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Source: Wildlife Biology, 13(2) : 150-158

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[150:IOECAF]2.0.CO;2

Importance of ecological compensation areas for small mammals in intensively farmed areas

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Aschwanden, J., Holzgang, O. & Jenni, L. 2007: Importance of ecological compensation areas for small mammals in intensively farmed areas. - Wildl. Biol. 13: 150-158.

Small mammals make up an important link in the food chain as many predator species feed on them. There are indications that small mammal populations in Europe are declining due to the intensification of agriculture. According to national legislation, farmers in Switzerland have to cultivate at least 7% of their land as ecological compensation areas and, thus, some alternative habitats that are possibly beneficial for small mammals have been created. In this study, we estimated the diversity and density of small mammals on two types of conventional farmland field types (artificial grassland and autumn-sown wheat) and three types of ecological compensation areas (wild-flower strips, herbaceous strips and low-intensity meadows) by use of capture-recapture in March, May and July 2003. The common vole *Microtus arvalis* was the most abundant and predominant species in all habitat types except in herbaceous strips, which harboured the highest diversity with six species caught. In March the density of small mammals was generally very low, but significantly higher in wild-flower (mainly due to common vole) and herbaceous strips than in the other habitat types. In wild-flower and herbaceous strips, densities increased strongly from March to May and in July. On autumn-sown wheat fields, a strong increase occurred only from May to July and was caused by common vole. On artificial grassland and low-intensity meadows, densities of small mammals (mainly common vole) increased only marginally with low-intensity meadows supporting slightly higher densities. Thus, habitats that were not mown each year supported the highest densities of small mammals. This demonstrates that ecological compensation areas, such as wild-flower and herbaceous strips, make up an important refuge for small mammals. They probably also have positive effects on populations of many predator species that depend on small mammals, particularly if a mosaic with mown surfaces is created.

Key words: density of small mammals, ecological compensation area, intensive agriculture, Microtus arvalis, vole

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Received 28 January 2005, accepted 20 March 2006

Associate Editor: Sigurður Snorrason

Small mammals constitute an important food resource for many avian and mammalian predator species. In Europe, the fossorial form of water vole *Arvicola terrestris* and many vole *Microtus* species are common and typical inhabitants of agricultural landscapes, yet many farming practices have negative short-term effects on these animals. Mowing and harvesting, for example, remove shelters and food (Tew & MacDonald 1993), and tillage destroys burrows. The intensification of agriculture in western Europe during the last decades may thus have resulted in a decline in vole populations and their predators. Indeed, there are indications that since the beginning of the 1980s the abundance of voles declined in agricultural landscapes of Germany and France (Kostrzewa & Kostrzewa 1993, Butet & Leroux 2001, Reichholf 2004). In these countries agricultural intensification is thought to have resulted in a decrease in the frequency and amplitude of the typical vole population cycles. A similar decline in vole populations may be assumed for agricultural areas in lowland Switzerland, although, to our knowledge, there is no study describing population dynamics of voles in this part of the country.

In order to counteract the loss of biodiversity in intensively farmed areas, farmers in Switzerland are bound by law to cultivate at least 7% of their land as 'ecological compensation areas', and they get subsidies for their ecological contribution (Harder 1998). Additional subsidies can be applied for if areas show a high ecological quality or are connected to each other (Oppermann & Gujer 2003). Legally approved ecological compensation areas, each with specific guidelines of cultivation and a subsidy, include for example: low-intensity meadows, litter meadows, hedgerows, wild-flower strips and traditional orchards.

Some ecological compensation areas like wild-flower strips and herbaceous strips are not mown or tilled each year. Potentially, such areas constitute a suitable habitat for small mammals typical of the farmland. On a farmland in northern Yorkshire UK, the total small mammal biomass in autumn, for example, was found to be three times higher on 6-m wide field margins than on conventional arable field edges (Shore et al. 2005). Untilled land strips serve as a refuge for small mammals during harvest of adjacent agricultural fields (Tew & MacDonald 1993, Baumann 1996, Tattersall et al. 1997). However, we are not aware of any study in which the density of small mammals in different types of ecological compensation areas and agriculturally used fields in their vicinity has been monitored over several months.

In our study, we examined whether ecological compensation areas support higher densities of small mammals than artificial grassland and autumn-sown wheat fields over the vegetation period from March to July. While most previous studies concentrated on one species or on one habitat type (Baumann 1996, Tattersall et al. 1997, Briner 2002, Shore et al. 2005) or applied different trapping designs for different habitat types, we used the same trapping design and a coherent capture-recapture analysis to estimate the densities of small mammals simultaneously on three different types of ecological compensation areas, on artificial grassland and autumn-sown wheat fields.

Material and methods

Study area and vegetation

We collected data in an intensively farmed plain (17 km^2) near Wauwil (47°10'N 8°02'E, 500 m a.s.l.) in central Switzerland during the summer of 2003. Since 1995, the ecological compensation areas in the whole region have been increased from 3.2 to 8% of the cultivated area (Graf 1999). In the study area, ecological compensation areas amounted to 4.3% of the agricultural acreage (low-intensity meadows 3.6%, wild-flower strips 0.4% and herbaceous strips 0.3%), while artificial grassland (49%), autumn-sown wheat (8.5%) and other cultures (38.2%) dominated the area.

The abundance of small mammals was studied on five different habitat types, three of which were ecological compensation areas (low-intensity meadows, wild-flower strips and herbaceous strips), and two were conventional farmland field types (artificial grassland and autumn-sown wheat). Wild-flower strips are arable fallows sown with seed mixtures of native plants. They were on average 15 m wide and 185 m long (i.e. covering 0.28 ha). Herbaceous strips consisted of different species of herbaceous plants: thistles *Cirsium* spp., common teasel *Dipsacus sylvestris*, St John's Wort *Hypericum perforatum*, common mallow *Malva sylvestris* and mulleins *Verbascum* spp. (5 × 320 m, i.e. covering on average 0.16 ha). They were bordered by hedgerows on one side and conventional field types on the other side (e.g. artificial grassland, maize fields or potato fields). Low-intensity meadows (64 × 100 m, i.e. covering on average 0.64 ha) in the study area are typical *Arrhenatheretum* (i.e. meadows dominated by tall oat grass). They are usually cut twice a year with the first cutting no sooner than 15 June. Application of liquid manure or other fertilizers is not allowed. Artificial grassland (0.88 ha on average) is dominated by white clover *Trifolium repens* and ryegrass *Lolium* sp. and form part of the ordinary crop rotation practice. It is cut at least five times between April and October and liquid manure is applied regularly. One artificial grassland was situated between a herbaceous strip, a maize field and two farm tracks. The second artificial grassland was bordered by farm tracks on three sides and by a potato field on the fourth side, and the third artificial grassland was situated between two farm tracks, another artificial grassland and a wetland reserve. Autumn-sown wheat fields which are harvested at the end of July covered an average area of 1.3 ha. They were machine harvested leaving little standing stubble. The wheat fields were mostly bordered by artificial grassland, potato fields and farm tracks.

For each of the five habitat types, three fields were chosen. During each trapping session (in March, May and July), the vegetation structure of each field was described on five randomly chosen squares (each of 1 m^2) as follows: a) vegetation height (in cm) was determined by measuring the 10th highest plant (to avoid measuring unusually high plants), b) vegetation density was determined by measuring the height (in cm) at which only 50% of a horizontal ruler, 1.7 cm wide and 100 cm long, was visible by watching vertically from above, c) percent cover of green vegetation, and d) dead plant material was estimated visually (at an accuracy of 5%).

Trapping of small mammals

The density of small mammals in each of the 15 fields (five habitat types with three replicates each) was determined using capture-recapture during three trapping sessions; one in March, one in May and one in July. In each field, we set 40 traps (Trip Trap with a nest box; we glued two metal washers to the outside of the trap door to ensure door shutting even during wet conditions). Because wild-flower and herbaceous strips were narrower than 10 m, we could not set traps in a square grid design. Therefore, the traps were placed along two straight lines 5 m apart. Along each line, 10 pairs of traps were set at 5-m intervals. Thus, the trapping rectangle covered an area of 45 × 5 m. In low-intensity meadow, artificial grassland and autumn-sown wheat, the borders of the trapping rectangle were at least 40 steps away from adjacent habitat types. In wild-flower and herbaceous strips, we were forced to set the trapping lines close to the edge of the strips.

We never set traps in freshly mown patches, and the vegetation height usually exceeded 20 cm, except for artificial grassland and low-intensity meadows in March when vegetation height was just below 20 cm. If there were indications of small mammal activity such as corridors or holes within a circle of a 50-cm radius around a trapping point, the traps were placed directly at such a sign. The openings of each trap pair were orientated into different directions. Each trapping session consisted of continuous trapping during 60 hours, starting in the evening (for three consecutive days and nights). Traps were checked every eight hours, starting at 23:00. Small mammals were lured with a piece of apple and a piece of mixed rolled oats, peanut butter and minced meat (Holzgang & Pfunder 2002), and a paper tissue was offered as nesting material. The animals were marked by locally cutting of the guard hair on the shoulder or on the back. Because the underhair is darker than the guard hair, the marking was visible as a dark spot in the fur. For every recapture round, the fur cutting was made at a different place (e.g. on the left shoulder, right lower back). By doing this, the time of the first and subsequent captures, respectively, were known for every recapture, and resulted in capture histories of eight time points for each trapping session.

Data analysis

The trapped individuals were assumed to live on a surface of 500 m^2 (50 × 10 m), which results from multiplying the length and width of the trapping rectangle after addition of a margin of 2.5 m on each side (Gurnell & Flowerdew 1994, Williams et al. 2002). The population size on each single field for each trapping session was estimated using closed capture-recapture models by use of the computer software CAPTURE (Otis et al. 1978). These models assume a closed population during the 60 hours of each trapping session, thus only capture probabilities needed to be calculated to estimate the number of individuals. We believe that the assumption of a closed population is valid, as it is quite improbable that there is much immigration or emigration within only three days. Separate analyses were performed for each field and trapping session. For 22 out of the 45 samples it was not possible to calculate population sizes by the use of CAPTURE due to too few recaptures. In these cases, the population sizes were estimated by use of the formula $N = C/(1 - (1 - P)^8)$ where C is the number of captures, P is the average of the capture probabilities (calculated using CAPTURE) of all samples of one trapping session and eight as exponent is the number of trap checks per trapping session. From the population estimates, we calculated the densities of small mammals (ha^{-1}) and the average density of the three fields sampled for each of the five habitat types with its standard error.

The common vole was the only species for which sufficient captures were obtained to estimate densities at a species-specific level. We estimated the proportion of common voles from the pooled overall density of all species of small mammals (see above) from the proportion of common voles caught and corrected for the species-specific capture probabilities as corrected proportion of common vole = (number of common vole/p (common vole))/(number of species 1/p (species 1)) + … + (number of species n/p (species n)), where p is the capture probability of each species pooled for May and July, respectively. This corrected proportion of common voles multiplied with the overall density of small mammals yielded the density of common voles and was calculated for each field.

Small mammal densities were analysed for their dependence on habitat type, month (trapping session), the interaction between habitat type and month and the four parameters of vegetation structure (height, density, cover of green vegetation and dead plant material) with an analysis of variance. Because the error variance did not show an equal distribution among the habitat types, an important criterion for the application of an analysis of variance was violated. Therefore, we used a weighted multifactorial analysis of variance (weighted least squares) according to Neter et al. (1990). The weight factor in such an analysis corresponds to the reciprocal value of the error variance.

Results

In total, we caught 349 different small mammal individuals at 738 occasions; thus an animal was on average captured twice. We caught the following six small mammal species: yellow-necked mouse *Apodemus flavicollis*, wood mouse *A. sylvaticus*, bank vole *Clethrionomys glareolus*, field vole *Mi-*

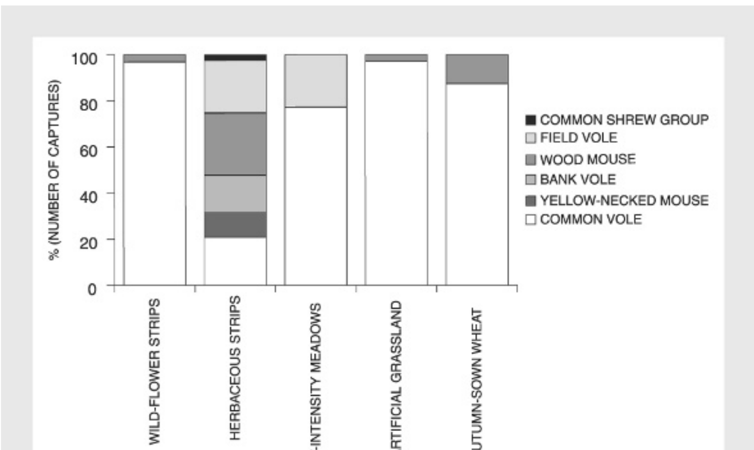

Figure 1. Species composition in the five habitat types, pooled over the three trapping sessions (N = 738 captures).

Table 1. Weighted analysis of variance of small mammal densities with respect to vegetation parameters, month (trapping session), habitat type and the interaction of habitat type*month (adjusted $R^2 = 0.86$, df = 17, F = 15.5, P < 0.001). B is the parameter estimate and SE (B) is the standard error of parameter estimate.

	B	SE (B)	df	Mean square	F	P
Intercept	742.46	90.14	1	12.101	11.895	0.002
Vegetation parameters						
Cover of dead plant material	1.27	0.94	1	1.836	1.805	0.192
Cover of green vegetation	0.18	0.71	1	0.062	0.061	0.807
Vegetation density	1.34	1.35	1	0.994	0.977	0.333
Vegetation height	-0.31	0.52	1	0.368	0.362	0.553
Month			2	14.761	14.510	< 0.001
Habitat type			4	10.871	10.685	< 0.001
Habitat type*month			7	12.283	12.074	< 0.001

crotus agrestis, common vole *M. arvalis* and some individuals of the common shrew *Sorex araneus* complex. Herbaceous strips were the only habitat type in which all six species were captured (60% voles, 38% *Apodemus* spp. and 2% shrews; Fig. 1). In all other habitat types, > 75% of the catches were common voles together with one additional species, the field vole on low-intensity meadows, or the wood mouse on wild-flower strips, artificial grassland and autumn-sown wheat.

Vegetation parameters had no significant effect on small mammal density (Table 1) or common vole density (Table 2), even when entered into the model before month (trapping session) and habitat type. But both small mammal and common vole density differed significantly between months and habitat types (see Tables 1 and 2), and these two effects were not independent of each other. The significant interaction term habitat type*month shows that the increase in small-mammal density over the three months differed between habitat types.

In March, the density of small mammals was low (averaging 27.0 ha^{-1} ± 22.0 SE) over all habitat types (Fig. 2). Nevertheless, wild-flower and herbaceous strips had a higher density (57.6 ha^{-1} ± 22.3 and 88.4 ha^{-1} ± 68.7, respectively) than low-intensity meadows (0 ha^{-1}), artificial grassland (8.2 ha^{-1} ± 8.1) and autumn-sown wheat (8.2 ha^{-1} ± 8.1). In all habitat types, the common vole was the only species that we caught at this time of year, except for herbaceous strips where the small-mammal density was made up by wood mouse and yellow-necked mouse. In May, a substantial increase to 486.6 ha^{-1} ± 292.4 and 630.2 ha^{-1} ± 289.6 was observed on wild-flower and herbaceous strips, respectively, whereas in the artificial grassland, autumn-sown wheat and low-intensity meadows, the increase was clearly less prominent (to 61.8 ha^{-1} ± 67.4, 78.8 ha^{-1} ± 11.9 and to 113.3 ha^{-1} ± 50.0, respectively; see Fig. 2). The common vole was the most abundant species on wild-flower strips (92% common voles), low-intensity meadows (85%) and artificial grassland (100%), whereas it was only a by-catch on herbaceous strips (7.5%) and autumn-sown wheat (21%). Even larger differences in small mammal densities between habitat types were estimated for July. On low-intensity meadows and artificial grassland, the density had increased slightly from 113.3 ha^{-1} to 140.0 ha^{-1} (± 82.6) and from

Table 2. Weighted analysis of variance of common vole densities with respect to vegetation parameters, month (trapping session), habitat type and the interaction of habitat type*month (adjusted $R^2 = 0.91$, df = 18, F = 24.3, P < 0.001). B is the parameter estimate and SE (B) is the standard error of parameter estimate.

	B	SE (B)	df	Mean square	F	P
Intercept	656.91	55.30	1	142069	6.613	<0.001
Vegetation parameters						
Cover of dead plant material	0.86	0.67	1	35650	1.660	0.209
Cover of green vegetation	0.72	0.66	1	25554	1.190	0.286
Vegetation density	0.80	1.22	1	9235	0.430	0.518
Vegetation height	-0.09	0.20	1	4025	0.187	0.669
Month			2	615296	28.642	<0.001
Habitat type			4	293716	13.67	< 0.001
Habitat type*month			8	380734	17.723	< 0.001

61.8 ha^{-1} to 84.0 ha^{-1}(± 54.0), respectively. In contrast, the densities of small mammals had increased further on wild-flower and herbaceous strips from May to July (from 486.6 ha^{-1} to 1046.6 ha^{-1} ± 123.5 and from 630.2 ha^{-1} to 836.4 ha^{-1} ± 457.6, respectively). During this period, an increase in density was also observed on autumn-sown wheat fields from 78.8 ha^{-1} to 561.3 ha^{-1} (± 201.7; see Fig. 2). In July, the proportion of common voles was > 80% of the total small mammal density in all habitat types, except in herbaceous strips where it amounted to 40%.

Discussion

Our study demonstrated large differences in species composition and seasonal abundance of small mammals between habitat types. The highest species diversity occurred in herbaceous strips with six species trapped. In all other habitat types, only two species were captured, with the common vole being the predominant species. Herbaceous strips are typical ecotones between hedges (including hedges along streams or channels) or woodland and agriculturally used land. This mosaic of different habitat types holds a diverse small-mammal community, and in the herbaceous strips we captured all the species typical for this habitat (Holzgang & Pfunder 2002). Clearly, bank vole, yellow-necked mouse and individuals of the common shrew complex, which prefer trees, bushes or dense undergrowth (Corbet & Ovenden 1982, Hausser 1995), moved from the adjacent hedge into the herbaceous strips where they were trapped. Also Baumann (1996) caught bank voles only in herbaceous strips adjacent to woodland. In wild-flower strips surrounded only by arable land, the common vole, typical of open land, was caught as well as the wood mouse, which moves also into open land with a good cover.

As expected, both the density of common voles and of all small mammals taken together generally increased over the study period from March to July. The common vole was the most abundant species on wild-flower strips, low-intensity meadows, artificial grassland and autumn-sown wheat, whereas it was only a bycatch on herbaceous strips. Although many tracks, particularly vole corridors, were observed in March, only a few individuals were caught. The estimated low density for March (27 ha^{-1}) corresponds to the findings of other studies, although the methods used differed. On fallows

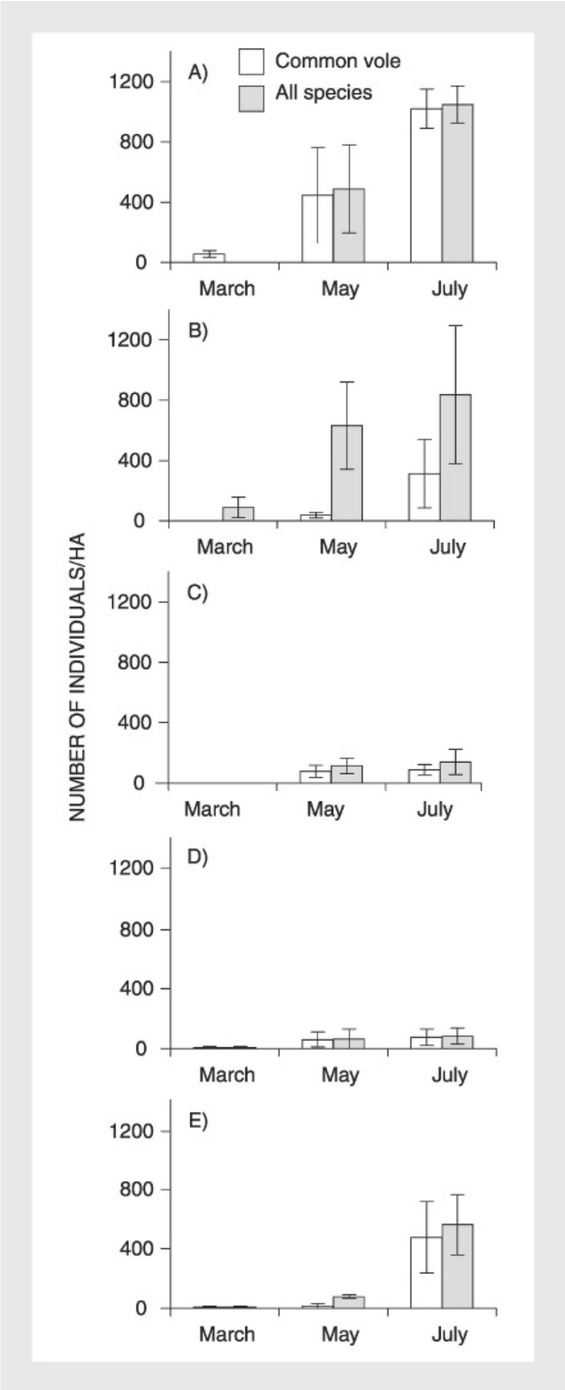

Figure 2. Mean densities of small mammal species (± SE) and mean densities of common voles (± SE), corrected for different capture probabilities, in the five habitat types (A) wild-flower strips, B) herbaceous strips, C) low-intensity meadows, D) artificial grassland and E) autumn-sown wheat) for March, May and July 2003. Capture probabilities: *M. arvalis* = 0.22, *M. agrestis* = 0.39, *A. sylvaticus* = 0.22, *A. flavicollis* = 0.25, *C. glareolus* = 0.19.

and orchards in West Germany, Boyce & Boyce (1988) estimated a vole density of 24 ha^{-1} for April 1982 (based on Minimum Number Alive). In western France, Butet & Leroux (2001) found vole densities between 0.8 and 87.6 ha^{-1} for April during 1986-1998 (pooled data based on the trap-night index for abandoned pastures, grazed and mown grassland and cereal crops). Gromadzki & Trojan (1971) estimated spring densities between 4.1 ha^{-1} and 33.8 ha^{-1} on cultivated fields and in refuge habitats in Poland in 1966 and 1967 (based on capture-marking-release).

The short vegetation might have offered only poor protection against predators (e.g. long-eared owl *Asio otus*, kestrel *Falco tinnunculus*, common buzzard *Buteo buteo*, red fox *Vulpes vulpes* and stoat *Mustela erminea*) and may have influenced the spatial behaviour of the small mammals resulting in reduced captures. Small mammals perceive tall vegetation as good protection (Tchabovsky et al. 2001). Under predation risk, which is high in short vegetation (Korpimäki et al. 1996, Longland & Price 1991, Jacob & Brown 2000, Sheffield et al. 2001), small mammals move faster, cover shorter distances (Lagos et al. 1995) and may reduce their home-ranges (Jacob & Hempel 2003). A reduced number of captures would influence the density of small mammal estimates negatively. For May and July, the effects of low vegetation cover can be excluded, as traps were only placed on fields with vegetation heights > 20 cm.

Compared to wild-flower and herbaceous strips, small mammal densities in autumn-sown wheat were very low in March and May, and increased only from May to July. The small mammals were probably exploiting this huge food resource shortly before harvest (i.e. at the end of July).

Densities of small mammals in artificial grassland remained at very low levels throughout the summer. Apparently, the regular cutting (first cut in April and afterwards about every five weeks until October) and subsequent application of liquid manure prevented the establishment of higher small-mammal densities. Populations of gray-tailed voles *Microtus canicaudus* on alfalfa fields are known to decline by about 50% after mowing (Edge et al. 1995).

Small-mammal and common-vole densities remained low for the whole study period in low-intensity meadows compared to wild-flower and herbaceous strips. Compared to artificial grassland, though, densities of small mammals and of common vole in May and July were twice as high. This may be the result of the lower frequency of mowing (only twice, first cut after 15th of June).

Many studies have shown that vole density is influenced by vegetation height, cover and litter (e.g. Ostfeld et al. 1985, Tattersall et al. 1997, Sheffield et al. 2001, Olson & Brewer 2003). Unexpectedly, we found no significant correlations between small mammal or common vole densities and parameters of vegetation structure in our study. Apparently, it was not vegetation structure, but habitat type that determined small-mammal densities in our study area. The habitat types differed in agricultural activities (mainly in the frequency of mowing and the application of liquid manure) and food availability (i.e. autumn-sown wheat). Therefore, it is likely that the density patterns of small mammals seen in our study area were mainly determined by the adverse effects of agricultural practices (i.e. mowing and liquid manure) and food availability.

Our study clearly demonstrated that ecological compensation areas not tilled or mown every year, such as wild-flower and herbaceous strips, support high densities of small mammals and can serve as a refuge in intensively farmed areas. Similarly, grassy field margins were found to harbour a higher small mammal biomass than conventional arable field edges in the UK (Shore et al. 2005). If connected to other semi-natural habitats (e.g. hedgerows), such ecological compensation areas may also increase the species diversity of small mammals. Regularly mowed ecological compensation areas (low-intensity meadows) support a lower diversity and density of small mammals.

The density of small mammals, in particular of the genera *Microtus* and *Arvicola*, directly determines the occurrence and abundance of many avian and mammalian predators. While some predators exploit small mammals opportunistically when their densities are high (e.g. red fox; Ferrari & Weber 1995, badger *Meles meles* and beech marten *Martes foina*; Niethammer & Krapp 2002), certain bird and mammal species are specialised predators that depend almost exclusively on them (e.g. stoat and weasel *Mustela nivalis*; Niethammer & Krapp 2002, long-eared owl; Mebs & Scherzinger 2000). Such specialised predators have a higher reproductive output or reproduce exclusively during periods of elevated small mammal densities (e.g. Wendland 1957, Niethammer & Krapp 2002). However, as shown in a study of the hunting behaviour of common kestrel and long-eared owl, it is not the absolute density of voles, but their accessibility, that determines where they hunt. Indeed, they mostly hunted on freshly mown grassland and also preferred freshly mown grassland bordering wild-flower and herbaceous strips (Aschwanden et al. 2005). Therefore, both refuge areas with high densities and a mosaic of freshly mown surfaces (preferably adjacent to high density areas) are important to support avian vole predators. Wild-flower and herbaceous strips are not only indirectly important for avian predators during summer, but also directly during winter as kestrels preferred wild-flower strips for hunting activities during the winter (Buner 1998).

In intensively farmed landscapes, ecological compensation areas, such as e.g. herbaceous and wild-flower strips, are of high value. As well as supporting highly productive and diverse small mammal communities, they support also a rich diversity and density of plants, insects and birds (Lys & Nentwig 1994, Jenny et al. 1998, Kleijn & Sutherland 2003, Walter et al. 2004) and thus are important to maintain biodiversity in agricultural landscapes.

Acknowledgements - we thank the Wauwiler Moos prison and local farmers for their information about the work planned on their fields (mowing and harvesting dates) and for allowing access to their farmland. Furthermore, we thank Thilo Tschersich, Vreni Mattmann and Marco Thoma for their assistance in the field and Marc Kéry and Michael Schaub for their support in data analysis. We also thank Verena Keller, Niklaus Zbinden, Roman Graf and Simon Birrer and two anonymous reviewers for commenting on an earlier draft of the manuscript. This study was part of the diploma thesis by Janine Aschwanden at the Zoological Institute, University of Zurich. We thank Heinz-Ulrich Reyer for his supervision and comments on the thesis.

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