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

Jonathan Jumeau^{1,2,3}†, Déborah Wolf², Léo Guthmann², Nicolas Gorlero², Françoise Burel³, Yves Handrich¹

¹ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

² Conseil Départemental du Bas-Rhin, Place du Quartier Blanc, 67964 Strasbourg, Cedex 9, France

³ Université de Rennes 1, CNRS, UMR 6553 ECOBIO, 35042 Rennes Cedex, France

† Corresponding author. Tel.: +33 06 07 62 33 63

E-mail address: jumeau.jonathan@gmail.com

Post-Print version

Published online 02 December 2017

Urban Ecosystems

<https://doi.org/10.1007/s11252-017-0721-y>

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² Conseil Départemental du Bas-Rhin, Place du Quartier Blanc, 67964 Strasbourg, Cedex 9, France

³ Université de Rennes 1, CNRS, UMR 6553 ECOBIO, 35042 Rennes Cedex, France

Running Title: New homes for badgers and foxes

Abstract

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

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

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

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

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

† Corresponding author. Tel.: +33 06 07 62 33 63

E-mail address: jumeau.jonathan@gmail.com

Introduction

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

of the war. For example, 700 000 bunkers were built in Albania in the second half of the 20th century (Bajrovic & Satter 2014; Ayers & Parangoni 2015). On a local scale, bunkers are clustered in small defensive lines located near strategic locations.

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

Few studies have explored the impact of bunkers on biodiversity. The reduced variations of temperatures in the wells of bunkers make them an ideal hibernation site for the Barbastelle bat (*Barbastella barbastellus*) (Sachanowicz & Zub 2002). In Germany, the one hundred bunkers and 32 kilometres of galleries making up the Festungsfront Oder-Warthe-Bogen bunker network are colonized by 37 000 bats from ten different species, possibly making it the artificial structure hosting the highest number of individuals in Europe (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 Tscharntke 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 20th 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

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

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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.

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

Materials and methods

Protocol

Studied area and bunkers

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

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

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

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

Local variables

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

were found by chance were also inspected. Geolocation was carried out using GPS (Bushnell Backtrack D-Tour). Freshness of evidence and the actual use of burrows were confirmed with a second visit to each bunker one month after the initial visit. The relative position of each burrow (inside or outside the bunker) was noted, as well as the type of badger sett ("central sett" including main, annexe and subsidiary burrows if they had three or more entrances and "outlier sett" if they had one or two entrances). The landscape type in which bunkers were found was also written down for each of them (*Forest, Grove* or *Crops*). We evaluated the accessibility of each bunker as follows:

- *Underground*: the bunker was entirely or almost entirely buried and all the entrances created by humans were underground. Only the roof was visible. No animal could reach it without digging;
- *Partially buried*: the bunker was partially buried and had one or more entrances created by humans where carnivorous species of the studied area could enter, but humans could not gain access without crawling;
- *Overground*: the bunker had at least one large human-made entrance that allowed easy access to both carnivores and humans.

Landscape analysis

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

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

Analysis

Method

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

Statistics

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

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

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

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

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

Results

Characteristics of bunkers

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

Table 1: Number of studied bunkers per accessibility type and main surrounding 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

Use of bunkers

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

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

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

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

Landscape analysis

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

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

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

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

The effect of accessibility

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

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

Comparison of groves with and without a bunker.

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

Discussion

Bunkers as habitat

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

The abundance of badgers in the studied area may be lower than that of foxes, as 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 km² 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.

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

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

Distribution of bunkers in the studied area

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

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

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

Towards an ecological management of bunkers

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

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

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

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

Conclusion

Bunkers are widely used as shelters by red foxes and European badgers. However, a high proportion of these military structures, especially on farmland, are in poor condition for their use as a habitat. The present study provides the necessary information to significantly improve the habitat potentiality of bunkers for the two most representative fossorial carnivore species living on Western European farmlands. Knowing the high number of bunkers concerned and their relatively equal distribution in the studied area, their management could help to slow the inexorable deterioration and homogenisation of the agricultural landscape.

Acknowledgements

We thank all the students who participated in this study and the anonymous reviewers for their comments on the previous version of this manuscript. We also thank Joanna Lignot and Lana Petrod for the English editing.

Author Contributions

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

Role of the funding source

This study was conducted through the CERISE project research and was funded by the French Minister of Ecology (DREAL Alsace) and the Departmental Council of the Bas-Rhin (CD67). They had no role in the study design, writing, collection, analysis and interpretation of data. They agree to the publication of this study.

Bibliography

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

- Bajrovic, I. & Satter, J. (2014). Albania: from bunkers to ballots. *J. Democr.*, 25, 142–153.
- Balestrieri, A., Cardarelli, E., Pandini, M., Remonti, L., Saino, N. & Prigioni, C. (2016). Spatial organisation of European badger (*Meles meles*) in northern Italy as assessed by camera-trapping. *Eur. J. Wildl. Res.*, 62, 219–226.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. & Edwards, P.J. (2008). Indicators for biodiversity in agricultural landscapes: A pan-European study. *J. Appl. Ecol.*, 45, 141–150.
- Bonfanti, P., Fregonese, A. & Sigura, M. (1997). Landscape analysis in areas affected by land consolidation. *Landsc. Urban Plan.*, 37, 91–98.
- Butet, A. & Leroux, A.B.A. (2001). Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biol. Conserv.*, 100, 289–295.
- Ciechanowski, M. & Sachanowicz, K. (2014). Fat Dormouse *Glis glis* (Rodentia: Gliridae) in Albania: Synopsis of Distributional Records with Notes on Habitat Use. *Acta Zool. Bulg.*, 66, 39–42.
- CIGAL. (2013). Données faune Alsace [WWW Document]. *Coopération pour l'information géographique en Alsace*. URL <https://www.cigalsace.org/portail/>
- Crossland, D. & Schöne, S. (2007). From Wehrmacht to Wildcats: World War II Bunkers Turn Into Wildlife Haven [WWW Document]. *SPIEGEL ONLINE*. URL <http://www.spiegel.de/international/germany/from-wehrmacht-to-wildcats-world-war-ii-bunkers-turn-into-wildlife-haven-a-507880.html>
- Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics, patterns of use and management implications. *J. Zool.*, 275, 190–200.
- Desjeux, Y., Dupraz, P., Kuhlman, T., Paracchini, M.L., Michels, R., Maignan, E. & Reinhard, S. (2014). Evaluating the impact of rural development measures on nature value indicators at different spatial levels: Application to France and the Netherlands. *Ecol. Indic.*, 59, 41–61.
- DeVault, T.L., Olson, Z.H., Beasley, J.C. & Rhodes, O.E. (2011). Mesopredators dominate competition for carrion in an agricultural landscape. *Basic Appl. Ecol.*, 12, 268–274.
- Dondina, O., Kataoka, L., Orioli, V. & Bani, L. (2016). How to manage hedgerows as effective ecological corridors for mammals: A two-species approach. *Agric. Ecosyst. Environ.*, 231, 283–290.
- Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic Appl. Ecol.*, 4, 129–138.

- Evans, L.E., Ardia, D.R. & Flux, J.E.C. (2009). Breeding synchrony through social stimulation in a spatially segregated population of European starlings. *Anim. Behav.*, 78, 671–675.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science* (80-.), 309, 570–4.
- Grashof-Bokdam, C.J. & van Langevelde, F. (2005). Green veining: Landscape determinants of biodiversity in European agricultural landscapes. *Landsc. Ecol.*, 20, 417–439.
- Hoffmann, M. & Sillero-Zubiri, C. (2016). *Vulpes vulpes*, Red Fox. *IUCN Red List Threat. Species 2016*, e.T23062A4, 1–10.
- Kaufmann, J. & Jurga, R. (1999). *Fortress Europe: European Fortifications Of World War II*. 1st edn. First Da Capo Press.
- König, C. (2013). Les ravageurs, menace pour nos céréales, 1–24.
- Kranz, A., Abramov, A.V., Herrero, J. & Maran, T. (2016). *Meles meles*. *IUCN Red List Threat. Species 2016*, 8235, e.T29673A45203002.
- Kurek, P., Kapusta, P. & Holeksa, J. (2013). Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecol. Res.*, 29, 1–11.
- Macdonald, D.W., Newman, C., Dean, J., Buesching, C.D. & Johnson, P.J. (2004). The distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field observations contradict the sett dispersion hypothesis. *Oikos*, 106, 295–307.
- Marton, M., Markolt, F., Szabo, L., Kozak, L., Lanszki, J., Patko, L. & Heltai, M. (2016). Den site selection of the European badger, *Meles meles* and the red fox, *Vulpes vulpes* in Hungary. *FOLIA Zool.*, 65, 72–79.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and bulldozers. *Nature*, 536, 146–145.
- Meia, J.-S. & Weber, J.-M. (1995). Home ranges and movements of red foxes in central Europe: stability despite environmental changes. *Can. J. Zool.*, 73, 1960–1966.
- Mermy, D.C., Guignat, H.S., Zammit, R., Heckenmeyer, E. & Lizée, M. (2011). *Inventaire départemental des cavités souterraines hors mines du Bas-Rhin*.
- Nowicki, F., Dadu, L., Carsignol, J., Bretau, J.-F. & Bielsa, S. (2008). Rapport bibliographique : Routes et chiroptères Etat des connaissances. *Les Rapp.*, 1–253.
- Odonat : Office des données naturalistes du Grand-Est. (2017). Atlas des espèces d'Alsace [WWW Document]. www.faune-alsace.org. URL http://www.faune-alsace.org/index.php?m_id=620
- Poschlod, P., Bakker, J.P. & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic Appl. Ecol.*, 6, 93–98.
- Redon (de), L., Le Viol, I., Jiguet, F., Machon, N., Scher, O. & Kerbiriou, C. (2015). Road network in an agrarian landscape: Potential habitat, corridor or barrier for small mammals? *Acta Oecologica*, 62, 58–65.

- Remonti, L., Balestrieri, A. & Prigioni, C. (2006). Factors determining badger *Meles meles* sett location in agricultural ecosystems of NW Italy. *Folia Zool.*, 55.1, 19–27.
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.*, 27, 265–71.
- Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.*, 39, 157–176.
- Rondinini, C., Ercoli, V. & Boitani, L. (2006). Habitat use and preference by polecats (*Mustela putorius* L.) in a Mediterranean agricultural landscape. *J. Zool.*, 269, 213–219.
- Roper, T.J. (1992). The structure and function of badger setts. *J. Zool.*, 227, 691–694.
- Roper, T.J., Tait, A.I., Fee, D. & Christian, S.F. (1991). Internal structure and contents of three badger (*Meles meles*) setts. *J. Zool.*, 225, 115–124.
- Sachanowicz, K. & Zub, K. (2002). Numbers of hibernating *Barbastella barbastellus* (Schreber, 1774) (Chiroptera, Vespertilionidae) and thermal conditions in military bunkers. *Mamm. Biol. - Zeitschrift für Säugetierkd.*, 67, 179–184.
- Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*, 21, 464–71.
- Sheperd, B.F. & Swihart, R.K. (1995). Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. *Can. J. Zool.*, 73, 2098–2105.
- Théou, P. & Bego, F. (2013). *Etude des populations de chiroptères de l'île de Sazani. Note naturaliste Initiative PIM.*
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecol. Lett.*, 8, 857–874.
- Velli, E., Bologna, M.A., Silvia, C., Ragni, B. & Randi, E. (2015). Non-invasive monitoring of the European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three different monitoring techniques and evaluation of their integration. *Eur. J. Wildl. Res.*, 61, 657–668.
- Warchałowski, M., Łupicki, D., Cichocki, J., Pietraszko, M., Rusek, A., Zawadzka, A. & Nikodem, M. (2013). Zimowanie nietoperzy Chiroptera w wybranych obiektach wolno stojących Frontu Fortecznego Łuku Odry i Warty. *Kulon*, 18, 139–147.
- van der Well, L. & van Beveren, A. (2016). Bunkersite.com [WWW Document]. URL <http://bunkersite.com/index.php>
- Wretenberg, J., Pärt, T. & Berg, Å. (2010). Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biol. Conserv.*, 143, 375–381.
- Zduniak, P., Czechowski, P. & Jedro, G. (2011). The effect of nesting habitat on reproductive output of the Barn Swallow (*Hirundo rustica*). A comparative study of populations from atypical and typical nesting habitats in western Poland. *BELGIAN J. Zool.*, 141, 38–43.
- Zollner, P.A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landsc. Ecol.*, 15, 523–533.

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

Jonathan Jumeau^{1,2,3†}, Déborah Wolf², Léo Guthmann², Nicolas Gorlero², Françoise Burel³, Yves Handrich¹

¹ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

² Conseil Départemental du Bas-Rhin, Place du Quartier Blanc, 67964 Strasbourg, Cedex 9, France

³ Université de Rennes 1, CNRS, UMR 6553 ECOBIO, 35042 Rennes Cedex, France

Running Title: New homes for badgers and foxes

Abstract

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

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

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

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

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

† Corresponding author. Tel.: +33 06 07 62 33 63

E-mail address: jumeau.jonathan@gmail.com

Introduction

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

of the war. For example, 700 000 bunkers were built in Albania in the second half of the 20th century (Bajrovic & Satter 2014; Ayers & Parangoni 2015). On a local scale, bunkers are clustered in small defensive lines located near strategic locations.

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

Few studies have explored the impact of bunkers on biodiversity. The reduced variations of temperatures in the wells of bunkers make them an ideal hibernation site for the Barbastelle bat (*Barbastella barbastellus*) (Sachanowicz & Zub 2002). In Germany, the one hundred bunkers and 32 kilometres of galleries making up the Festungsfront Oder-Warthe-Bogen bunker network are colonized by 37 000 bats from ten different species, possibly making it the artificial structure hosting the highest number of individuals in Europe (Warchałowski et al. 2013; Jan Cichocki in AFP 2014). Small terrestrial mammals like the edible dormouse (*Glis glis*) also colonize bunkers (Ciechanowski & Sachanowicz 2014).

Bunkers can improve the quality of life and the survival of birds such as the common starling (*Sturnus vulgaris* ; Evans, Ardia, & Flux, 2009) or the barn swallow (*Hirundo rustica* ; Zduniak, Czechowski, & Jedro, 2011). However, bunkers do not generally appear to be an optimal habitat. This is illustrated by an Albanian island where chiropterans were rare despite an abundance of bunkers; however, the rarity of this species on the island may also be explained by the remoteness of the island and the good habitat quality on the mainland (Théou & Bego 2013). To our knowledge, only one study has focused on the presence of carnivores in bunkers (Crossland & Schöne 2007).

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

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

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

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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.

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

Materials and methods

Protocol

Studied area and bunkers

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

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

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

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

Local variables

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

were found by chance were also inspected. Geolocation was carried out using GPS (Bushnell Backtrack D-Tour). Freshness of evidence and the actual use of burrows were confirmed with a second visit to each bunker one month after the initial visit. The relative position of each burrow (inside or outside the bunker) was noted, as well as the type of badger sett ("central sett" including main, annexe and subsidiary burrows if they had three or more entrances and "outlier sett" if they had one or two entrances). The landscape type in which bunkers were found was also written down for each of them (*Forest, Grove* or *Crops*). We evaluated the accessibility of each bunker as follows:

- *Underground*: the bunker was entirely or almost entirely buried and all the entrances created by humans were underground. Only the roof was visible. No animal could reach it without digging;
- *Partially buried*: the bunker was partially buried and had one or more entrances created by humans where carnivorous species of the studied area could enter, but humans could not gain access without crawling;
- *Overground*: the bunker had at least one large human-made entrance that allowed easy access to both carnivores and humans.

Landscape analysis

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

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

Analysis

Method

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

Statistics

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

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

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

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

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

Results

Characteristics of bunkers

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

Table 1: Number of studied bunkers per accessibility type and main surrounding 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

Use of bunkers

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

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

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

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

Landscape analysis

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

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

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

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

The effect of accessibility

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

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

Comparison of groves with and without a bunker.

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

Discussion

Bunkers as habitat

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

The abundance of badgers in the studied area may be lower than that of foxes, as 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 km² 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.

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

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

Distribution of bunkers in the studied area

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

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

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

Towards an ecological management of bunkers

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

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

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

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

Conclusion

Bunkers are widely used as shelters by red foxes and European badgers. However, a high proportion of these military structures, especially on farmland, are in poor condition for their use as a habitat. The present study provides the necessary information to significantly improve the habitat potentiality of bunkers for the two most representative fossorial carnivore species living on Western European farmlands. Knowing the high number of bunkers concerned and their relatively equal distribution in the studied area, their management could help to slow the inexorable deterioration and homogenisation of the agricultural landscape.

Acknowledgements

We thank all the students who participated in this study and the anonymous reviewers for their comments on the previous version of this manuscript. We also thank Joanna Lignot and Lana Petrod for the English editing.

Author Contributions

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

Role of the funding source

This study was conducted through the CERISE project research and was funded by the French Minister of Ecology (DREAL Alsace) and the Departmental Council of the Bas-Rhin (CD67). They had no role in the study design, writing, collection, analysis and interpretation of data. They agree to the publication of this study.

Bibliography

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

- Bajrovic, I. & Satter, J. (2014). Albania: from bunkers to ballots. *J. Democr.*, 25, 142–153.
- Balestrieri, A., Cardarelli, E., Pandini, M., Remonti, L., Saino, N. & Prigioni, C. (2016). Spatial organisation of European badger (*Meles meles*) in northern Italy as assessed by camera-trapping. *Eur. J. Wildl. Res.*, 62, 219–226.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. & Edwards, P.J. (2008). Indicators for biodiversity in agricultural landscapes: A pan-European study. *J. Appl. Ecol.*, 45, 141–150.
- Bonfanti, P., Fregonese, A. & Sigura, M. (1997). Landscape analysis in areas affected by land consolidation. *Landsc. Urban Plan.*, 37, 91–98.
- Butet, A. & Leroux, A.B.A. (2001). Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biol. Conserv.*, 100, 289–295.
- Ciechanowski, M. & Sachanowicz, K. (2014). Fat Dormouse *Glis glis* (Rodentia: Gliridae) in Albania: Synopsis of Distributional Records with Notes on Habitat Use. *Acta Zool. Bulg.*, 66, 39–42.
- CIGAL. (2013). Données faune Alsace [WWW Document]. *Coopération pour l'information géographique en Alsace*. URL <https://www.cigalsace.org/portail/>
- Crossland, D. & Schöne, S. (2007). From Wehrmacht to Wildcats: World War II Bunkers Turn Into Wildlife Haven [WWW Document]. *SPIEGEL ONLINE*. URL <http://www.spiegel.de/international/germany/from-wehrmacht-to-wildcats-world-war-ii-bunkers-turn-into-wildlife-haven-a-507880.html>
- Davison, J., Huck, M., Delahay, R.J. & Roper, T.J. (2008). Urban badger setts: characteristics, patterns of use and management implications. *J. Zool.*, 275, 190–200.
- Desjeux, Y., Dupraz, P., Kuhlman, T., Paracchini, M.L., Michels, R., Maignan, E. & Reinhard, S. (2014). Evaluating the impact of rural development measures on nature value indicators at different spatial levels: Application to France and the Netherlands. *Ecol. Indic.*, 59, 41–61.
- DeVault, T.L., Olson, Z.H., Beasley, J.C. & Rhodes, O.E. (2011). Mesopredators dominate competition for carrion in an agricultural landscape. *Basic Appl. Ecol.*, 12, 268–274.
- Dondina, O., Kataoka, L., Orioli, V. & Bani, L. (2016). How to manage hedgerows as effective ecological corridors for mammals: A two-species approach. *Agric. Ecosyst. Environ.*, 231, 283–290.
- Duelli, P. & Obrist, M.K. (2003). Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic Appl. Ecol.*, 4, 129–138.

- Evans, L.E., Ardia, D.R. & Flux, J.E.C. (2009). Breeding synchrony through social stimulation in a spatially segregated population of European starlings. *Anim. Behav.*, 78, 671–675.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science* (80-.), 309, 570–4.
- Grashof-Bokdam, C.J. & van Langevelde, F. (2005). Green veining: Landscape determinants of biodiversity in European agricultural landscapes. *Landsc. Ecol.*, 20, 417–439.
- Hoffmann, M. & Sillero-Zubiri, C. (2016). *Vulpes vulpes*, Red Fox. *IUCN Red List Threat. Species 2016*, e.T23062A4, 1–10.
- Kaufmann, J. & Jurga, R. (1999). *Fortress Europe: European Fortifications Of World War II*. 1st edn. First Da Capo Press.
- König, C. (2013). Les ravageurs, menace pour nos céréales, 1–24.
- Kranz, A., Abramov, A.V., Herrero, J. & Maran, T. (2016). *Meles meles*. *IUCN Red List Threat. Species 2016*, 8235, e.T29673A45203002.
- Kurek, P., Kapusta, P. & Holeksa, J. (2013). Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecol. Res.*, 29, 1–11.
- Macdonald, D.W., Newman, C., Dean, J., Buesching, C.D. & Johnson, P.J. (2004). The distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field observations contradict the sett dispersion hypothesis. *Oikos*, 106, 295–307.
- Marton, M., Markolt, F., Szabo, L., Kozak, L., Lanszki, J., Patko, L. & Heltai, M. (2016). Den site selection of the European badger, *Meles meles* and the red fox, *Vulpes vulpes* in Hungary. *FOLIA Zool.*, 65, 72–79.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E.M. (2016). The ravages of guns, nets and bulldozers. *Nature*, 536, 146–145.
- Meia, J.-S. & Weber, J.-M. (1995). Home ranges and movements of red foxes in central Europe: stability despite environmental changes. *Can. J. Zool.*, 73, 1960–1966.
- Mermy, D.C., Guignat, H.S., Zammit, R., Heckenmeyer, E. & Lizée, M. (2011). *Inventaire départemental des cavités souterraines hors mines du Bas-Rhin*.
- Nowicki, F., Dadu, L., Carsignol, J., Bretau, J.-F. & Bielsa, S. (2008). Rapport bibliographique : Routes et chiroptères Etat des connaissances. *Les Rapp.*, 1–253.
- Odonat : Office des données naturalistes du Grand-Est. (2017). Atlas des espèces d'Alsace [WWW Document]. www.faune-alsace.org. URL http://www.faune-alsace.org/index.php?m_id=620
- Poschlod, P., Bakker, J.P. & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic Appl. Ecol.*, 6, 93–98.
- Redon (de), L., Le Viol, I., Jiguet, F., Machon, N., Scher, O. & Kerbiriou, C. (2015). Road network in an agrarian landscape: Potential habitat, corridor or barrier for small mammals? *Acta Oecologica*, 62, 58–65.

- Remonti, L., Balestrieri, A. & Prigioni, C. (2006). Factors determining badger *Meles meles* sett location in agricultural ecosystems of NW Italy. *Folia Zool.*, 55.1, 19–27.
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.*, 27, 265–71.
- Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.*, 39, 157–176.
- Rondinini, C., Ercoli, V. & Boitani, L. (2006). Habitat use and preference by polecats (*Mustela putorius* L.) in a Mediterranean agricultural landscape. *J. Zool.*, 269, 213–219.
- Roper, T.J. (1992). The structure and function of badger setts. *J. Zool.*, 227, 691–694.
- Roper, T.J., Tait, A.I., Fee, D. & Christian, S.F. (1991). Internal structure and contents of three badger (*Meles meles*) setts. *J. Zool.*, 225, 115–124.
- Sachanowicz, K. & Zub, K. (2002). Numbers of hibernating *Barbastella barbastellus* (Schreber, 1774) (Chiroptera, Vespertilionidae) and thermal conditions in military bunkers. *Mamm. Biol. - Zeitschrift für Säugetierkd.*, 67, 179–184.
- Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*, 21, 464–71.
- Sheperd, B.F. & Swihart, R.K. (1995). Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. *Can. J. Zool.*, 73, 2098–2105.
- Théou, P. & Bego, F. (2013). *Etude des populations de chiroptères de l'île de Sazani. Note naturaliste Initiative PIM.*
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecol. Lett.*, 8, 857–874.
- Velli, E., Bologna, M.A., Silvia, C., Ragni, B. & Randi, E. (2015). Non-invasive monitoring of the European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three different monitoring techniques and evaluation of their integration. *Eur. J. Wildl. Res.*, 61, 657–668.
- Warchałowski, M., Łupicki, D., Cichocki, J., Pietraszko, M., Rusek, A., Zawadzka, A. & Nikodem, M. (2013). Zimowanie nietoperzy Chiroptera w wybranych obiektach wolno stojących Frontu Fortecznego Łuku Odry i Warty. *Kulon*, 18, 139–147.
- van der Well, L. & van Beveren, A. (2016). Bunkersite.com [WWW Document]. URL <http://bunkersite.com/index.php>
- Wretenberg, J., Pärt, T. & Berg, Å. (2010). Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biol. Conserv.*, 143, 375–381.
- Zduniak, P., Czechowski, P. & Jedro, G. (2011). The effect of nesting habitat on reproductive output of the Barn Swallow (*Hirundo rustica*). A comparative study of populations from atypical and typical nesting habitats in western Poland. *BELGIAN J. Zool.*, 141, 38–43.
- Zollner, P.A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landsc. Ecol.*, 15, 523–533.

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Table 1: *Number of studied bunkers per accessibility type and main surrounding 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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Figure 1: *Location of defensive lines in Europe* (according to Kaufmann & Jurga 1999).

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

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.