou, P. & Bego, F. (2013). *Etude des populations de chiroptères de l'île de Sazani. Note*  
29 500 *naturaliste Initiative PIM.*  
30
- 31 501 Tscharncke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape  
32 502 perspectives on agricultural intensification and biodiversity - Ecosystem service  
33 503 management. *Ecol. Lett.*, 8, 857–874.  
34
- 35 504 Velli, E., Bologna, M.A., Silvia, C., Ragni, B. & Randi, E. (2015). Non-invasive monitoring of the  
36 505 European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three  
37 506 different monitoring techniques and evaluation of their integration. *Eur. J. Wildl. Res.*,  
38 507 61, 657–668.  
39
- 40 508 Warchałowski, M., Łupicki, D., Cichocki, J., Pietraszko, M., Rusek, A., Zawadzka, A. & Nikodem,  
41 509 M. (2013). Zimowanie nietoperzy Chiroptera w wybranych obiektach wolno stojących  
42 510 Frontu Fortecznego Łuku Odry i Warty. *Kulon*, 18, 139–147.  
43
- 44 511 van der Well, L. & van Beveren, A. (2016). Bunkersite.com [WWW Document]. URL  
45 512 <http://bunkersite.com/index.php>  
46
- 47 513 Wretenberg, J., Pärt, T. & Berg, Å. (2010). Changes in local species richness of farmland birds  
48 514 in relation to land-use changes and landscape structure. *Biol. Conserv.*, 143, 375–381.  
49
- 50 515 Zduniak, P., Czechowski, P. & Jedro, G. (2011). The effect of nesting habitat on reproductive  
51 516 output of the Barn Swallow (*Hirundo rustica*). A comparative study of populations from  
52 517 atypical and typical nesting habitats in western Poland. *BELGIAN J. Zool.*, 141, 38–43.  
53
- 54 518 Zollner, P.A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in  
55 519 fragmented agricultural landscapes. *Landsc. Ecol.*, 15, 523–533.  
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# 1 The use of military bunkers by the European badger and red fox in Western Europe

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6 **Running Title:** New homes for badgers and foxes

## 7 Abstract

8 Intensification of agriculture and land consolidation policy induced the removal of most  
9 natural features from farmland, reducing the habitat of many wild species. Abandoned WWII  
10 bunkers, unaffected by land consolidation, are a potential shelter for wildlife and could be  
11 used as burrows by carnivores such as European badgers and red foxes.

12 We explored 182 abandoned bunkers in a farmland area in eastern France in summer 2016.  
13 Bunkers were located in crops, forests, or groves. Over a three-month period, signs of  
14 presence, the number and type of burrows inside the bunkers and in their immediate vicinity  
15 were noted. Environmental variables were obtained using GIS, and binomial models were  
16 created to reveal parameters influencing bunker use by badgers and foxes. The degree of  
17 bunkers burrowing was used as a co-variable. Twenty-one groves without bunkers were also  
18 studied in order to estimate the added value of bunkers in groves.

19 Badger and fox tracks were found on 34% of the sites, and burrows on 24% of them with  
20 similar rates for badgers and foxes. Animals used partially buried bunkers more than  
21 underground or overground bunkers. The sizes of annual crops and urban areas around the  
22 bunker were positively correlated with bunker use. The presence of a bunker in groves was  
23 positively correlated with the presence of burrows in groves.

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24 As bunkers were widely used by badgers and foxes, they may improve conservation in  
25 intensive farming landscapes. We recommend the management of these ruins to facilitate the  
26 sustainable installation of a variety of species.

27 *Keywords:* refuges, artificial habitat, military fortifications, farmlands, burrows

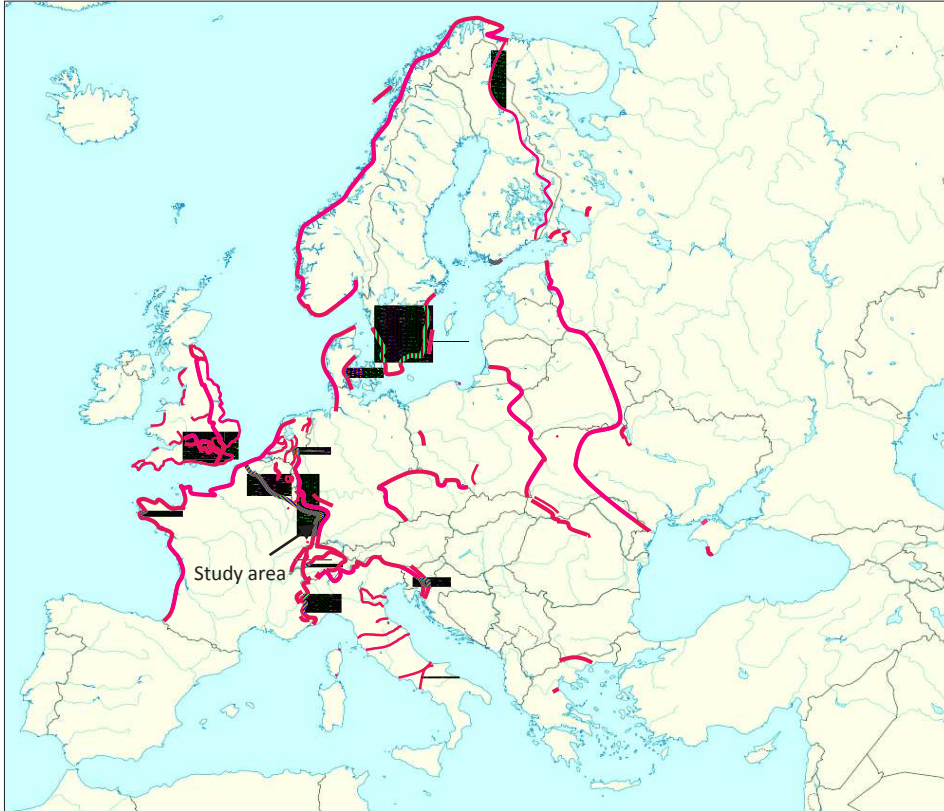
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## 30 Introduction

31 A huge number of military fortifications were built before and during the Second World  
32 War, often located close to border areas like the Maginot Line or the Atlantic Wall. These  
33 concrete bunkers (English), Blockhäuser (German) or casemates (French) are often located  
34 underground, either by design or due to burying over time. They have a small number of  
35 rooms, and the largest constructions have a well to collect water (van der Well & van Beveren  
36 2016). Entrances to the larger defence bunkers are hard to reach, either due to ditches or  
37 because they are completely underground. The entrances of bunkers used as storage units or  
38 as garrisons (blockhouses) are larger and easier to reach. At the end of the war, these  
39 structures were often abandoned. They are currently in a good state of conservation but are  
40 less accessible. This is particularly true on farmland, where bunkers have been covered by  
41 successive ploughing. As they were built in defensive or support lines, bunkers are widely  
42 dispersed, covering large areas of land (Mermy et al. 2011). In Europe, they are found from  
43 the Stalin Line in the East to the Atlantic Wall and the GHQ line in the West. There is no  
44 precise inventory of these structures, but the number present along the different defensive  
45 lines represented in **Figure 1** could be estimated between 120 000 and 200 000. Although the  
46 majority of bunkers were constructed before and during WW2, some were built after the end

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47 of the war. For example, 700 000 bunkers were built in Albania in the second half of the 20<sup>th</sup>  
48 century (Bajrovic & Satter 2014; Ayers & Parangoni 2015). On a local scale, bunkers are  
49 clustered in small defensive lines located near strategic locations.  
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58 **Figure 1:** Location of defensive lines in Europe (according to Kaufmann & Jurga 1999).  
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60 Few studies have explored the impact of bunkers on biodiversity. The reduced variations  
61 of temperatures in the wells of bunkers make them an ideal hibernation site for the  
62 Barbastelle bat (*Barbastella barbastellus*) (Sachanowicz & Zub 2002). In Germany, the one  
63 hundred bunkers and 32 kilometres of galleries making up the Festungsfront Oder-Warthe-  
64 Bogen bunker network are colonized by 37 000 bats from ten different species, possibly  
65 making it the artificial structure hosting the highest number of individuals in Europe  
66 (Warchałowski et al. 2013; Jan Cichocki in AFP 2014). Small terrestrial mammals like the  
edible dormouse (*Glis glis*) also colonize bunkers (Ciechanowski & Sachanowicz 2014).  
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67 Bunkers can improve the quality of life and the survival of birds such as the common starling  
68 (*Sturnus vulgaris* ; Evans, Ardia, & Flux, 2009) or the barn swallow (*Hirundo rustica* ; Zduniak,  
69 Czechowski, & Jedro, 2011). However, bunkers do not generally appear to be an optimal  
70 habitat. This is illustrated by an Albanian island where chiropterans were rare despite an  
71 abundance of bunkers; however, the rarity of this species on the island may also be explained  
72 by the remoteness of the island and the good habitat quality on the mainland (Théou & Bego  
73 2013). To our knowledge, only one study has focused on the presence of carnivores in  
74 bunkers (Crossland & Schöne 2007).

75       Urbanisation and the intensification of agriculture in developed countries led to the  
76 creation of landscapes that are solely dedicated to agricultural production. Current intensive  
77 agriculture landscapes are characterized by large monospecific farm plots (Foley et al. 2005;  
78 Tschardt et al. 2005), where pesticide use is common. The habitat quality and biodiversity  
79 of these environments are usually low (Benton et al. 2003; Maxwell et al. 2016). During the  
80 second half of the 20<sup>th</sup> century, land consolidation policy led to the removal of natural  
81 habitats such as wetlands or copses (Bonfanti et al. 1997; Butet & Leroux 2001; Robinson &  
82 Sutherland 2002). This continuing agricultural intensification mainly has a negative impact on  
83 biodiversity (Poschlod et al. 2005; Desjeux et al. 2014 ; Benton et al., 2003). However, bunkers  
84 found in these areas can play a role in preserving semi-natural elements in their vicinity such  
85 as hedges, pathway verges and groves, which can all be used by a variety of species in  
86 including mesopredators (Dondina et al. 2016), or can even be used by animal species as  
87 alternative habitats.

88       The red fox (*Vulpes vulpes*) and the European badger (*Meles meles*) are probably the most  
89 common fossorial carnivores in Western European farmlands (Hoffmann & Sillero-Zubiri  
90 2016; Kranz et al. 2016). In stable ecosystems, these mesopredators regulate agricultural

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91 pests which have a huge impact on the productivity of agricultural areas or entail damage to  
92 food stocked in warehouses and silos (König 2013). They also limit the dispersion of invasive  
93 species, as illustrated by the reduction in the populations of American mink (*Neovison vison*)  
94 by the red fox in Fennoscandia (Ritchie et al. 2012). Scavenging by foxes is considered as an  
95 ecosystemic service by providing sanitary services (Sekercioglu 2006; DeVault et al. 2011). The  
96 European badger provides services such as the dissemination of seeds and their resurfacing  
97 from the soil seed bank, and abandons burrows that will then be used by other mammal  
98 species (Kurek et al. 2013).

99 Burrow use is very different in these two species, which both use a number of burrows  
100 that are spread across their territory. The red fox mainly has small burrows with one or two  
101 entrances. The badger has a variety of burrows (called “setts”) that vary in size and function.  
102 The main sett is large with up to hundred entrances and can be very old, sometimes having  
103 been used by several generations of badgers (Roper et al. 1991). There is one main sett per  
104 group territory, where breeding occurs. Annexe and subsidiary setts have fewer entrances  
105 and are located near the main burrow. Outlier setts are located on the edge of the territory  
106 and have just one or two entrances (Roper 1992). While the main sett is used for breeding,  
107 thermoregulation and avoiding predators, the benefits provided by outlier burrows remain  
108 unclear. They could play a role in regulating ectoparasite load, reducing the incidence of  
109 breeding suppression and minimizing the costs of travelling through the territory (Davison et  
110 al. 2008).

111 We hypothesized that bunkers are used as outlier burrows by both of these fossorial  
112 species but that entrances located at an accessible height are necessary for this to occur.

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113 The objectives of this study were (1) to quantify the proportion of bunkers used by  
114 European badgers and by red foxes, (2) to identify how these species use them, and (3) to  
115 understand the factors associated with this use.

## 116 **Materials and methods**

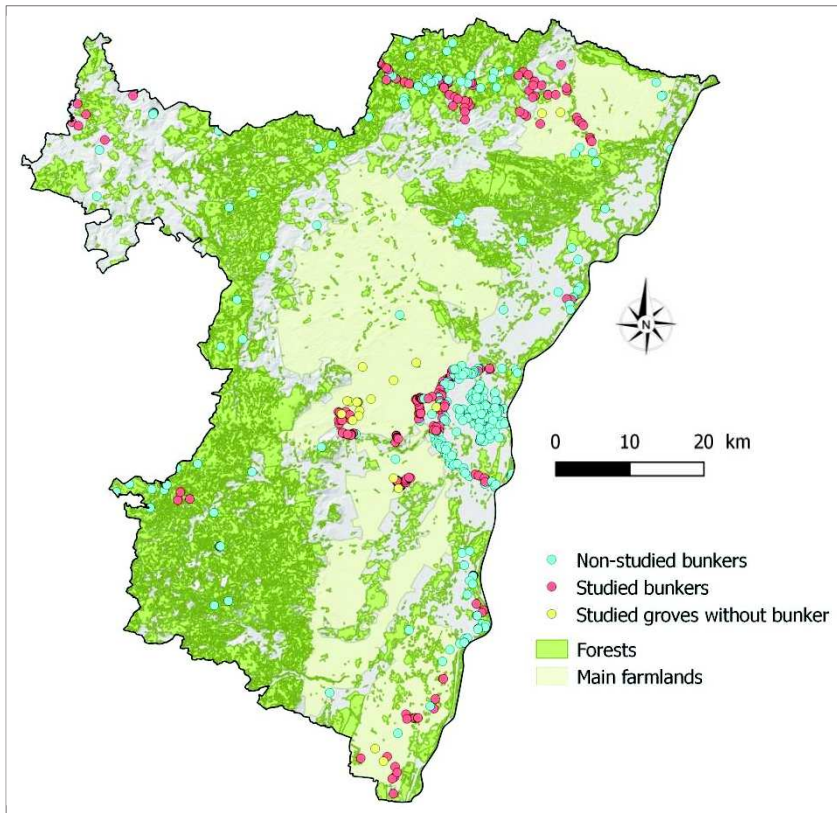
### 117 **Protocol**

#### 118 *Studied area and bunkers*

119 The military bunkers studied are located on the German defensive line of Strasbourg and  
120 at the eastern extremity of the Maginot Line, located in the Bas-Rhin (Alsace, Grand Est,  
121 France). The annual average temperature of Bas-Rhin is 10.4 °C. Annual precipitation is about  
122 700 mm/y with an average altitude of 150 m. Bunkers are scattered throughout the territory,  
123 with the majority located on farmland that is mainly composed of corn and wheat crops with  
124 rare groves. In this study, a *grove* was defined as a small group of trees (>3 m high) with a size  
125 between 0.01 and 1 ha, with or without an understorey. If the area exceeded 1ha, the  
126 landscape type was considered to be *forest*. Six hundred and fourteen fortifications have  
127 been found and geolocated in this region, but this list is non-exhaustive and the overall  
128 number could be far higher (Mermy et al. 2011). Indeed, new bunkers are regularly found  
129 through archaeological excavations.

130 Not all the bunkers were studied; those located within towns and cities were excluded  
131 from the present study. The remaining bunkers (N=120) were randomly sampled to obtain a  
132 representation of all the bunkers in the studied area. In addition to the 120 selected bunkers,  
133 a further 62 bunkers were found during inspections. The analyses therefore concern a total of  
134 182 bunkers (**Figure 2**). Twenty-one groves without bunkers and surrounded by crops were  
135 also studied over the same period in order to compare their attractiveness with that of groves

136 with bunkers. Groves within one km of selected bunkers were randomly selected to ensure  
1 the same environmental type.  
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3 137 the same environmental type.  
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33 139 **Figure 2:** Location of the 182 bunkers and the 21 groves without bunkers  
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36 140 *Local variables*  
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38 141 Up to ten bunkers were inspected during daytime by groups of two to four field assistants  
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41 142 trained to identify signs of use by animals. Geographically close bunkers were inspected  
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43 143 during a randomly chosen day between June and August 2016. Any footprints and evidence of  
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45 144 the presence of badgers and foxes (fur, prey leftovers, faeces, burrows, freshly dug earth or  
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47 145 footprints) were identified within a 10 to 20 m range around and inside the bunkers. The  
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49 146 freshness of this evidence was assessed to evaluate the recentness of bunker use (latrine,  
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51 147 faeces and food, newly dug and humid ground). Badger and fox burrows were differentiated  
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53 148 by multiple signs including the number, shape and size of the entrances, odour, and presence  
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56 149 of in-proximity latrines and footprints (Marton et al. 2016). Any unidentified bunkers which  
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150 were found by chance were also inspected. Geolocation was carried out using GPS (Bushnell  
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3 151 Backtrack D-Tour). Freshness of evidence and the actual use of burrows were confirmed with  
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5 152 a second visit to each bunker one month after the initial visit. The relative position of each  
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7 153 burrow (inside or outside the bunker) was noted, as well as the type of badger sett (“central  
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9  
10 154 sett” including main, annexe and subsidiary burrows if they had three or more entrances and  
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12 155 “outlier sett” if they had one or two entrances). The landscape type in which bunkers were  
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15 156 found was also written down for each of them (*Forest, Grove or Crops*). We evaluated the  
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18 157 accessibility of each bunker as follows:

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21 158 • *Underground*: the bunker was entirely or almost entirely buried and all the entrances  
22  
23  
24 159 created by humans were underground. Only the roof was visible. No animal could reach  
25  
26  
27 160 it without digging;
- 28  
29 161 • *Partially buried*: the bunker was partially buried and had one or more entrances created  
30  
31  
32 162 by humans where carnivorous species of the studied area could enter, but humans  
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34  
35 163 could not gain access without crawling;
- 36  
37 164 • *Overground*: the bunker had at least one large human-made entrance that allowed easy  
38  
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40 165 access to both carnivores and humans.

#### 41 42 43 166 *Landscape analysis*

44  
45 167 GIS was used to map landscape elements within an 800 m radius of each bunker. This  
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47  
48 168 corresponds to an average badger home range in western Europe, and represents a smaller  
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51 169 home range than the red fox (Meia & Weber 1995; Balestrieri et al. 2016). The distance to the  
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54 170 nearest landscape element of each type was computed, and the size of each landscape  
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56 171 element type was calculated within each 800 m radial buffer. Landscape elements types were  
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59 172 as follows: watercourses, ponds and lakes, groves, hardwood forests, scrublands, mixed  
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173 forests, plantations, resinous forests, riparian forests, meadows, vineyards, urban area and  
174 annual crops (CIGAL© data (CIGAL 2013), accuracy 1/10 000). The average distance between  
175 bunkers of a same small defensive line was measured, as well as the size of all the groves.

## 176 Analysis

### 177 Method

178 Four dependent variables were used: (1) the use or non-use of the bunker/grove (use was  
179 considered to occur if any evidence of badger or fox presence was observed), (2) the  
180 presence of a burrow inside a bunker or in its immediate vicinity, (3) the presence of currently  
181 occupied burrows (also called burrow in use) indicated by fresh evidence of their use, and (4)  
182 the type of badger sett (central/outlier). These dependent variables were used for bunkers  
183 and for groves without bunkers.

### 184 Statistics

185 Generalized linear binomial models (GLM $\beta$ ) were used to explain the variations of dependent  
186 variables of bunkers, using the following variables as co-variables:

- 187 • The percentage of each landscape element type in each 800m radial buffer;
- 188 • The nearest distance to each landscape element type;
- 189 • The accessibility of each bunker (*underground, partially buried, overground*).

190 The three first dependent variables were also used to compare groves with and without a  
191 bunker. To explain their variations, GLM $\beta$  were also used with the following variables as co-  
192 variables:

- 193 • The size of the grove;
- 194 • The absence/presence of a bunker in the grove;
- 195 • The species (fox, badger or both of these species).

196 Collinear variables were identified and removed using a stepwise procedure based on the  
 197 Variance Inflation Factor (VIF), associated with ACP and Spearman tests. Models were  
 198 selected using AIC backward elimination/forward selection. Modalities of variables were  
 199 compared with a Tuckey-HSD post-hoc test. Statistics were performed with R software  
 200 (v3.3.0) and GIS analysis using QGIS (v2.18.3). The significance threshold was set to  $p < 0.05$ .

## 201 Results

### 202 *Characteristics of bunkers*

203 Nineteen bunkers were located in groves (10.44%), 57 in forests (31.32%) and 106 on  
 204 crops (58.24%). Accessibility type was more balanced, with 39 underground bunkers  
 205 (21.43%), 60 partially buried bunkers (32.97%) and 83 overground bunkers (45.60%)(**Table 1**).  
 206 Only five underground bunkers were located in groves and in forests. The small defensive  
 207 lines in the studied area were composed of an average 9.4 bunkers ( $\pm 2.3$  SE,  $N=15$ ), with an  
 208 average inter-distance of 389 metres ( $\pm 64.64$  SE).

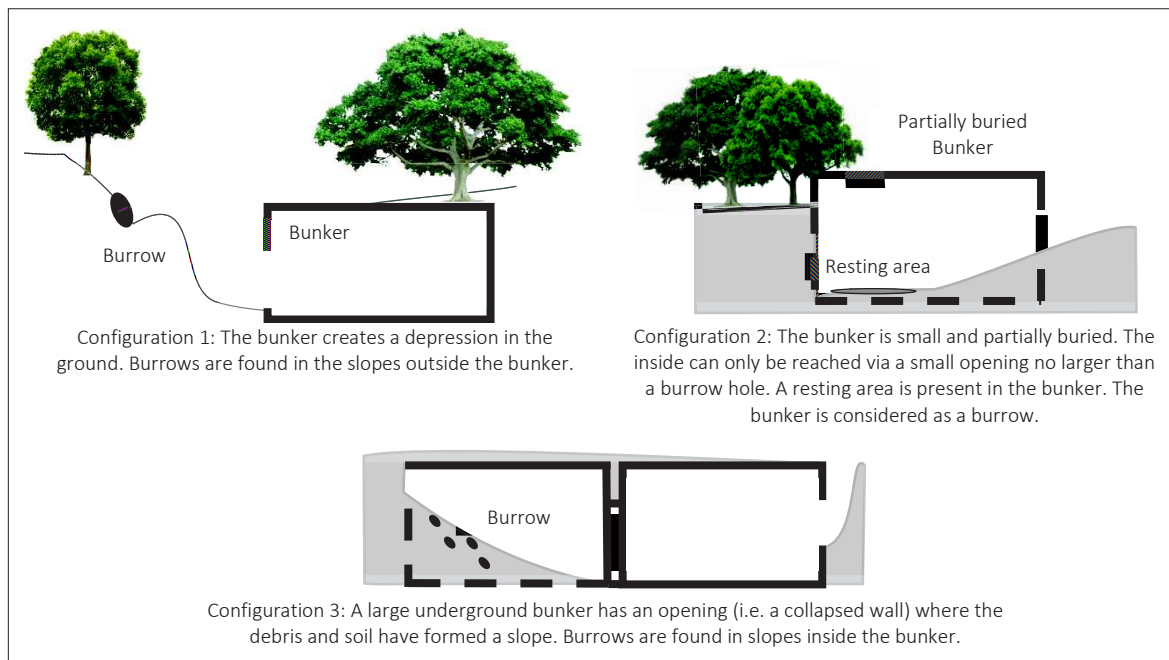
209 **Table 1:** *Number of studied bunkers per accessibility type and main surrounding*  
 210 *landscape.*

Surroundings	Underground	Partially buried	Overground	Total
Crop	34	26	46	106
Grove	2	11	6	19
Forest	3	23	31	57
Total	39	60	83	182

### 212 *Use of bunkers*

213 Evidence of badger or fox presence was found in 61 of the 182 studied bunkers  
 214 (33.52%). Each species used a significantly similar number of bunkers ( $W = 21214$ ,  $p=0.357$ ).  
 215 Burrows were found on 43 sites (23.63%), 30 (69.77%) of which were still occupied at the  
 216 time of the study. We found 18 (41.86%) burrows inside the bunkers and 25 (58.14%) outside.

217 Twenty-seven badger setts were found inside or in the vicinity of bunkers, of which 20 (74%)  
 218 were outlier burrows and seven (26%) were central burrows. Five of these seven central  
 219 burrows were found outside the bunkers. "Resting areas" composed of hay and badger/fox  
 220 fur were found inside nine small partially buried bunkers. The latter were considered as  
 221 outlier burrows in the analyses but with no assigned species. We identified three different  
 222 burrow configurations in relation to the bunkers, as illustrated in **Figure 3**.



**Figure 3:** *The three different configurations of burrows observed in this study.*

233 On eight sites (4.4%), bunkers were used by humans (house, wood/tractor storage, waste  
 234 disposal site). In two bunkers, several underferd amphibians were found with a number of  
 235 dead animals of different species trapped in underground rooms that could only be reached  
 236 using a ladder.

237 *Landscape analysis*

238 Selection of collinear variables resulted in 14 collinear groups. The 14 main  
 239 explanatory variables were extracted (**Table 2**). Data for both species were pooled to obtain  
 240 sufficient data for landscape analysis.

241 **Table 2:** List of used environmental variables

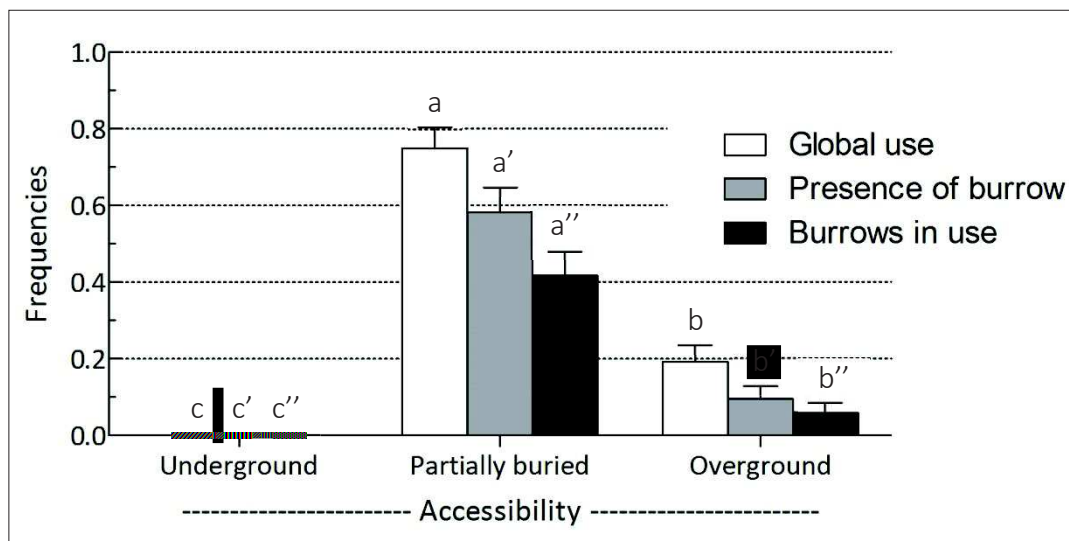
Distance to:	Watercourses, Ponds and lakes, Scrublands, Vineyards
Size of:	Groves, watercourses, annual crops, ponds and lakes, scrublands, mixed forests, meadows, urban area, orchards, vineyards

242 The use of bunkers and the use of groves without bunkers were both positively  
 243 correlated to the annual crop size in the surrounding buffers (least significant values:  $Z=2.831$ ;  
 244  $p<0.01$ ). Both types of use were also negatively correlated to the distance to annual crops by  
 245 a significant negative correlation between the annual crop size and distance to annual crops  
 246 ( $\rho=-0.905$ ;  $p<0.01$ ).

247 The presence of burrows and the number of burrows in use were positively correlated  
 248 to annual crop size (least significant values:  $Z=3.044$ ;  $p<0.01$ ) and to the size of urban area  
 249 (least significant values:  $Z=3.148$ ;  $p<0.01$ ).

250 *The effect of accessibility*

251 The accessibility of bunkers had a significant effect on use ( $\chi^2=72.074$ ,  $df=2$ ,  $p<0.01$ ), on  
 252 the presence of burrows ( $\chi^2=54.877$ ,  $df=2$ ,  $p<0.01$ ) and on the number of burrows in use  
 253 ( $\chi^2=35.037$ ,  $df=2$ ,  $p<0.01$ ) (Figure 4).



254

255 **Figure 4:** *Effects of the accessibility of bunkers on their use by animals (global use shown in*  
256 *white, presence of burrows in grey, and presence of burrows in use in black), for each of the*  
257 *three accessibility categories. Error bars are standard errors.*

258

259 *Comparison of groves with and without a bunker.*

260 Use of groves was not correlated to the presence of a bunker ( $\chi^2=0.523$ ,  $df=1$ ,  $p=0.469$ ).

261 There were more burrows ( $\chi^2=10.354$ ,  $df=1$ ,  $p<0.01$ ) and more burrows in use ( $\chi^2=5.107$ ,  $df=1$ ,  
262  $p=0.02$ ) when a bunker was present. The area of the groves had no effect on grove use, on  
263 the presence of burrows and on the number of burrows in use (most significant values:  $Z=-$   
264  $0.361$ ;  $p=0.718$ ). Among the eleven species-determined burrows found in groves, seven were  
265 badger setts and two were fox burrows.

## 266 **Discussion**

### 267 *Bunkers as habitat*

268 Bunkers form a network of habitats which provide resources for wildlife. The presence of  
269 burrows in over one third of the studied bunkers and a relatively high occupation rate suggest  
270 that badgers and foxes have had to adapt to a man-made habitat due to the reduction in their  
271 natural environment. These are not the only carnivorous species using bunkers; wildcats (*Felis*  
272 *silvestris*) are also known to inhabit a large number of bunkers (Crossland & Schöne 2007).  
273 Camera traps could be a more appropriate tool to study this type of discrete species in forest  
274 bunkers (Anile et al. 2009; Velli et al. 2015). This technique could also allow a more precise  
275 quantification of bunker use and an evaluation of the effect of human disturbance.

276 The abundance of badgers in the studied area may be lower than that of foxes, as  
277 badgers were less observed than foxes in non-exhaustive naturalist local surveys (Data 2008-

2017; 2 185 observations of badgers vs 3 036 observations of foxes (1.39 times more) in the  
4 755 km<sup>2</sup> of the studied area; Odonat, 2017). If these figures are correct, the observation of  
equal use of bunkers by each species in this study thus suggests that badgers are particularly  
attracted by these remaining habitats in highly changed landscapes. These animals also have a  
greater network of burrows than foxes, with setts that are composed of different types of  
chamber. Most of the badger burrows found were outlier setts, characterized by few  
entrances and usually a nest chamber. A similar configuration was found in partially buried  
bunkers. They were regularly used by badgers and foxes. As nesting sites were found inside  
these partially buried bunkers, we considered the latter to be burrows.

Partially buried bunkers provide shelter. However, entirely buried bunkers were never  
used by the studied species, indicating that visible human-made openings are needed to  
make them accessible to these animals. This observation suggests that badgers and foxes do  
not dig to reach the underground rooms, even when the bunker roof is visible. Partially buried  
bunkers could be habitat opportunities requiring an initial physical effort to gain access, yet  
they are not particularly sought after by these species. Foxes and badgers can also use  
bunkers that are highly accessible and can be easily entered by humans, but the quality of  
these shelters seems lower than that provided by partially buried bunkers. This difference in  
quality could be explained by the larger size of inner rooms, the luminosity and human  
disturbances, all of which are greater when bunkers are not buried (Aaris-Sørensen 1987).  
When burrows were found inside or in the vicinity of these highly accessible bunkers, it was  
always in cases where the structures created a ground depression outside the bunker or  
when a large amount of dirt was found inside. In both cases, a dirt slope was present, in which  
burrows had been dug.

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301 A higher number of burrows and burrows in use were found in areas with larger  
302 annual crops and greater urbanisation. The destruction of natural habitats for the benefit of  
303 crops and urban area may force badgers and foxes to live in bunkers, which are preserved  
304 from overly intense human action (Remonti et al. 2006). Bunkers may represent safe areas  
305 where foxes and badgers could rest, feed and reproduce, i.e. a source of refuge on farmland.  
306 The importance of refuge habitats has already been raised for other carnivores, such as the  
307 polecat in the Mediterranean landscape (Rondinini et al. 2006). They also provide resources  
308 for other species such as birds, plants, spiders, insects and other mammals (Sheperd &  
309 Swihart 1995; Zollner 2000; Benton et al. 2003; Duelli & Obrist 2003; Grashof-Bokdam & van  
310 Langevelde 2005; Billeter et al. 2008; Wretenberg et al. 2010; Redon (de) et al. 2015).

311 Wildlife obtains different services from bunkers and groves without bunkers when  
312 they use them as refuge habitats. Indeed, the presence of a bunker in a grove increased the  
313 probability of finding a burrow and a burrow in use there. A major difference between these  
314 two landscape elements was the presence of slopes created by ground depression around  
315 bunkers.

#### 316 *Distribution of bunkers in the studied area*

317 Few bunkers were found in groves. These were mainly small bunkers used for storage and  
318 were hidden from the enemy when constructed in wooded areas. However, as other storage  
319 bunkers were found on crops, we presume that land consolidation strategy has ensured the  
320 maintenance of groves. Administratively speaking, if the presence of a bunker made a piece  
321 of land “uncultivable” on the land registry plan, the piece of land remained registered as such  
322 and the bunker and grove were both preserved in their natural state. If not, the piece of land  
323 became cultivable and farmers were free to plant crops around the bunker. Moreover, the  
324 use of land for crops has led to the burial of bunkers, as shown by the high number of

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3 325 underground bunkers found on farmland. As carnivores do not dig to reach buried bunkers,  
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5 326 these structures have lost their habitat potentiality.

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8 327 As bunkers were built around strategic points in small defensive lines, they form a  
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10 328 network of potential shelters for wildlife. The distance between the successive bunkers of one  
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12 329 small defensive line allows badgers to have three or four outlier burrows in their territory,  
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14 330 whilst foxes have even more.

15 331 *Towards an ecological management of bunkers*

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19 332 Although bunkers are widely used by carnivores, they are often unhealthy structures,  
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21 333 with stagnant water containing high numbers of mosquitoes and animal carcasses. Hygienic  
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23 334 conditions are usually poor, and it is unlikely that animals can live in these places for long  
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25 335 periods of time. The frequent presence of frogs trapped in bunker chambers that are only  
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27 336 reachable by a ladder merits attention and should be notified to the competent authorities to  
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29 337 ensure that the concerned bunkers are made safe, especially when they represent a danger  
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31 338 for children in urban areas.

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35 339 Some trees were found close to the bunkers, even in middle of large crops fields. They  
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37 340 did not provide enough cover to form a grove but provided roosting areas for avian  
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39 341 mesopredators. Furthermore, preserved groves located on farmland can be used by these  
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41 342 species, including corvids, hawks, buzzards and owls. There was no evidence of badgers or  
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43 343 foxes around bunkers that did not have visible human-made openings, suggesting that access  
44  
45 344 was insufficient.

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49 345 These results show that bunkers are currently used by wildlife, but some have lost  
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51 346 their habitat potentiality. This situation can be changed and improved by the management of  
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53 347 bunkers which would be advantageous not only for badger and foxes but also for a variety of  
54  
55 348 other species. First, the accessibility of bunkers with large apertures should be reduced by



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3 350 leaving only small holes such as those used by carnivores and bats (Nowicki et al. 2008).  
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5 351 Indeed, even when entirely surrounded by scrubland, bunkers with large human-made  
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7 352 openings are attractive to people who sometimes put these spaces to surprising use, such as  
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9 353 the exhibition of thousands of hubcaps we found in one bunker. The surroundings of bunkers  
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11 354 located on cropland should be included on the land registry plan to ensure their  
12  
13 355 management. A ground depression should be created around underground bunkers to  
14  
15 356 excavate them and create slopes that can be used by wildlife to create burrows and settle  
16  
17 357 (Macdonald et al. 2004). Burrows were found inside or in the vicinity of 35 of the 99 bunkers  
18  
19 358 that had a slope (35.4%). This means that if all the studied bunkers (182) were managed with  
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21 359 a slope, 64 potential burrows could be expected, and hundreds could be observed if all the  
22  
23 360 bunkers in the study area (at least 614) managed in the same way. The planting of trees  
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25 361 would create small groves around the bunkers to provide benefits for avian predators. Finally,  
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27 362 certain interesting bunkers located close to urban areas could be video-equipped as an  
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35 awareness-raising project to educate people about wildlife.

### 363 **Conclusion**

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39 364 Bunkers are widely used as shelters by red foxes and European badgers. However, a  
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42 365 high proportion of these military structures, especially on farmland, are in poor condition for  
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44 366 their use as a habitat. The present study provides the necessary information to significantly  
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46 367 improve the habitat potentiality of bunkers for the two most representative fossorial  
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48 368 carnivore species living on Western European farmlands. Knowing the high number of  
49  
50 369 bunkers concerned and their relatively equal distribution in the studied area, their  
51  
52 370 management could help to slow the inexorable deterioration and homogenisation of the  
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54 371 agricultural landscape.

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### 376 **Author Contributions**

377 All authors approve this version of the manuscript. They agree to be accountable for  
378 the aspects of the work that they conducted, and will ensure that any questions related to the  
379 accuracy or integrity of any part of their work are appropriately investigated and resolved. JJ  
380 conceived the idea and design methodology; JJ, DW, NG and LG collected the data; JJ and LG  
381 carried out data analysis; JJ, YH and FB organised the writing of the manuscript. All authors  
382 played an active part in the drafting of the manuscript and gave their final approval for  
383 publication.

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388 data. They agree to the publication of this study.

### 389 **Bibliography**

- 390 Aaris-Sørensen, J. (1987). Past and present distribution of badgers *Meles meles* in the  
391 Copenhagen area. *Biol. Conserv.*, 41, 159–165.
- 392 AFP. (2014). Forgotten war site now a bat cave [WWW Document]. *IOL*. URL  
393 <http://www.iol.co.za/news/forgotten-war-site-now-a-bat-cave-1672065>
- 394 Anile, S.T., Bizzarri, L.O. & Ragni, B.E. (2009). Camera trapping the European wildcat (*Felis*  
395 *silvestris silvestris*) in Sicily (southern Italy): Preliminary results. *Hystrix Ital. J. Mammal.*,  
396 20, 55–60.
- 397 Ayers, B. & Parangoni, I. (2015). Industrial heritage in albania: an assessment. *Ind. Archaeol.*  
398 *Rev.*, 37, 111–122.

- 399 Bajrovic, I. & Satter, J. (2014). Albania: from bunkers to ballots. *J. Democr.*, 25, 142–153.
- 1  
2 400 Balestrieri, A., Cardarelli, E., Pandini, M., Remonti, L., Saino, N. & Prigioni, C. (2016). Spatial  
3 401 organisation of European badger (*Meles meles*) in northern Italy as assessed by camera-  
4 402 trapping. *Eur. J. Wildl. Res.*, 62, 219–226.
- 5  
6 403 Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat  
7 404 heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- 8  
9 405 Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J.,  
10 406 Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H.,  
11 407 Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F.,  
12 408 Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M.,  
13 409 Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans,  
14 410 M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. & Edwards, P.J. (2008).  
15 411 Indicators for biodiversity in agricultural landscapes: A pan-European study. *J. Appl. Ecol.*,  
16 412 45, 141–150.
- 17  
18 413 Bonfanti, P., Fregonese, A. & Sigura, M. (1997). Landscape analysis in areas affected by land  
19 414 consolidation. *Landsc. Urban Plan.*, 37, 91–98.
- 20  
21 415 Butet, A. & Leroux, A.B.A. (2001). Effects of agriculture development on vole dynamics and  
22 416 conservation of Montagu’s harrier in western French wetlands. *Biol. Conserv.*, 100, 289–  
23 417 295.
- 24  
25 418 Ciechanowski, M. & Sachanowicz, K. (2014). Fat Dormouse *Glis glis* (Rodentia: Gliridae) in  
26 419 Albania: Synopsis of Distributional Records with Notes on Habitat Use. *Acta Zool. Bulg.*,  
27 420 66, 39–42.
- 28  
29 421 CIGAL. (2013). Données faune Alsace [WWW Document]. *Coopération pour l’information*  
30 422 *géographique en Alsace*. URL <https://www.cigalsace.org/portail/>
- 31  
32 423 Crossland, D. & Schöne, S. (2007). From Wehrmacht to Wildcats: World War II Bunkers Turn  
33 424 Into Wildlife Haven [WWW Document]. *SPIEGEL ONLINE*. URL  
34 425 <http://www.spiegel.de/international/germany/from-wehrmacht-to-wildcats-world-war-ii-bunkers-turn-into-wildlife-haven-a-507880.html>
- 35  
36 426  
37 427 Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics,  
38 428 patterns of use and management implications. *J. Zool.*, 275, 190–200.
- 39  
40 429 Desjeux, Y., Dupraz, P., Kuhlman, T., Paracchini, M.L., Michels, R., Maignan, E. & Reinhard, S.  
41 430 (2014). Evaluating the impact of rural development measures on nature value indicators  
42 431 at different spatial levels: Application to France and the Netherlands. *Ecol. Indic.*, 59, 41–  
43 432 61.
- 44  
45 433 DeVault, T.L., Olson, Z.H., Beasley, J.C. & Rhodes, O.E. (2011). Mesopredators dominate  
46 434 competition for carrion in an agricultural landscape. *Basic Appl. Ecol.*, 12, 268–274.
- 47  
48 435 Dondina, O., Kataoka, L., Orioli, V. & Bani, L. (2016). How to manage hedgerows as effective  
49 436 ecological corridors for mammals: A two-species approach. *Agric. Ecosyst. Environ.*, 231,  
50 437 283–290.
- 51  
52 438 Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: the  
53 439 contribution of seminatural habitat islands. *Basic Appl. Ecol.*, 4, 129–138.
- 54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 440 Evans, L.E., Ardia, D.R. & Flux, J.E.C. (2009). Breeding synchrony through social stimulation in a  
1 441 spatially segregated population of European starlings. *Anim. Behav.*, 78, 671–675.  
2
- 3 442 Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe,  
4 443 M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J.,  
5 444 Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global  
6 445 consequences of land use. *Science (80-. )*, 309, 570–4.  
7
- 8  
9 446 Grashof-Bokdam, C.J. & van Langevelde, F. (2005). Green veining: Landscape determinants of  
10 447 biodiversity in European agricultural landscapes. *Landsc. Ecol.*, 20, 417–439.  
11
- 12 448 Hoffmann, M. & Sillero-Zubiri, C. (2016). *Vulpes vulpes*, Red Fox. *IUCN Red List Threat. Species*  
13 449 *2016*, e.T23062A4, 1–10.  
14
- 15 450 Kaufmann, J. & Jurga, R. (1999). *Fortress Europe: European Fortifications Of World War II*. 1st  
16 451 edn. First Da Capo Press.  
17
- 18 452 König, C. (2013). Les ravageurs, menace pour nos céréales, 1–24.  
19
- 20 453 Kranz, A., Abramov, A.V., Herrero, J. & Maran, T. (2016). *Meles meles*. *IUCN Red List Threat.*  
21 454 *Species 2016*, 8235, e.T29673A45203002.  
22
- 23 455 Kurek, P., Kapusta, P. & Holeksa, J. (2013). Burrowing by badgers (*Meles meles*) and foxes  
24 456 (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest.  
25 457 *Ecol. Res.*, 29, 1–11.  
26
- 27  
28 458 Macdonald, D.W., Newman, C., Dean, J., Buesching, C.D. & Johnson, P.J. (2004). The  
29 459 distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field  
30 observations contradict the sett dispersion hypothesis. *Oikos*, 106, 295–307.  
31
- 32 461 Marton, M., Markolt, F., Szabo, L., Kozak, L., Lanszki, J., Patko, L. & Heltai, M. (2016). Den site  
33 462 selection of the European badger, *Meles meles* and the red fox, *Vulpes vulpes* in  
34 463 Hungary. *FOLIA Zool.*, 65, 72–79.  
35
- 36  
37 464 Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and  
38 465 bulldozers. *Nature*, 536, 146–145.  
39
- 40 466 Meia, J.-S. & Weber, J.-M. (1995). Home ranges and movements of red foxes in central  
41 467 Europe: stability despite environmental changes. *Can. J. Zool.*, 73, 1960–1966.  
42
- 43 468 Mermy, D.C., Guignat, H.S., Zammit, R., Heckenmeyer, E. & Lizée, M. (2011). *Inventaire*  
44 469 *départemental des cavités souterraines hors mines du Bas-Rhin*.  
45
- 46  
47 470 Nowicki, F., Dadu, L., Carsignol, J., Bretaud, J.-F. & Bielsa, S. (2008). Rapport bibliographique :  
48 471 Routes et chiroptères Etat des connaissances. *Les Rapp.*, 1–253.  
49
- 50 472 Odonat : Office des données naturalistes du Grand-Est. (2017). Atlas des espèces d'Alsace  
51 473 [WWW Document]. [www.faune-alsace.org](http://www.faune-alsace.org). URL [http://www.faune-alsace.org/index.php?m\\_id=620](http://www.faune-alsace.org/index.php?m_id=620)  
52 474 [alsace.org/index.php?m\\_id=620](http://www.faune-alsace.org/index.php?m_id=620)  
53
- 54 475 Poschlod, P., Bakker, J.P. & Kahmen, S. (2005). Changing land use and its impact on  
55 476 biodiversity. *Basic Appl. Ecol.*, 6, 93–98.  
56
- 57  
58 477 Redon (de), L., Le Viol, I., Jiguet, F., Machon, N., Scher, O. & Kerbiriou, C. (2015). Road  
59 478 network in an agrarian landscape: Potential habitat, corridor or barrier for small  
60 479 mammals? *Acta Oecologica*, 62, 58–65.  
61  
62  
63  
64  
65

- 480 Remonti, L., Balestrieri, A. & Prigioni, C. (2006). Factors determining badger *Meles meles* sett  
1 481 location in agricultural ecosystems of NW Italy. *Folia Zool.*, 55.1, 19–27.  
2
- 3 482 Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012).  
4 483 Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.*, 27, 265–  
5 484 71.  
6
- 7 485 Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity  
8 486 in Great Britain. *J. Appl. Ecol.*, 39, 157–176.  
9
- 10 487 Rondinini, C., Ercoli, V. & Boitani, L. (2006). Habitat use and preference by polecats ( *Mustela*  
11 488 *putorius* L.) in a Mediterranean agricultural landscape. *J. Zool.*, 269, 213–219.  
12
- 13 489 Roper, T.J. (1992). The structure and function of badger setts. *J. Zool.*, 227, 691–694.  
14
- 15 490 Roper, T.J., Tait, A.I., Fee, D. & Christian, S.F. (1991). Internal structure and contents of three  
16 491 badger ( *Meles meles* ) setts. *J. Zool.*, 225, 115–124.  
17
- 18 492 Sachanowicz, K. & Zub, K. (2002). Numbers of hibernating *Barbastella barbastellus* (Schreber,  
19 493 1774) (Chiroptera, Vespertilionidae) and thermal conditions in military bunkers. *Mamm.*  
20 494 *Biol. - Zeitschrift für Säugetierkd.*, 67, 179–184.  
21
- 22 495 Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*,  
23 496 21, 464–71.  
24
- 25 497 Sheperd, B.F. & Swihart, R.K. (1995). Spatial dynamics of fox squirrels ( *Sciurus niger* ) in  
26 498 fragmented landscapes. *Can. J. Zool.*, 73, 2098–2105.  
27
- 28 499 Théou, P. & Bego, F. (2013). *Etude des populations de chiroptères de l'île de Sazani. Note*  
29 500 *naturaliste Initiative PIM.*  
30
- 31 501 Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape  
32 502 perspectives on agricultural intensification and biodiversity - Ecosystem service  
33 503 management. *Ecol. Lett.*, 8, 857–874.  
34
- 35 504 Velli, E., Bologna, M.A., Silvia, C., Ragni, B. & Randi, E. (2015). Non-invasive monitoring of the  
36 505 European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three  
37 506 different monitoring techniques and evaluation of their integration. *Eur. J. Wildl. Res.*,  
38 507 61, 657–668.  
39
- 40 508 Warchałowski, M., Łupicki, D., Cichocki, J., Pietraszko, M., Rusek, A., Zawadzka, A. & Nikodem,  
41 509 M. (2013). Zimowanie nietoperzy Chiroptera w wybranych obiektach wolno stojących  
42 510 Frontu Fortecznego Łuku Odry i Warty. *Kulon*, 18, 139–147.  
43
- 44 511 van der Well, L. & van Beveren, A. (2016). Bunkersite.com [WWW Document]. URL  
45 512 <http://bunkersite.com/index.php>  
46
- 47 513 Wretenberg, J., Pärt, T. & Berg, Å. (2010). Changes in local species richness of farmland birds  
48 514 in relation to land-use changes and landscape structure. *Biol. Conserv.*, 143, 375–381.  
49
- 50 515 Zduniak, P., Czechowski, P. & Jedro, G. (2011). The effect of nesting habitat on reproductive  
51 516 output of the Barn Swallow (*Hirundo rustica*). A comparative study of populations from  
52 517 atypical and typical nesting habitats in western Poland. *BELGIAN J. Zool.*, 141, 38–43.  
53
- 54 518 Zollner, P.A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in  
55 519 fragmented agricultural landscapes. *Landsc. Ecol.*, 15, 523–533.  
56  
57  
58  
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1 **Table 1:** *Number of studied bunkers per accessibility type and main surrounding*  
2 *landscape.*

Surroundings	Underground	Partially buried	Overground	Total
Crop	34	26	46	106
Grove	2	11	6	19
Forest	3	23	31	57
Total	39	60	83	182

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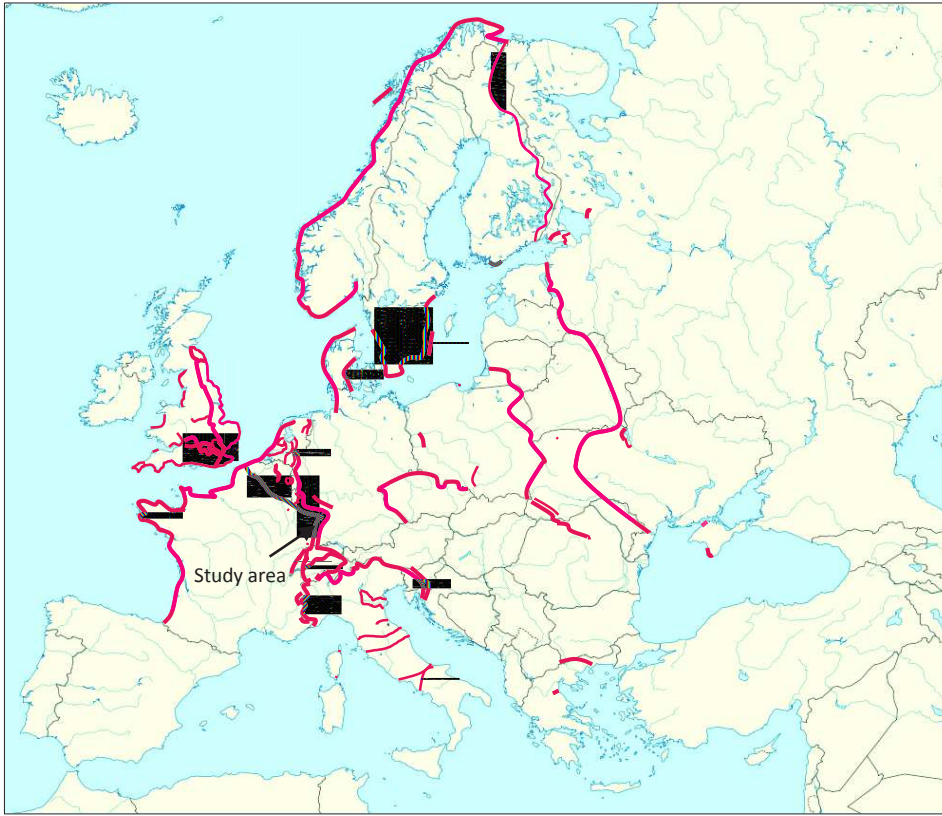
6 **Table 2:** *List of used environmental variables*

Distance to:	Watercourses, Ponds and lakes, Scrublands, Vineyards
Size of:	Groves, watercourses, annual crops, ponds and lakes, scrublands, mixed forests, meadows, urban area, orchards, vineyards

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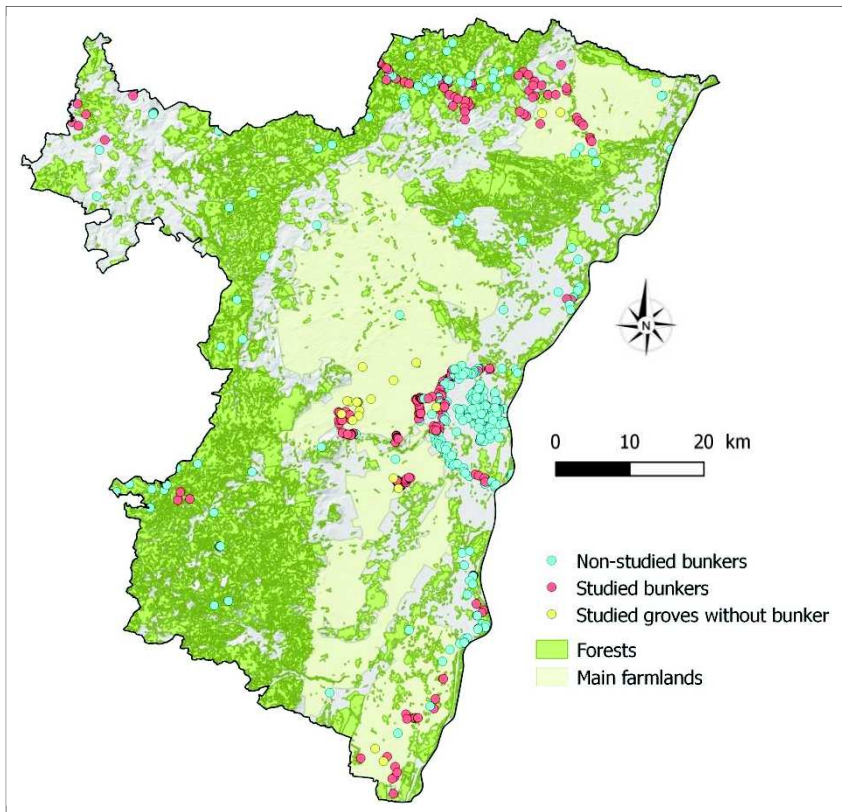


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**Figure 1:** Location of defensive lines in Europe (according to Kaufmann & Jurga 1999).



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Figure 2: Location of the 182 bunkers and the 21 groves without bunkers

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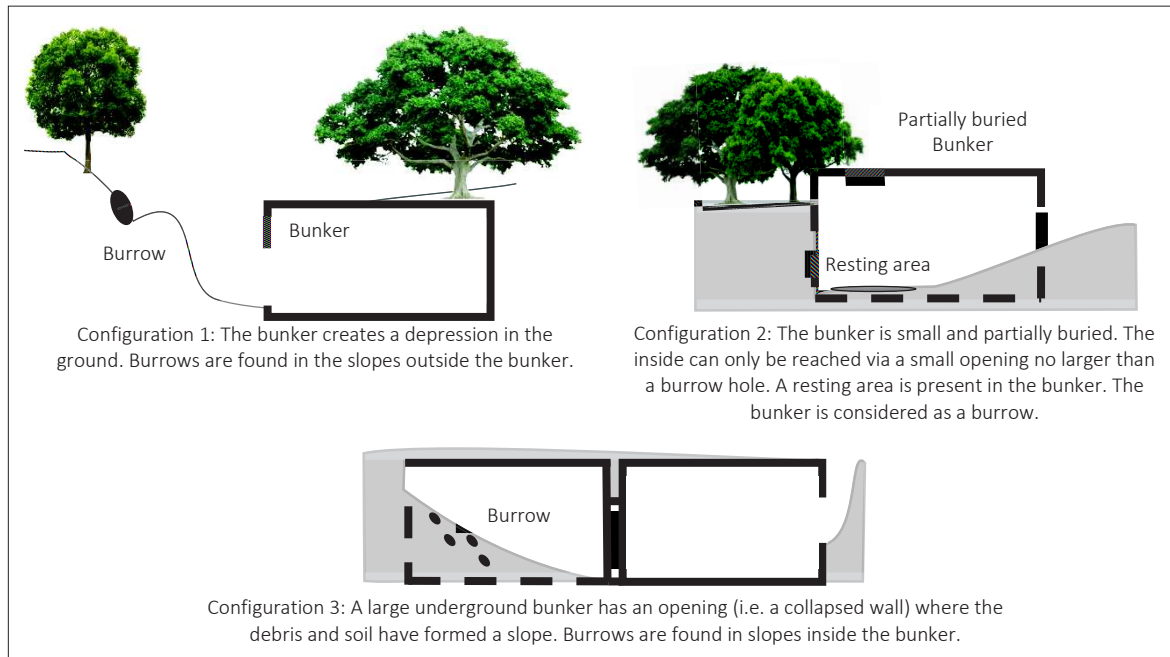
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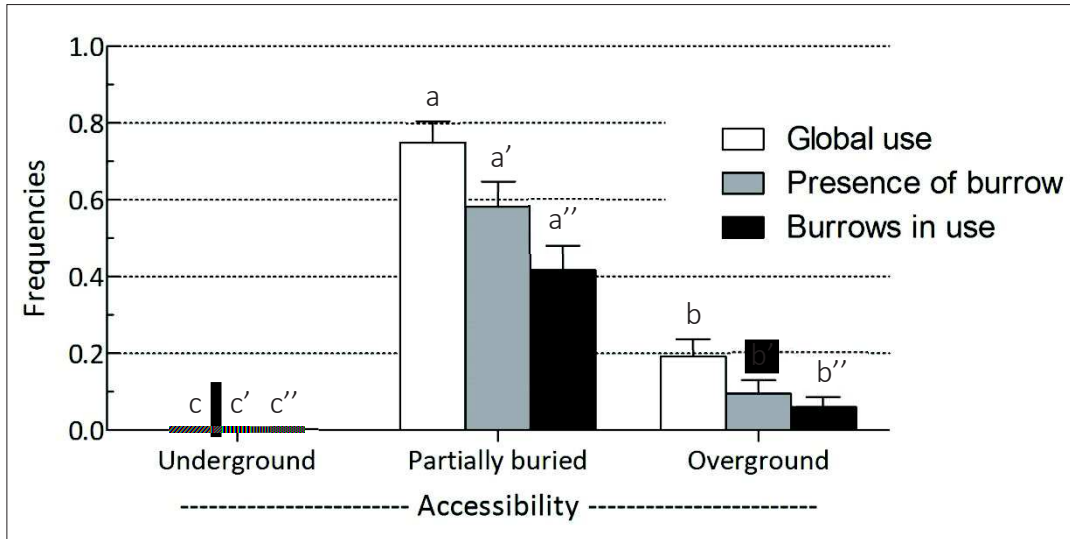
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24 **Figure 3:** *The three different configurations of burrows observed in this study.*

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27 **Figure 4:** *Effects of the accessibility of bunkers on their use by animals (global use shown in*  
 28 *white, presence of burrows in grey, and presence of burrows in use in black), for each of the*  
 29 *three accessibility categories. Error bars are standard errors.*

