



Increasing brown hare (*Lepus europaeus*) densities in farmland without predator culling: results of a field experiment in Switzerland

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Abstract

In a field experiment in Northwestern Switzerland, we managed one part of each of four experimental areas in order to improve leveret (*Lepus europaeus*) survival and used the remaining part as control. The experimental areas were dominated by arable farming with a high diversity of different crops. Potential leveret predators were numerous and not controlled by gamekeeping. Management elements were wildflower patches, partly with an optimized antipredator design, and wider-sown cereals (to allow hares to enter the fields from May to July). We assumed that leverets are relatively safe in these two types of fields because these are seldom processed by agricultural machinery and potential leveret predators rarely forage there. The management lasted 7 years in two experimental areas and 3 years in the other two. Hare numbers and locations were monitored by spotlight counts, starting at least 3 years before the beginning of the experiment. In three out of the four experimental areas, we found a more positive development of hare densities in the managed area compared to the control area. Furthermore, the distribution of the hares within the experimental areas could be best described by a model including the percentage of wildflower patches, the percentage of arable land, and the percentage of cereals in wider-sown rows suggesting that hares predominantly occupied the surroundings of the management elements. We conclude that—irrespective of high predator densities—brown hare populations in agricultural landscapes with previously low hare densities can be considerably increased by offering a total area of about 3% wider-sown winter cereals or wildflower patches within the agriculturally used area.

Keywords Brown hare (*Lepus europaeus*) · Field experiment · Agriculture · Predation

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Introduction

Differences in population densities of brown hare (*Lepus europaeus*) in time and space are strongly influenced by different survival of leverets (Keith 1981; Pépin 1989; Marboutin et al. 2003). Most common causes of mortality in leverets are wet weather (Hackländer et al. 2002a; Hoffmann 2003; Smith et al. 2005), agricultural machinery (Kaluzinski and Pielowski 1976; Milanov 1996), and predation by foxes *Vulpes vulpes* (Reynolds and Tapper 1995) or other carnivore mammals (wild and domestic), raptors of about the size of a buzzard, larger owl species, corvids, and wild boar *Sus scrofa* (Averianov et al., 2003). In the only published study that compared these mortality factors in leverets, predators were the most important mortality factor in northern Germany (Voigt 2010). Leveret mortality in different agricultural landscapes between birth and the start of the hunting season in autumn was estimated 71–84% (Pielowski 1975), 63–95% (Möller 1977), 73–84% (Frylestam 1980), 70–80% (Hansen 1992), 50–75% (Pépin 1989), and 71–86% (Marboutin et al. 2003).

Considering both the importance of leveret mortality for hare population density and the role of predators as mortality factor, systematic culling of predators is a traditional and often successful management tool to improve brown hare populations in parts of Europe like England (Reynolds and Tapper 1996; Tapper and Yalden 2010) or Germany (Kalchreuther 2003; Spittler 2014). Panek et al. (2006) have demonstrated the positive influence of fox culling on brown hare populations in Poland, and field experiments in England have shown that hare density can be increased by professional “gamekeeping” (systematic culling of foxes, cats, stoats, crows, and other carnivores; Reynolds et al. 2010).

To be effective, culling must be done rigorously (Reynolds and Tapper 1996). To increase brown hare density from 12 to 48 per km² in a total area of 35 km² in northern Germany, a total of 234 foxes, 864 cats, 836 stoats, 766 weasels, and 1129 crows and magpies had to be killed within 10 years (Kalchreuther 2003). In Northwestern Switzerland, there is no tradition of gamekeeping. Stoats and weasels are protected by law and systematically shooting the numerous domestic cats in the fields would not be tolerated by the people living in the countryside in Switzerland. In addition, culling makes only sense when perpetuated continuously; when gamekeeping is stopped, or reduced in effort, predator numbers immediately recover and hare numbers start decreasing (Reynolds et al. 2010). For these reasons, but also because we find it questionable to cull great numbers of predators only to increase the density of one popular target species, we tried to find alternatives to increase hare densities.

Instead of reducing the number of potential predators, we tried to increase the area where leverets are relatively safe from predators. Fernex et al. (2011) showed that potential leveret predators explore mainly the margins of different types of fields and also the inner parts of meadows and bare or freshly tilled fields, but to a lesser extent the inner parts of cereal fields and wildflower patches. A higher activity of predators at the margins compared to the inner parts of wildflower patches was also shown by Hummel et al. 2017. Additionally, wildflower patches near forests, hedges, and settlement areas are more often visited by predators than those in greater distance to these structures (Hummel et al. (2017). The inner parts of cereal fields are not only rarely visited by predators, but in addition, the risk of injury by agricultural machinery is almost absent until harvest. The problem with these fields is the dense stand of the crops, making it difficult to be entered by hares from May until harvest in July (Rühe 1999). These are the months with the highest numbers of leverets (Marboutin et al. 2003). Our hypothesis was that leveret survival and thereby brown hare numbers can be positively influenced by making cereal fields accessible to hares in spring and summer, by increasing the percentage of wildflower patches in a given area and by optimizing their margin-to-inner-relation and their placement in the landscape. To

examine this hypothesis, we motivated farmers to offer the above-mentioned types of land-use in four experimental areas. We analysed whether the subsequent changes in hare numbers in these managed areas were larger than in the adjoining control areas, where normal land use continued. We further inferred the spatial distribution of hares within the study area and asked whether hares predominantly occupied the land-use types that we assumed to be accessible to hares in spring and summer.

Material and methods

Study areas

We chose five study areas amongst the 58 sites of the Swiss brown hare monitoring (SBHM, Zellweger-Fischer et al. 2011), located in intensively used farmland of the Swiss lowland. Each study area consisted of two or three plots. Except for the study area “Wenslingen” (see below), the land-use of one plot per study areas was managed in favour of brown hares (i.e. managed plots), while the land-use of the remaining plots did not receive a special management (i.e. control plots). Because farmers assisted the projects on a voluntary basis, the choice of managed and control plots within each study area was not random. As managed plot, we have chosen the plots where we first found sufficient participants amongst the local farmers. For the study area “Wenslingen” we did not find enough farmers that agreed to take part in the project. The study thus included 14 plots distributed over five study areas with one managed plot in four of the five study areas (Fig. 1). The five study areas were (1) “Reinach” (identification codes: “BL02 HOPPHASE”, “BL02REST”, “BL07Z”), 47° 28' 50 N–7° 35' 08 E; (2) “Laufen” (“BL05 HOPPHASE”, “BL05”, “BL05Z”), 47° 25' 15 N–7° 31' 32 E; (3) “Aristau” (“AG02”, “AG03”, “AG04”), 47° 17' 31 N–8° 22' 23 E; (4) “Selzach” (“SO01”, “SO02”, “BE20”), 47° 11' 52 N–7° 28' 12 E; and (5) “Wenslingen” (“BL04”, “BL06Z”) 47° 26' N,–7° 54' E. Aerial views with exact delimitations of experimental and control areas for the four study areas with managed plots are given as supplementary material (Appendix A). The climate of all study areas is influenced by the Atlantic Ocean with mild winters and precipitations in all months with a maximum from May to August (for temperatures see Table 1).

All study areas are intensively cultivated with mainly arable production and a smaller proportion of permanent grassland for dairy farming. Some small pieces of forest, hedges, and small creeks lay between the fields. In Switzerland, an agri-environmental scheme (AES) with several types of ecological compensation areas (ECA) was introduced in 1993, including meadows farmed at a low intensity, traditional orchards, hedgerows, and wild flower areas (Zellweger-Fischer et al. 2011). Local authorities further promote ECA.

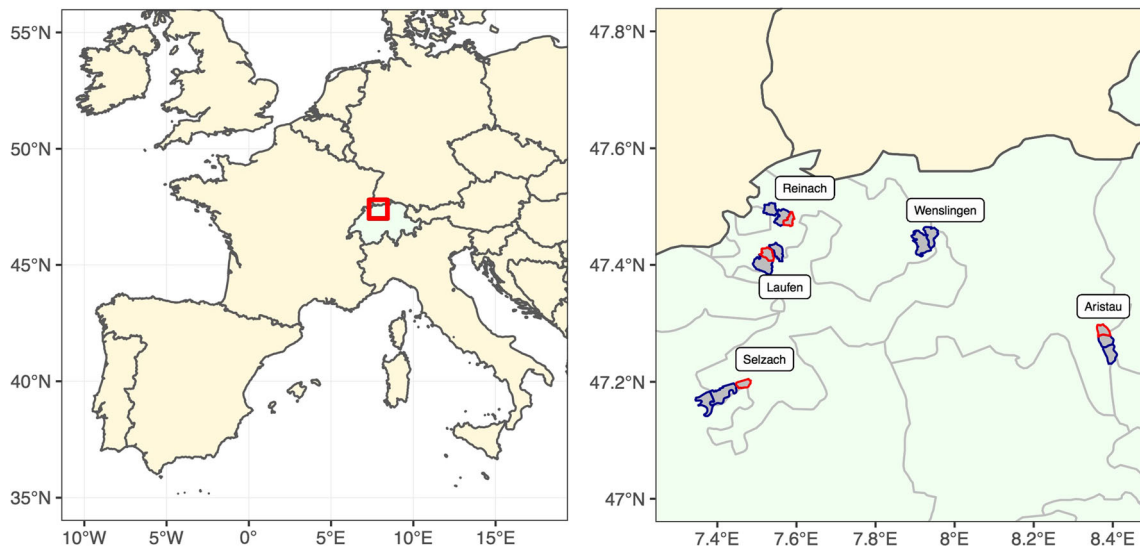


Fig. 1 Location of Northwestern Switzerland in Europe (left side) and the the experimental areas in Northwestern Switzerland (right side). Managed areas are displayed in red and control areas blue respectively. Note that there was no managed area in “Wenslingen”

The intensity of arable production is generally comparable to the neighbouring EU countries, but due to ownership structure and topography, most fields are smaller in the Swiss lowland compared to those in Germany or France (around 1 ha, Meichtry-Stier et al. 2014). Since 1999, the proof of ecological performance (PEP) is a precondition for Swiss farmers to get any subsidies. The PEP includes regulations for crop rotation and fertilizing. At least 7% of a farm’s utilised agricultural area has to be managed as ECA. Each farm must cultivate in any year at least four different crops. Five- to 7-year rotations

with often 2 years improved grassland are common. As a consequence, in most lowland regions between 20% and 40% of the arable area consists of improved grassland. Small-field sizes and complex rotations result in a mosaic of different crops (see aerial photos in the [supplementary material](#)). Table 1 gives some information on land use in the study areas.

There has been no hunting of brown hares in the study areas for many years. Except for the managed plot in “Selzach”, hare densities at the beginning of the experiment

Table 1 Some characteristics of the study areas. All data about land use are from own mappings in 2015 (parts of control areas in 2010). Temperatures are from the nearest meteorological stations of MeteoSchweiz 1981–2010 (MeteoSchweiz 2018). Total land used for agriculture in “Aristau” and “Selzach” control areas are from Zellweger-Fischer 1015. Densities of foxes are from the original field protocols of the

Swiss brown hare monitoring (two spotlight counts at each site every year in early spring, see Zellweger-Fischer 2015) and not corrected for imperfect detection. Hare densities are calculated from more than two spotlight counts for most areas (see methods section); data for “Reinach” and “Laufen” for winters 2007/08, 2008/09, and 2009/10 and for “Aristau” and “Selzach” for Winters 2010/2011, 2011/12, and 2012/13

Study areas	Reinach		Laufen		Aristau		Selzach	
	Man	Cont	Man	Cont	Man	Cont	Man	Cont
Altitude (m above sea level at centre)	311	315	432	405	381	385	429	430
Mean annual temperature (°C)	10.5	10.5	9.1	9.1	9.6	9.6	9.0	9.0
Mean temperature January (°C)	1.6	1.6	0.2	0.2	0.5	0.5	0.0	0.0
Mean temperature July (°C)	19.7	19.7	18.4	18.4	19.0	19.0	18.5	18.5
Total land used for agriculture (ha)	185	770	347	858	324	1059	290	1810
Proportion arable (improved grassland excluded)	0.36	0.53	0.38	0.29	0.34	–	0.74	–
Proportion cereals	0.20	0.24	0.24	0.20	0.13	–	0.44	–
proportion grassland (improved and unimproved)	0.49	0.37	0.54	0.66	0.52	–	0.21	–
Proportion wildflower strips	0.08	0.01	0.04	0.02	0.01	–	0.01	–
Mean density of foxes seen during hare counts (ind/km ²)	2.1	3.3	1.9	2.4	3.8	–	1.6	–
Mean hare density before experiment (ind/km ²)	3.6	2.7	1.8	1.2	6.2	4.8	17.7	8.4

were low (Table 1) when compared to other lowland farming areas in Europe (Averianov et al. 2003), but comparable to other parts of lowland Switzerland (Zellweger-Fischer 2015).

Predators

Potential leveret predators upon leverets at the study sites are badger (*Meles meles*), stone marten (*Martes foina*), domestic cat (*Felis silvestris catus*), domestic dog (*Canis lupus familiaris*), pine marten (*Martes martes*), European polecat (*Mustela putorius*), red fox (*Vulpes vulpes*), wild boar (*Sus scrofa*), black kite (*Milvus migrans*), carrion crow (*Corvus corone*), common buzzard (*Buteo buteo*), raven (*Corvus corax*), eagle owl (*Bubo bubo*), grey heron (*Ardea cinerea*), kestrel (*Falco tinnunculus*), long-eared owl (*Asio otus*), red kite (*Milvus milvus*), rook (*Corvus frugilegus*), tawny owl (*Strix aluco*), white stork (*Ciconia ciconia*) (Fernex et al. 2011), stoat (*Mustela erminea*), weasel (*Mustela nivalis*), and wild cat (*Felis silvestris*) (author's unpublished data).

Traditionally, there exists no systematic gamekeeping in Northwestern Switzerland, and trapping is not practised at all. The local hunters shot occasionally some foxes (*Vulpes vulpes*), badgers (*Meles meles*), and exceptionally also stone martens (*Martes foina*) (see Table 2). Only in one of the four experimental sites ("Laufen"), the numbers of foxes and badgers shot was higher than the numbers of predators found dead. Cats, stoats, weasels, pine martens, and polecats were not hunted at all. Carrion crows were regularly shot, mainly from flocks of non-breeders. However, there was little effect of this shooting on the overall density of carrion crows. The mean number of 410 crows shot per year from 2006 to 2015 in the 518 km² of the canton Basel-Landschaft corresponds to only 8% of the estimated breeding population (2000–3000 breeding pairs, unpublished estimation from the Swiss breeding bird atlas team); the high but unknown number of non-breeding flocking crows is not included in this calculation.

Because of favourable habitats and low hunting pressure, densities of predators are high (see Table 1 for foxes seen during spotlight counts). As only a part of the fox population is visible during the spotlight counts in a mixed landscape

which includes small forests, hedges, and built-over areas, Table 1 underestimates winter densities of foxes. All experimental areas are surrounded by residential areas and interspersed by farms, which results in many cats and dogs in the fields. However, we have no data on their numbers and the time they spend there. In the study by Fernex et al. (2011) done in the study area "Reinach", about twice as much baits were found in the fields by cats and free-running dogs compared to foxes, which gives an idea on the frequent presence of these potential leveret predators. Camera traps placed close to wildflower strips throughout the canton Basel-Landschaft (including the study areas "Reinach" and "Laufen") recorded the following relative abundance of predators (given are percentages of all records of predators): cats (44%), foxes (24%), badgers (14%), and dogs (5%) (Hummel et al. 2017).

Unpublished data of D. Weber and N. Beerli from a study site of 18 ha within the "Reinach" managed area revealed an average number of 4.8 carrion crows, 0.4 white storks, and 0.6 Grey herons present during daytime from April to August. This figure translates to 27 crows, 2.2 storks, and 3.3 herons per 100 ha. Twenty-seven crows is a bit more than the estimated average density of about ten breeding pairs per 100 ha for all study areas (Knaus et al. 2018). The difference can be explained by the occasional presence of flocks of non-breeders.

Hare-friendly agricultural practices

Cereals in wider-sown rows: autumn-sown cereals (mainly wheat, but also barley) were sown using seed drills manipulated in such a way, that after three sown rows, the next two rows were omitted, followed by three rows, two lacking rows and so on. This resulted in cereal fields with a striped pattern, and the use of only 60% of the normal seed quantity per surface unit (see Fig. 2). We made no further restrictions to the treatment of the wider-sown cereal fields. Fertilizing was alike as in normal cereal fields, and most of the experimental fields received one herbicide treatment in early spring. In accordance with the common practice in the experimental areas, growth regulators, insecticides, and fungicides were not used

Table 2 Hunting pressure upon predators and at the study areas. Data from the reports of the hunting societies to the state administration for the years 2006–2015 (Reinach), 2009–2015 (Laufen), 2010–2015 (Aristau, Selzach)

Study areas	Reinach	Laufen	Aristau	Selzach
Total area of hunting grounds including experim. site (ha)	1971	2261	1826	688
Mean number of foxes shot per year (ind/100 ha)	1.4	1.5	1.1	0.9
Mean number of foxes found dead per year (ind/100 ha)	1.4	0.7	1.2	1.4
Mean number of badgers shot per year (ind/100 ha)	0.5	0.5	0.1	0.0
Mean number of badgers found dead per year (ind/100 ha)	0.4	0.1	0.1	0.3
Mean number of stone martens shot per year (ind/100 ha)	0.0	0.0	0.0	0.1
Mean number of stone martens dead per year (ind/100 ha)	0.3	0.1	0.0	0.2



Fig. 2 Winter wheat in wider-sown rows in the “Reinach” managed area in spring. Also note the wildflower patch in the background on the right

in the majority of the experimental fields. The locations of the experimental cereal fields were chosen by the farmers amongst the cereal fields according to their long-term rotation scheme. Although farmers were offered a compensation for their extra work and cost and the presumptive loss in yield, it was difficult to find enough participants. Therefore, we did not achieve the desired total of about 3% of the agriculturally used area as wider-sown cereals in all of the four managed experimental sites at the beginning of the experiment. On the other side, we allowed some highly motivated farmers to also implement wider-sown cereals in nearby areas of the control sites. After 4 years, wider-sown cereals were given up as a management tool in the “Laufen” experimental area in order to have one experimental area with only wildflower patches as a management tool and also due to limited financial resources. The percentage of cereals in wider-sown rows in the experimental areas in every year is given in Table 3.

Wildflower patches Wildflower areas, mostly implemented as strips of a few meters large, are a part of the established Swiss agri-environmental scheme. They are often about 6 m large and sown with a prescribed wildflower mix (Zellweger-Fischer et al. 2011). Farmers are obligated to let them more or less untouched for a period of 6 to 8 years. We asked farmers in the “Reinach” and “Laufen” management plots to increase the area of wildflower strips, to improve their outline (forming shorter but larger patches) and to install them at places with low predation pressure (not alongside forests, hedges, watercourses roads, and tracks). Due to the long contractual periods (6 to 8 years) and a limited motivation to implement wildflower patches, this transformation was a slow process. In “Reinach”, with a high proportion already at the beginning of the experiment; the proportion of wildflower areas increased from 6.4% (2008) to 7.6% (2015) of the total land used for agriculture. Due to the better shape of the patches, the proportion of “inner” area of wildflower patches (> 5 m distance to the margin) increased from 3.7% (2008) to 4.9% (2015) of the total land used for agriculture. In “Laufen”, wildflower areas increased from 1.6% (2008) to 3.7% (2015), whereas the proportion of “inner” wildflower area increased from 0.6 (2008) to 2.4% (2015).

Additional measures To prevent the numerous domestic dogs from entering cereal fields, some of them (wider-sown ones and others) were electrically fenced in the “Reinach” managed plot (two electric wires 30 cm and 70 cm above ground) from January or February until April in the years 2012 to 2015. Fencing encompassed 5.6 ha on average (3.0% of the land used for agriculture). In 2012 and 2013, there was an additional fenced area in the “Reinach” control plots (2.7% of the total land used for agriculture). From 2008 to 2013, a farmer in the “Laufen” managed plot tested several measures for hay

Table 3 Total area of cereals in wider-sown rows in the different years of the experiment as a percentage of the total area used for agriculture

Study areas	Reinach		Laufen		Aristau		Selzach	
	Man	Cont	Man	Cont	Man	Cont	Man	Cont
Experimental treatment (managed or control)								
Wider-sown cereals in 2008 (year of harvest), % of site	0	0	0	0	0	0	0	0
Wider-sown cereals in 2009 (year of harvest), % of site	1.9	0	0	0	0	0	0	0
Wider-sown cereals in 2010 (year of harvest), % of site	0	0	1.4	0	0	0	0	0
Wider-sown cereals in 2011 (year of harvest), % of site	2.1	0	1.8	0.3	0	0	0	0
Wider-sown cereals in 2012 (year of harvest), % of site	2.9	0	1.9	0.3	0	0	0	0
Wider-sown cereals in 2013 (year of harvest), % of site	2.7	0.5	1.8	0.3	1.1	0	2.6	0
Wider-sown cereals in 2014 (year of harvest), % of site	3.2	0.9	0	0	1.6	0	4.7	0
Wider-sown cereals in 2015 (year of harvest), % of site	2.1	0.1	0	0	3.4	0	3.4	0

meadow cultivation intended to protect leverets from mowing machines on 4.1 to 4.8% of the total land used for agriculture. Because no positive effect on hare distribution or numbers was detected, these measures in the hay meadows of “Laufen” were not continued.

Land-use mapping

The land use was classified and mapped on-site with the help of a land register map and aerial photographs. The classification comprised 29 habitat types (see Schai-Braun et al. 2013). Land-use mapping was done in 2009, 2010, and 2011 in both “Reinach” and “Laufen” managed and control areas, in 2013, 2014, and 2015 in the managed areas of “Reinach”, “Aristau”, and “Selzach” and a large part of the “Reinach” control area, and in 2015 in the “Laufen” managed and control area. Land use maps were digitized using a geographic information system (GIS; ESRI 2015. ArcGIS Desktop: Release 10.3.3. Redlands, CA: Environmental Systems Research Institute).

Hare numbers and locations

As a part of the Swiss brown hare monitoring (SBHM, Zellweger-Fischer et al. 2011), spotlight counts were done after dusk in the agricultural land on roads from a car driving at a speed of about 10 km per hour in all experimental areas twice between late February and early April in every year. Spotlight counting transects were fixed and not changed during the study. The position of each hare was mapped and later digitized. A facsimile of an original field protocol showing transect route and mapped animals is given as supplementary material in appendix A. SBHM-transects were defined based on the existing road network in a way that should allow to illuminate and observe the complete agricultural land of the study area. However, due to sight obstacles like hedgerows and tall vegetation on some fields and to varied topography, parts of the study area were not illuminated by the spotlight and therefore, some of the hares present in the experimental areas escaped detection. As a consequence, the degree of hare-detectability is partly site-specific. According to Dietrich (2010), between 20 and 90% of the total number of hares present are seen in the standard spotlight counts of the SBHM. For analysis, hare counts therefore should be corrected for imperfect detection (see below).

Two additional spotlight counts on the same transects were made in the managed areas and in several years in the control areas “Reinach” and “Laufen” between mid-October and mid-December and additional spotlight counts, mainly in the managed areas, were made in winter when possible to increase the reliability of the data. The total number of spotlight counts from 2006/07 to 2015/16 is 49 in “Reinach” managed area, 47 in “Laufen” managed area, 39 in “Reinach” control area, and 33 in “Laufen” control area. In the other experimental

areas, these figures are (from 2013/14 to 2015/16): 16 in “Aristau” managed area, 15 in “Selzach” managed area, and 6 in both “Aristau” and “Selzach” control areas.

Analysing total hare population over time

With this analysis, we aimed to test the hypothesis that hare populations increased more (or decreased less) after hare-friendly measures have been implemented in the managed plots compared to the trend in hare populations in control plots. Since the amount of cover for hares and thus the probability to detect hares may vary between study sites, we used a binomial-mixture model to estimate the total number of hares at a plot taking imperfect detection into account (Kéry and Royle 2015). An important prerequisite of binomial-mixture models are repeated counts within a period where one can assume a closed population (that is no hares die, emigrate, immigrate, or are born). We assumed that hare population in winter may be considered as closed, because in 33 cases from our five areas (including “Wenslingen”) for which we have hare counts from both late autumn and following spring, the average number of hares counted in spring was 1.02 times the number of hares counted in the preceding autumn (SE = 0.08). We thus used all hare counts of one winter in a given plot as repeated measurement of the total hare population in this plot during that winter. Since we assume a closed population, little variation in the repeated counts would suggest that detection probabilities are either very high (counts are always close to the true population size) or very low (counts are always close to zero). In contrast, strong variation in repeated counts would suggest intermediate or variable detection probabilities. Note that distance sampling, which is another method that is often used to account for detection probability in hare counts, does not depend on repeated counts. However, distance sampling usually assumes random distribution of hares with respect to the transect locations which is likely violated because detection probability in areas adjacent to roads/track seems lower than further away (Zellweger-Fischer et al. 2011). The general behaviour and assumptions of binomial-mixture models as well as the distinctions to distance-sampling are well explained in Kéry and Royle (2015), and binomial-mixture models have been applied to estimate hare populations in Switzerland (Zellweger-Fischer et al. 2011). Our model allowed the detection probabilities of hares to differ between study areas (i.e. an average detection probability is estimated per study area). Further, we allow the detection probability of each count to vary around the mean detection probability of the study area. For each plot, we separately estimated the total number of hares during the first winter (i.e. separate intercepts per each plot), but assumed that the temporal trend of hare populations was the same in the plots within a study area (i.e. separate linear trends for each study area). Further, we added a parameter to estimate how much the temporal trend

of the control areas (and the temporal trend prior to the implementation of the hare management) increased from the winter after hare-friendly measures were implemented. We estimated such a management effect for each study area separately.

To estimate the model parameters, we used the program JAGS, which is based on Markov-chain Monte Carlo methods (Plummer 2003). For all parameters, we used weakly informative priors (Gelman et al. 2017). For example, for the log-scale intercept of the average true numbers of hares, we used a normal distribution with mean = 2.3 and standard deviation = 1.5. This corresponds to a distribution with ten hares as the most likely value but a range of likely values that cover the range from about 1 to 200 hares. The entire model including the used prior distributions is written in the “BUGS” language and given in Appendix B. We ran two parallel chains and assessed convergence with the Gelman-Rubin Index (Brooks and Gelman 1998). We estimated the posterior distribution at 10,000 iterations, excluding the first 5000 and using only every second of the remaining iterations.

Analysing hare distribution across space

With this analysis, we aimed to infer whether land-use variables affected the spatial distribution of hares in winter. During hare counting, all hare observations were noted on a map, and it is these locations of hare observations that we analysed here. Note, that in contrast to the previous analyses, we do not account for the effect of detection probability although we are aware that hares are less likely to be detected further away from the transect line. The location of the different land-use types will be largely independent of the transect line, and we thus believe that issues of detection probability will not strongly bias the results.

A regular grid (500 m × 500 m) was laid over the entire study area. The cell size of 25 ha was chosen in the magnitude of small home-range sizes of European hares in agricultural landscapes (see for an overview Smith et al. 2005) and since other habitat analysis of hare distribution in Switzerland had chosen the same grid size (Schai-Braun et al. 2013; Meichtry-Stier et al. 2014), which allows good comparison of results. The grid was aligned with the Swiss coordinate system. Each grid cell with more than 50% in the study area and that had at least 10 ha of open land was used in the analysis. The limit of 10 ha was chosen arbitrarily in order to eliminate cells with open land which was much smaller than normal home-ranges of hares. Based on land-use mapping, we calculated the following parameters for each grid cell: share of arable land, share of cereals, share of cereals with gaps, share of wildflower patches, share of wildflower patches designed for hares, share of ecological meadows, and length of border lines formed by hedges and forests. The shares refer to the open land area within the study area. The average of the observed hare densities was also calculated for each grid cell. All data

were finally z -transformed so that the effect sizes could be compared between the variables (Schielzeth 2010).

The data were analysed with mixed linear models (LMM). The mean hare density per ha open area was the dependent variable. The above-mentioned land-use variables were included as predictor variables. In this analysis, we were interested how the hares were distributed according to the different land-use types available in the study regions, and we did not want to explain the differences in hare numbers between the regions. We thus subtracted region average from each measure of land-use share in a grid cell. The resulting numbers thus indicated whether the land-use share was below or above the regional average. In order to account for repeated measurement, the grid cell ID, the area, and the winter were additionally considered as three random effects in the model. The AIC was used as a criterion to gradually simplify the full model. The simplification was stopped when the difference in AIC was > 2 .

Results

The mean experimental area-specific model estimates for the detection probability p of a hare in one spotlight count were $p = 0.54$ (95%-credible interval 0.41–0.65) in “Reinach”, $p = 0.40$ (0.21–0.54) in “Laufen”, $p = 0.48$ (0.27–0.63) in “Aristau”, and $p = 0.51$ (0.36–0.67) in “Selzach”. The detection probability gives how likely we are to detect an average hare in the study sites. Thus, if there are ten hares present in the study site and we are likely to detect each of them with $p = 0.5$, then we will count in average five hares per spotlight count. Figure 3 shows the development of the estimated hare densities in the four study areas where hare management could be implemented both for the total of the managed and control plots. In three out of the four experimental areas, the total number of hares increased more after the implementation of hare management than in control plots. The difference in the temporal trend of the log transformed number of hares after the implementation of hare management minus the trend in control plots (values > 0 indicating management success) was 0.15 (95%-credible interval 0.03–0.27) for “Reinach”, 0.12 (–0.04–0.28) for “Laufen”, –0.18 (–0.54–0.20) for “Aristau” and 0.26 (0.04–0.47) for “Selzach”. So for “Selzach” and “Reinach” the trend attributable to management is definitely positive. For “Laufen”, it is probably positive but 95% credible intervals include zero. For “Aristau”, any management effect is small (Fig. 3) but definitely not positive.

Influences of different landscape elements on the winter distribution of the hares within the experimental areas and the “Wenslingen” site are given in Table 4. In the best model, the percentage of wildflower patches, the percentage of arable land, and the percentage of cereals in wider-sown rows

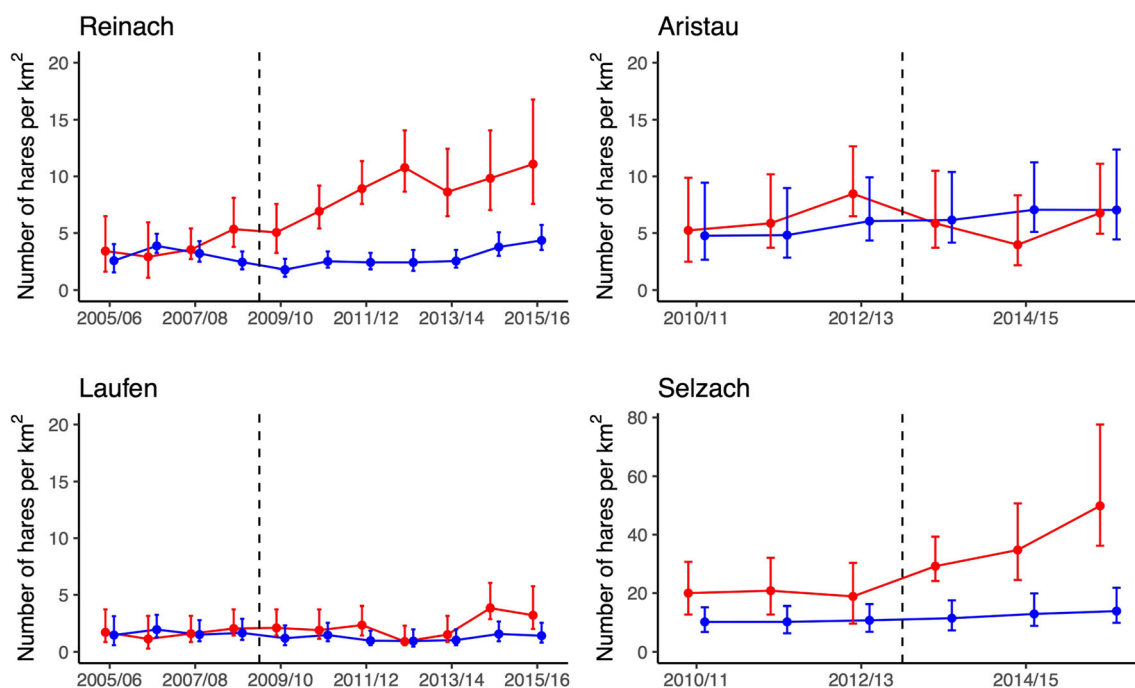


Fig. 3 Development of the estimated hare densities (number of hares per km² agriculturally used area in winter) over the study period in the four study areas where hare management could be implemented. Given are mean and 95%-credible intervals for the managed plots (red) and control

plots (blue). The vertical dashed lines give the starting of the hare management. Note the different scales for densities for the “Selzach” study area

positively influenced hare presence. The other variables tested had no strong influence (i.e. estimated effect size close to zero and a 95%-credible intervals that covered zero).

Discussion

We conclude from our experiment that in three out of four experimental areas, hare-friendly management led to a significant increase in hare densities within a few years. There was no need to reduce the high number of potential leveret predators to reach this result. We can only speculate about the reasons why the offer of wider-sown cereals had no positive

influence in the fourth experimental area “Aristau”. One obvious presumption is an insignificant quantity of wider-sown cereals in the first 2 years of the experiment (farmers contributed only 3.6 and 5.3 ha, about one half of the striven quantity of 10 ha; in the third year with 11 ha (3% of the managed area) of wider-sown cereals hare numbers started to increase). Further, the small population of hares in the managed areas at the beginning might have been influenced by stochastic events (about 8 individuals at the beginning in Laufen and about 24 in Aristau; Table 1). Such stochastic events may include wet weather in the days after the birth of leverets, a bad choice of the birth place by the female hare (ignoring different predation risks), accidental death of adult females,

Table 4 Explaining the winter distribution of hares within the study areas (including “Wenslingen”) in 500 m × 500 m grid cells with land use in the preceding summer using the best model. The column “in model” shows if a variable is part of the best model based on the AIC-

values. Effect strength is given based on the full model with all variables. *p* values of excluded variables have been estimated based on the last model which contained this variable

Variable	In model	Effect strength	<i>p</i> value
Area used as wildflower strips or patches (%)	Yes	0.004	0.03
Area used as arable land (%)	Yes	0.003	0.11
Area with wider-sown cereals (%)	Yes	0.003	0.04
Area used as isolated and large wildflower patches (%)	No	−0.001	0.43
Length of hedgerows and forest edges (m)	No	0.001	0.35
Area with cereals (normal + wider-sown) (%)	No	0.000	0.95
Area with extensively managed hay meadows (%)	No	0.000	0.99

diseases (e.g. several cases of tularemia were found in the “Laufen” area and its surroundings during our study), and others. Finally, we cannot exclude unknown antagonistic factors operating in the managed, but not in the control area “Aristau” in the years 2013 and 2014 or in “Laufen” in the year 2012.

The positive effects on hare densities were likely caused by wider-sown cereals (“Selzach”), wildflower patches (“Laufen”), or a combination of both (“Reinach”). Interestingly, we found no effect of wider-sown cereals in Laufen in the years 2010 to 2013, which might be due to an insufficient quantity of this measure or to other unknown reasons (see above). The winter distribution of hares across all experimental areas (including controls and study site “Wenslingen”) could best be explained by the percentage of arable land, wildflower patches, and wider-sown cereals in the previous vegetation period suggesting that hares prefer to stay within these managed areas also during winter.

The positive effect of wildflower patches might be due to a better survival of leverets thanks to the complete absence of processing by agricultural machinery; the opportunity to hide under vegetation especially in the early months of the year when agricultural crops provide almost no cover; and the low frequency of predator visits (except alongside the margins; Fernex et al. 2011, Hummel et al. 2017). Denise Karp (unpublished data) found a lower survival rate of leverets with increasing distance to wildflower patches. Positive effects of wildflower strips on hare densities and distributions have already been found in different regions of Europe (see Smith et al. 2005) and in Switzerland (Meichtry-Stier et al. 2014). According to Perron (2012), a total of more than 1% wildflower areas positively influenced the development of hare populations in Northwestern Switzerland. Meichtry-Stier found a positive development of hare densities in their study site with a mean percentage of 3.2% wildflower patches and none in the study sites with only 1.7% and 1.9% wildflower patches respectively. In a study encompassing 58 sites in lowland Switzerland, Zellweger-Fischer et al. (2011) found no influence of wildflowers and set-asides on brown hare density. They explained this somewhat surprising finding with the rarity of such elements in their study sites (only 0.2% on average). In our experimental area “Laufen”, hare densities increased, after the wildflower area was raised from 1.6 to 3.7% of the total area used for agriculture. As the margins of wildflower strips are systematically exploited by potential leveret predators (Fernex et al. 2011), especially when near forests, hedges, or settlements (Hummel et al. 2017), one would also expect an influence of the wildflower patches’ outline and its location within a diverse agricultural landscape. Indeed, leveret survival was better when the leverets used optimized wildflower patches compared to conventionally managed wildflower strips (Karp 2016). In our analysis of the distribution of hares within the managed and the control sites, we

found however no such effect. This might be due to the almost exclusive presence of those elements in the managed areas of two out of the five sites, where this analysis was conducted.

Until harvest, the inner parts of cereal fields seem to be very unattractive for potential leveret predators (Fernex et al. 2011; Beerli 2013), possibly because they offer almost no voles (Aschwanden et al. 2007) or other interesting prey or because preycatching there is difficult. Therefore, leverets in cereal fields might be relatively safe from predators, when compared to grassland and other agricultural areas. The percentage of cereal fields has been found to be an important factor explaining differences in brown hare densities across landscapes (see Smith et al. 2005 for an overview) and this might mainly be due to the relative safety of the leverets in such fields. The decline of brown hares in many parts of Europe has been attributed to an intensification of agriculture (Smith et al. 2005). One possibly very important element of this intensification, which has received only marginal attention by those discussing the reasons of the brown hare decline, is the limited accessibility of cereal fields for hares as shown by Rühle (1999). Stands of the cereal plants in modern fields are too dense to be easily accessed by hares which render cereal fields useless as birth places for leverets just in the months of the most important recruitment. Wider-sown cereals are a simple and efficient method to increase the offer of relatively predator-free areas as breeding places for hares without influencing the rotations or land-use mosaic of a farm. We found it a very effective method to increase hare numbers in some places. In the “Selzach” area, hare density more than doubled after we had offered between 2.6 and 4.7% wider-sown cereals for 3 years. According to our results, we recommend a proportion of at least 2.5% of wider-sown winter cereals of the total arable land as measure to improve leveret survival and indirectly hare density. The measure is inexpensive, because the wheat plants compensate for the lower seed density by increasing the number of stalks and the size of the ears. According to estimations of the farmers who participated in our experiment, seeding only 60% of the normal seed quantity results in an average loss of 16% of the wheat harvest.

We conclude that—irrespective of high predator densities—brown hare populations in agricultural landscapes with comparatively low initial hare densities can be considerably increased by simply offering a total of about 3% wider-sown winter cereals or wildflower patches within the agriculturally used area. The key point seems to be, that we do not need to add brown hare “habitats” but high-value requisites within the already existing habitat. In other words, our measures did not increase the quantity but improve the quality of habitats. Where leveret mortality is the reason of low hare density additional machine- and predator-safe places for the leverets might be a successful management option. In regions where leveret mortality is limited by other factors than predators or agricultural machinery (e.g. lack of lipid-rich food for

lactating female hares, Hackländer et al. 2002b), or where insufficient survival of adults is the reason of low hare densities, the measures proposed in our work would possibly not be effective to increase hare populations.

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References

- Aschwanden J, Holzgang O, Jenni L (2007) Importance of ecological compensation areas for small mammals in intensively farmed areas. *Wildl Biol* 13:150–158
- Averianov A, Niethammer J, Pegel M (2003) *Lepus europaeus* Pallas, 1778 – Feldhase. In: Krapp F (ed) *Handbuch der Säugetiere Europas, Band 3/II: Hasentiere Lagomorpha*. Aula-Verlag, Wiebelsheim, pp 35–104
- Berli N (2013) Räumliches Verhalten potenzieller Junghasenprädatoren. Bachelor thesis, Institut NLU, University Basel
- Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat* 7:434–455
- Dietrich A (2010) Auswertung von Scheinwerferzählungen mit Binomial mixture Modellen am Beispiel der Feldhasenzählungen *Lepus europaeus* in der Schweiz. Master thesis, Universität für Bodenkultur Vienna
- Fernex A, Nagel P, Weber D (2011) Sites with reduced predation risk to young hares within an agricultural landscape. *Mammalia* 75(4):395–397. <https://doi.org/10.1515/MAMM.2011.053>
- Frylestam B (1980) Reproduction in the European hare in southern Sweden. *Holarctic Ecology* 3:74–80
- Gelman A, Simpson D, Betancourt M (2017) The prior can often only be understood in the context of the likelihood. *Entropy* 19(10):555
- Hackländer K, Arnold W, Ruf T (2002a) Postnatal development and thermoregulation in the precocial European hare (*Lepus europaeus*). *J Comp Physiol B* 172:183–190
- Hackländer K, Tataruch F, Ruf T (2002b) The effect of dietary fat content on lactation energetics in the European hare (*Lepus europaeus*). *Physiol Biochem Zool* 75:19–28
- Hansen K (1992) Reproduction in European hare in Danish farmland. *Acta Theriol* 37:27–34
- Hoffmann D (2003) Populationsdynamik und -entwicklung des Feldhasen in Schleswig-Holstein im Beziehungsgefüge von Klima, Prädation und Lebensraum. Dissertation, Universität Trier
- Hummel S, Meyer L, Hackländer K, Weber D (2017) Activity of potential predators of European hare (*Lepus europaeus*) leverets and ground-nesting birds in wildflower strips. *Eur J Wildl Res* 63(1–13). <https://doi.org/10.1007/s10344-017-1158-6>
- Kalchreuther H (2003) Die Sache mit der Jagd. 5., neu bearbeitete und erweiterte Auflage. Paul Parey, Hamburg und Berlin
- Kaluzinski J, Pielowski Z (1976) The effect of technical agricultural operations on the hare population. In: Z. Pielowski Pucek Z (ed). *Ecology and management of European hare populations*. Państwowe Wydawnictwo Rolnicze i Lesne, pp 205–211
- Karp D (2016) Prewaning survival of brown hare leverets (*Lepus europaeus*). In: Kelly P, Phillips S, Smith A, Browning C (ed.). *Proceedings of the 5th world lagomorph conference*, Turlock, California, July 11–15, 2016 Endangered Species Recovery Program, California State University Stanislaus, p 35
- Keith LB (1981) Population dynamics of hares. In: Myers K, MacInnes CD (eds) *proceedings of the world lagomorph conference held in Guelph, Ontario august 1979*. University of Guelph, Ontario, pp 395–440
- Kéry M, Royle JA (2015) *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS: volume 1: prelude and static models*. Academic Press
- Knaus P, Antoniazza S, Wechsler S, Guélat J, Kéry M, Strebel N, Sattler T (2018) Schweizer Brutvogelatlas 2013–2016. Verbreitung und Bestandsentwicklung der Vögel in der Schweiz und im Fürstentum Liechtenstein. Schweizerische Vogelwarte, Sempach
- Marboutin E, Bray Y, Peroux R, Mauvy B, Lartigues A (2003) Population dynamics in European hare: breeding parameters and sustainable harvest rates. *J Appl Ecol* 40:580–591
- Meichtry-Stier KS, Jenny M, Zellweger-Fischer J, Birrer S (2014) Impact of landscape improvement by agri-environment scheme options on densities of characteristic farmland bird species and brown hare (*Lepus europaeus*). *Agric Ecosyst Environ* 189:101–109
- MeteoSchweiz (2018) Klimanormwerte. <http://www.meteoschweiz.admin.ch/home/klima/schweizer-klima-im-detail/klima-normwerte/klimadiagramme-und-normwerte-pro-station.html> (16.10.2018)
- Milanov ZB (1996) Effects of mowing fodder plants on small game populations in central Bulgaria. In: Botev N (ed) *Proceedings of the international union of game biologists XXII congress September 4–8 1995 Sofia, Bulgaria*. Pensoft, Sofia, Moscow, St. Petersburg, pp 394–397
- Möller D (1977) Zur postnatalen Mortalität des Feldhasen in der Deutschen Demokratischen Republik. *Beiträge zur Jagd- und Wildforschung* 10:247–254
- Panek M, Kamieniarsz R, Bresinski W (2006) The effect of experimental removal of red foxes *Vulpes vulpes* on spring density of brown hares *Lepus europaeus* in western Poland. *Acta Theriol* 51:187–193
- Pépin D (1989) Variation in survival of brown hare (*Lepus europaeus*) leverets from different farmland areas in the Paris basin. *J Appl Ecol* 26:13–23
- Perron M (2012) Bestandsentwicklung des Feldhasen in Abhängigkeit der Landschaftsfragmentierung im Kanton Aargau. Master thesis, Zürcher Hochschule für Angewandte Wissenschaften, Wädenswil
- Pielowski Z (1975) Charakterystyka ekologiczna populacji zajaca *Lepus europaeus* Pallas, 1778. *Roczniki Akademii Rolniczejw Poznaniu. Prace Habiliacyjne* 65:5–33
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the third international workshop on distributed statistical computing*, March 20–22. Technische Universität Wien, Vienna, p 203
- Reynolds JC, Tapper SC (1995) Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its

- potential impact on annual population growth. *Wildl Biol* 1:145–158
- Reynolds JC, Tapper SC (1996) Control of mammalian predators in game management and conservation. *Mammal Rev* 26:127–156
- Reynolds JC, Stoate C, Brockless MH, Aebischer NJ, Tapper SC (2010) The consequences of predator control for brown hares (*Lepus europaeus*) on UK farmland. *Eur J Wildl Res* 56:541–549
- Rühe F (1999) Effect of stand structures in arable crops on brown hare (*Lepus europaeus*) distribution. *Gibier Faune Sauvage* 16:317–337
- Schai-Braun S, Weber D, Hackländer K (2013) Spring and autumn habitat preferences of active European hares (*Lepus europaeus*) in an agricultural area with low hare density. *Eur J Wildl Res* 59:387–397
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113
- Smith RK, Vaughan Jennings N, Harris S (2005) A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Rev* 35:1–24
- Spittler H (2014) Was sind die Gründe für den Rückgang von Hase und Fasan?. S. 13–20 In: OÖ Landesjagdverband (ed) OÖ Niederwild-Symposium: Hat das Niederwild noch Zukunft? Oberösterreichischer Landesjagdverband, St. Florian
- Tapper S, Yalden D (2010) The Brown hare. The Mammal Society, Southampton
- Voigt U (2010) Zur Raumnutzung und Mortalitätsursachen bei Junghasen (*Lepus europaeus*). In: Godt J, Lang J, Rosenthal G (eds) Fachtagung Feldhase. Ergebnisse der “Fachtagung Feldhase – der aktuelle Stand der Feldhasenforschung” 19.–20. März 2010 in Kassel. Lutra Verlags- und Vertriebsgesellschaft, Tauer, pp 83–92
- Zellweger-Fischer J (2015) Schweizer Feldhasenmonitoring 2015. Schweizerische Vogelwarte, Sempach
- Zellweger-Fischer J, Kéry M, Pasinelli G (2011) Population trends of brown hares in Switzerland: the role of land-use and ecological compensation areas. *Biol Conserv* 144:1364–1373

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