

Janine Aschwenden · Simon Birrer · Lukas Jenni

Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)?

Received: 23 December 2004 / Revised: 25 February 2005 / Accepted: 1 March 2005 / Published online: 11 May 2005
© Dt. Ornithologen-Gesellschaft e.V. 2005

Abstract Common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*) in intensively farmed areas in Switzerland decreased markedly as a result of declining vole (*Microtus* spp.) populations. In order to counteract the loss of biodiversity in intensively farmed areas, the Swiss agri-environment scheme stipulates several types of ecological compensation areas, which together should take up 7% of the farmland. Among them are wild flower and herbaceous strips, which are not mown every year and which in summer support up to 8 times more small mammals than ordinary fields and grassland. This study investigates whether kestrels and long-eared owls preferentially hunt on ecological compensation areas and whether preferred hunting areas are related to the density of small mammals or to the density and height of the vegetation. Both kestrels and long-eared owls mainly hunted on freshly mown low-intensity meadows and artificial grassland, despite low densities of small mammals. Therefore, vegetation structure was more important for the selection of hunting sites than prey abundance. However, both predators preferred to hunt on freshly mown grassland and meadows bordering a wild flower or herbaceous strip. Voles from these strips probably invaded the adjacent freshly mown grassland and became an easy prey for kestrels and owls. In intensively farmed regions, ecological compensation areas, particularly those not mown each year, are an important refuge for small mammals, although in summer the small mammals are not directly accessible to hunting birds. Hence, a mosaic of different habitat types with grassland mown at different times of the year to-

gether with undisturbed strips is best suited to provide a year-round supply of accessible food for vole hunters.

Keywords Agri-environment scheme · *Asio otus* · Ecological compensation area · *Falco tinnunculus* · Hunting preference

Introduction

The common kestrel (*Falco tinnunculus*) has been reported to have declined in many European countries, most probably because its main prey, voles (*Microtus* spp.), have decreased as a result of the intensification of farming (Hagemejer and Blair 1997). In Switzerland, the numbers of kestrels remained stable in the traditionally farmed mountain areas, but declined in the intensively farmed lowlands up to the end of the 1980s and have remained at low levels since (Schmid 1990; Schmid et al. 2001). Similarly, the long-eared owl (*Asio otus*), another avian predator feeding mainly on voles, seems to have declined in agricultural Europe for the same reason as the kestrel, although data are much scarcer and less conclusive (Illner 1988; Hagemejer and Blair 1997). In Switzerland, the few available local population trends, the percentage of long-eared owls among all raptors and owls brought to bird care centres, and the numbers at winter roosts, all indicate declining numbers (Birrer 2003). The density of common voles (*Microtus arvalis*) affects the populations of the two avian predators in many ways. In areas and years with many voles, breeding density and breeding success are higher (Korpimäki 1984; Korpimäki and Norrdahl 1991; Village 1998; Henrioux 1999), breeding starts earlier during the year and clutch size is larger (Ziesemer 1973; Korpimäki 1984; Wijnandts 1984; Kostrzewa and Kostrzewa 1993). There are indications that the population of common voles in France and Germany has declined in intensively farmed areas (Kostrzewa and Kostrzewa 1993; Butet and Leroux 2001), which suggests a comparable decline

Communicated by F. Bairlein

J. Aschwenden (✉)
Weizackerstrasse 25, 8405 Winterthur, Switzerland
E-mail: aschwanja@gmx.ch

S. Birrer · L. Jenni
Swiss Ornithological Institute, 6204 Sempach, Switzerland
E-mail: simon.birrer@vogelwarte.ch
E-mail: lukas.jenni@vogelwarte.ch

for the lowlands of Switzerland. Therefore, the main reason for declining numbers of kestrels and long-eared owls in lowland Switzerland is probably the reduced availability of their main prey, the common vole.

In order to counteract the loss of biodiversity in intensively farmed areas, farmers in Switzerland are bound by law to cultivate 7% of their land as ecological compensation areas and are subsidised for this ecological contribution (Harder 1998). Within this agri-environment scheme, additional subsidies can be applied for if areas show a high ecological quality or are connected to each other (Oppermann and Gujer 2003). Legally approved ecological compensation areas, each with special guidelines for cultivation and subsidy, are, e.g., low-intensity meadows, litter meadows (nutrient-poor wet meadows mown in late summer or autumn), hedgerows, wild flower strips and traditional orchards.

Because some ecological compensation areas like wild flower strips and herbaceous strips are not mown every year, they support a much higher density of small mammals than conventional farmland. In the study area in summer, small mammal densities in wild flower and herbaceous strips were on average about 8 times higher than on low-intensity meadows and artificial grassland (Aschwanden et al., in preparation). Other studies have shown that untilled land serves as a refuge for small mammals during harvest of adjacent agricultural fields (Baumann 1996; Tattersall et al. 1997). Buner (1998) also concluded (by counting holes of voles) that wild flower strips supported higher densities during the winter months than other areas and were, therefore, preferred by hunting kestrels.

In this study, we investigated whether ecological compensation areas that support high densities of voles are indeed preferred as hunting places by kestrels and long-eared owls. As is well known, it is not prey density, but prey profitability, which primarily determines where predators hunt (Stephens and Krebs 1986). Prey profitability is strongly related to prey availability or accessibility and, in the case of voles as prey, depends on vegetation structure (e.g. Baker and Brooks 1981; Bechard 1982). We therefore analysed whether preferred hunting places were related to the density of small mammals or the density and height of the vegetation.

Methods

Study area

Data were collected during summer 2003 in an intensively farmed plain near Wauwil (47°10'N, 8°02'E) in Central Switzerland (see Birrer 1993 for more details). Since 1995, the Swiss Ornithological Institute increased the ecological compensation areas in co-operation with local farmers from 3.2% to 8% of the cultivated area (Graf 1999).

In 2003, the study area was mapped and the availability of different habitat types was determined with a GIS. Five habitat types were potential hunting habitats for both predators: the three types of ecological compensation areas, which were wild flower strips (0.4% of agricultural acreage), herbaceous strips (0.3%) and low-intensity meadows (3.6%), and the two conventional field types of artificial grassland (49.0%) and autumn-sown wheat (8.5%). All other field types, like maize, potatoes, etc., were grouped into the category "others" (38.2%).

Wild flower strips are arable fallow sown with seed mixtures of wild plants and had an average size of 15×185 m (0.28 ha). Herbaceous strips (on average 0.16 ha, 5×320 m) bordered hedgerows on one side and were adjacent to conventional fields on the other side. Low-intensity meadows with 0.64 ha on average (64×100 m) are grassland which is mown for the first time in the season only after 15 June, without application of liquid manure or other fertilisers. Artificial grassland (0.88 ha on average) is part of the crop rotation, usually gets mown several times from April to October and liquid manure is applied regularly. The average size of autumn-sown wheat fields was 1.3 ha and they were harvested at the end of July.

For each of the five habitat types, three replicates were chosen and their vegetation structure was described on five randomly chosen squares (1 m²), once each in March, May and July as follows: (1) vegetation height (in cm) was determined by measuring the tenth highest plant (to avoid measuring unusually high plants); (2) vegetation density was determined by measuring the height (in cm) at which 50% of a horizontal stick (observed vertically from above) was visible; and (3) cover of green vegetation and dead plant material was visually estimated in steps of 5%. In addition, meadows and grassland were divided into three categories: freshly mown, not freshly mown (< 20 cm high) and not freshly mown (> 20 cm high). The proportion of these three categories in the study area was determined every week. For each meadow, we also determined whether it bordered a wild flower or herbaceous strip or not.

Birds and foraging observations

Three pairs of kestrels were breeding in the study area. They were followed by car and observed with binoculars. Totals of 146 locations of hunting attempts, 322 locations of hovering flights and 191 locations of perched birds, 659 observation points in all, were recorded on a map (scale 1:25,000) together with the habitat type and the hunting success. When the kestrels were perched, the habitat type which was overseen by the kestrels was recorded.

Four pairs of long-eared owls were known to live in the study area and three breeding locations with begging young owls were found. When the adult long-eared owls left the nesting site at sunset, they were followed by car

and observed with an ambient light intensifier (3× magnification) as long as possible. Every hunting activity, usually observed at a distance of <200 m, was recorded on a map (scale 1:25,000) together with habitat type and hunting success. When the owls were perch hunting, every perch location was recorded on the map together with the habitat type which was overseen by the owl.

Observations took place from mid-May until the end of July 2003. Kestrels could be observed between 0730 and 2030 hours, whereas all hunting observations of owls were done before midnight.

Statistical analysis

For kestrels, 75% of the observations could be clearly assigned to one of the six individuals. This was possible when the kestrels were observed leaving or arriving at the nest box or when they were flying towards or away from the nest box. Males and females were distinguishable by their plumage characters. The other 25% of the observations could not be assigned to individuals, because the kestrels sometimes flew too fast or too high to be followed continuously. These observations were allotted to individuals by dividing the study area into three home ranges, each containing one nest with the observation points of the corresponding kestrel pair. Preferred hunting habitats were determined by compositional analysis (Aebischer et al. 1993), using the computer program Resource Selection for Windows, Version 1.00 Beta 8.4 (Leban 1999). The observation points of one individual were related to the surface of habitat types available in the corresponding home range.

Because it was not possible to distinguish individual long-eared owls and to determine their home ranges, a compositional analysis according to Aebischer et al. (1993) could not be applied. Instead, in order to get an idea which habitat types were preferred for hunting activities, the ratios of use by the owls to availability in the area used were calculated. A ratio higher than one

indicates that this habitat type was used more frequently than expected from its availability. The null hypothesis that use was according to availability was tested with a χ^2 -test. Because observation points need to be independent for a χ^2 -test, only observation points at different locations, which had a minimum interval of 3 min, were used (see White and Garrot 1990). Within 3 min it should have been possible for long-eared owls to choose freely between the habitat types available in the study area.

For kestrels, multivariate logistic regression (with backward elimination of non-significant terms) was used to evaluate whether hunting success was affected by habitat type, presence of neighbouring wild flower or herbaceous strips, vegetation height, vegetation density and hunting mode (hovering and perch).

Results

Common kestrel

Habitat types

Kestrels hunted mostly on artificial grassland (74% of 659 locations: hunting attempts, hovering flights and habitat types within view of kestrels when perched taken together) and on low-intensity meadows (22%), while 2, 0 and 1% of observations were on wild flower strips, herbaceous strips and other habitats, respectively (Fig. 1a). The use of habitat types for hunting activities (hunting attempts, hovering flights and habitats observed when perched) was significantly different from habitat type availability (compositional analysis $\lambda=0.0007$, $P<0.001$, Table 1). Low-intensity meadows were used 6.4 times more frequently for hunting than expected from their availability, wild flower strips 6.2 times and artificial grassland 1.6 times more frequently (Fig. 1a). Low-intensity meadows were significantly preferred over artificial grassland, while there was no significant difference between the remaining habitat types (Table 1).

Fig. 1 Comparison of habitat type availability and use (in %) for hunting activities of **a** common kestrels (*Falco tinnunculus*) ($n=146$ hunting attempts + 322 hover flights + 191 perch locations) and **b** long-eared owls (*Asio otus*) ($n=41$ hunting attempts + 36 perch locations)

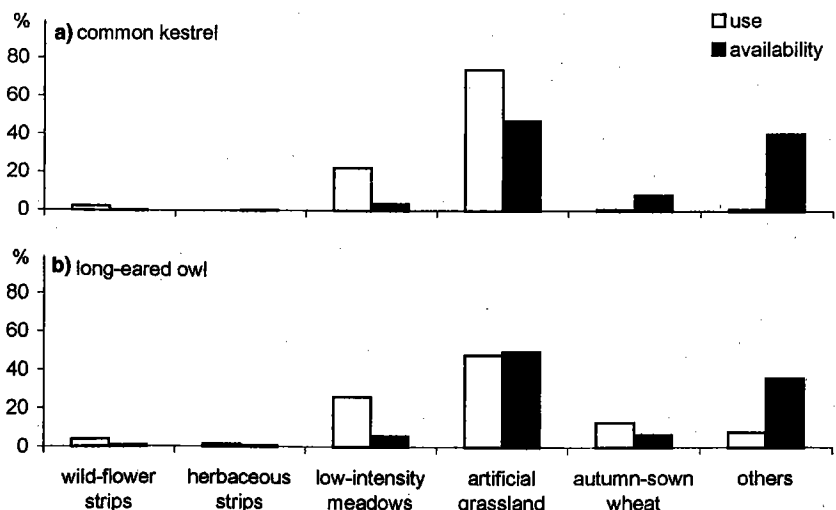


Table 1 Compositional analysis comparing the use of different habitat types by hunting common kestrels (*Falco tinnunculus*) with availability in their home ranges

Habitat type	Wild flower strips	Herbaceous strips	Low-intensity meadows	Artificial grassland	Autumn-sown wheat	Others	Rank
Wild flower strips		1.70	-2.26*	-2.05*	2.01	2.02	3
Herbaceous strips	-1.70		-14.85**	-44.08**	0.40	1.50	2
Low-intensity meadows	2.26*	14.85**		2.63**	3.91**	5.42**	5
Artificial grassland	2.05*	44.08**	-2.63**		3.91**	5.15**	4
Autumn-sown wheat	-2.01	-0.40	-3.91**	-3.91**		0.75	1
Others	-2.02	-1.50	-5.42**	-5.15**	-0.75		0

Total significance: $\lambda=0.0007$, $P<0.001$. The matrix of t -values comparing all habitat types against each other with indication of their significance ($*P<0.1$, $**P<0.05$) is given. A significantly positive t -value indicates that the habitat type in the first column is

preferred over the habitat type indicated in the first line. In the last column, the ranking of habitat types according to preference by kestrels is given, highest rank indicating the most preferred habitat type

Vegetation height of meadows and grassland

Because most hunting activity occurred on low-intensity meadows and on artificial grassland, and because these habitat types differed considerably in vegetation height as a result of mowing, we analysed whether there was a preference by kestrels for a certain sward height when hunting. Compositional analysis showed significant differences in the use by kestrels compared to the availability of different sward heights ($\lambda=0.0052$, $P<0.001$, Table 2). Sixty-five per cent of the hunting activity occurred on freshly mown grassland (Fig. 2a). Freshly mown low-intensity meadows were used 14.5 times more frequently than expected from their availability and freshly mown artificial grassland 2.5 times more frequently (Fig. 2a). Swards higher than 20 cm were used less than expected, in particular the artificial grassland.

habitat availability and use when dividing up the freshly mown grassland into those bordering a wild flower or herbaceous strip and those not adjacent to such strips (compositional analysis $\lambda=0.0548$, $P<0.05$, Table 3). Freshly mown low-intensity meadows bordering a wild flower or herbaceous strip were used 55 times more frequently than expected from their availability (Fig. 3a), and they were significantly preferred over the other grassland types (Table 3). Freshly mown artificial grassland adjacent to strips was used 6.3 times more frequently than expected, freshly mown low-intensity meadows not bordering a strip 7.4 times and freshly mown artificial grassland not bordering a strip 2.0 times more frequently, but there was no significant difference in preference to the remaining grassland types (Table 3).

Effect of neighbouring wild flower strips or herbaceous strips

Because the density of small mammals on low-intensity meadows and artificial grassland, the habitat types most frequently used by kestrels, was much lower than in wild flower and herbaceous strips (Aschwanden et al., in preparation), we tested whether kestrels preferred to hunt on grassland bordering a wild flower or herbaceous strip. Clearly, there was a significant difference between

Hunting effort and success

During a total of 28.9 h in 109 observation periods (mean observation period 16 min), 146 hunting attempts were observed (5.0 h^{-1}), among them 48 successful ones and 7 with unknown result (1.7–2.0 successful hunts per h, success rate 33–38%). Fifty-one per cent of the hunting attempts were from hovering flights, 49% from perches. The 48 successful hunting attempts occurred only on low-intensity meadows (13) and on artificial grassland (35) (Fig. 4). Comparing successful and unsuccessful hunting attempts, there were no significant

Table 2 Compositional analysis comparing the use of different habitat types by hunting common kestrels for low-intensity meadows and artificial grassland divided by sward height

Habitat type	Low-intensity meadows			Artificial grassland			Rank
	Freshly mown	< 20 cm	> 20 cm	Freshly mown	< 20 cm	> 20 cm	
Low-intensity meadows							
Freshly mown		5.44**	2.73**	2.40*	3.83**	4.82**	5
< 20 cm	-5.44**		-1.01	-4.10**	-3.62**	-3.58**	0
> 20 cm	-2.73**	1.01		-2.64**	-1.85	-1.63	1
Artificial grassland							
Freshly mown	-2.40*	4.10**	2.64**		2.25*	4.06**	4
< 20 cm	-3.83**	3.62**	1.85	-2.25*		1.77	3
> 20 cm	-4.82**	3.58**	1.63	-4.06**	-1.77		2

Total significance: $\lambda=0.0052$, $P<0.001$. The matrix of t -values comparing all habitat types against each other with indication of their significance ($*P<0.1$, $**P<0.05$) is given. See also notes to Table 1

Fig. 2 Comparison of availability and use for hunting activities of **a** common kestrels ($n=142$ hunting attempts + 176 perch locations + 296 hover flights) and **b** long-eared owls ($n=33$ hunting attempts + 23 perch locations) in relation to sward height of low-intensity meadows and artificial grassland

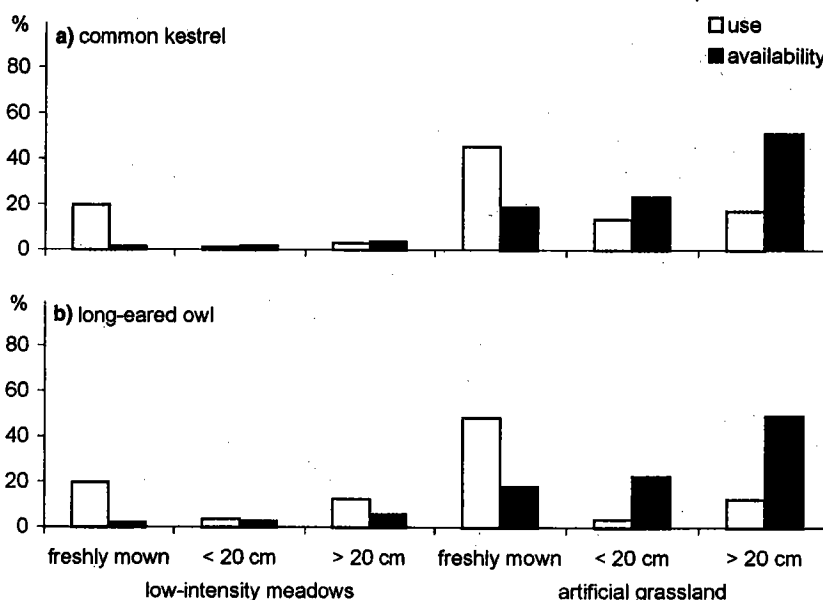


Table 3 Compositional analysis comparing the use of different habitat types by hunting common kestrels for low-intensity meadows and artificial grassland divided by sward height, by presence (+) or absence (-) of neighbouring wild flower or herbaceous strips

Habitat type	Low-intensity meadows freshly mown		Artificial grassland freshly mown		Artificial grassland and low-intensity meadows not freshly mown		Rank
	+	-	+	-	+	-	
Low-intensity meadows freshly mown							
+		3.00**	3.30**	3.50**	3.45**	4.85**	5
-	-3.00**		1.25	-0.09	3.21**	0.97	3
Artificial grassland freshly mown							
+	-3.30**	-1.25		-0.43	2.05	0.67	2
-	-3.50**	0.09	0.43		1.20	4.36**	4
Artificial grassland and low-intensity meadows not freshly mown							
+	-3.45**	-3.21**	-2.05	-1.20		-0.23	0
-	-4.85**	-0.97	-0.67	-4.36**	0.23		1

Total significance: $\lambda=0.0548$, $P < 0.05$. The matrix of t -values comparing all habitat types against each other with indication of their significance ($*P < 0.1$, $**P < 0.05$) is given. See also notes to Table 1

effects of habitat type, presence of neighbouring wild flower or herbaceous strips, vegetation height, vegetation density and hunting mode (hovering and perch) (logistic regression analysis).

Long-eared owl

Habitat types

Most hunting activity of long-eared owls occurred on artificial grassland (48%) and on low-intensity meadows (26%), while 13% of observations were in autumn-sown wheat, 4% in wild flower strips, 1% in herbaceous strips and 8% in other habitat types (out of a total of 84 hunting attempts and 60 locations of perched birds). Long-eared owls used habitat types not according to their availability ($\chi^2=87.9$, $df=5$, $P < 0.001$), but used low-intensity meadows 4.5 times more frequently than expected from availability, wild flower strips six times more frequently (but with only three hunting observations) and autumn-sown wheat two times more

frequently (Fig. 1b). Artificial grassland was used almost according to availability, and other habitat types were used less than expected (Fig. 1b).

Vegetation height of meadows and grassland

Long-eared owls showed preferences in the use of grassland according to vegetation height and type ($\chi^2=140.4$, $df=5$, $P < 0.001$). Freshly mown low-intensity meadows were used 9.4 times and freshly mown artificial grassland 2.7 times more frequently than expected (Fig. 2b). Long-eared owls also preferred low-intensity meadows > 20 cm, but only before 15 June when there were no freshly mown low-intensity meadows available yet.

Effect of neighbouring wild flower strips or herbaceous strips

Long-eared owls hunted more often than expected on low-intensity meadows and artificial grassland that

Fig. 3 Comparison of availability and use for hunting activities of **a** common kestrels ($n=142$ hunting attempts + 176 perch locations + 296 hover flights) and **b** long-eared owls ($n=33$ hunting attempts + 23 perch locations) in habitat types with (+) or without (-) adjacent wild flower or herbaceous strips

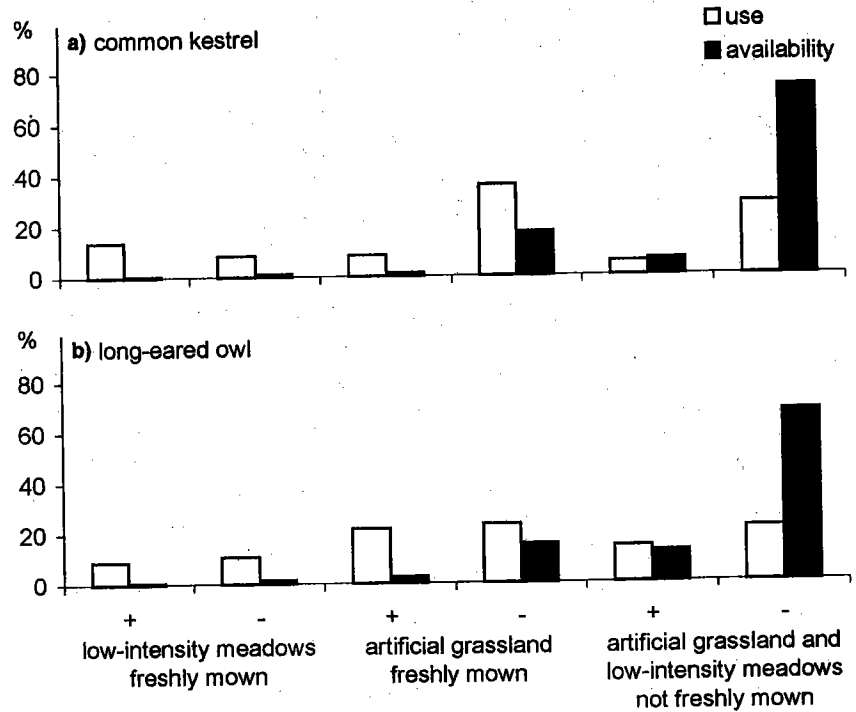
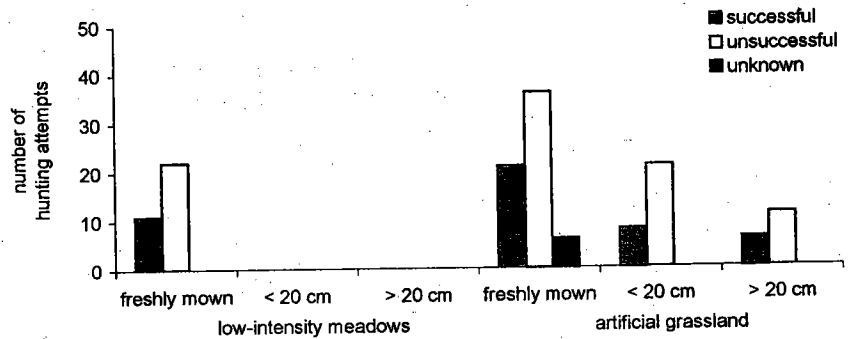


Fig. 4 Hunting success of common kestrels. Number of successful and unsuccessful hunting attempts ($n=142$)



bordered a wild flower or a herbaceous strip than on such habitats not bordering a wild flower or a herbaceous strip. This was significant for freshly mown surfaces ($\chi^2=28.05$, $df=1$, $P<0.001$, $n=36$ hunting attempts) as well as for taller vegetation ($\chi^2=9.32$, $df=1$, $P<0.01$, $n=20$). Long-eared owls used freshly mown surfaces bordering wild flower or herbaceous strips 15.8 times (low-intensity meadows) and 8.5 times (artificial grassland) more frequently than expected (Fig. 3b). Meadows and grassland not freshly mown and bordering a wild flower or herbaceous strip were used according to availability, while those not bordering a strip were clearly not preferred (Fig. 3b).

Hunting effort and success

Hunting long-eared owls were observed during a total of 5.9 h in 32 uninterrupted periods (mean 11 min per period). Out of 84 hunting attempts (14.4 h^{-1}), only 7 (8%) were successful and in 6 (7%) the result was

unknown (1.2–2.2 successful hunts per h). Seventy-nine per cent of the hunting attempts were from owls in flight and 21% from perched owls. The 7 successful hunts occurred on freshly mown artificial grassland (4), freshly mown low-intensity meadows (2) and 1 on a wild flower strip. The low number of successful hunts prevented a statistical analysis.

Discussion

Neither kestrels and long-eared owls hunted in the different habitat types according to their availability. Both study species hunted most frequently on low-intensity meadows and artificial grassland. Here, densities of small mammals amounted to only about 12% of the small mammal densities observed in July in wild flower ($1,046 \text{ ha}^{-1}$) and herbaceous (836 ha^{-1}) strips and 20% of those in autumn-sown wheat (561 ha^{-1}) (Aschwan- den et al., in preparation). Therefore, the use of the different habitat types for hunting was not related to

prey density, as was observed in several small mammal eating species of birds (ferruginous hawk, *Buteo regalis*, Wakeley 1978; red-tailed hawk, *B. jamaicensis*, and rough-legged buzzard, *B. lagopus*, Baker and Brooks 1981; Swainson's hawk, *B. swainsoni*, Bechard 1982; American kestrel, *Falco sparverius*, Sheffield et al. 2001; common buzzard, *B. buteo*, common kestrel, grey heron, *Ardea cinerea*, and white stork, *Ciconia ciconia*, in northern Germany, Hämker and Borstel 2003).

Among the mainly used artificial grassland and low-intensity meadows, kestrels and long-eared owls clearly preferred those freshly mown. It appeared that small mammals on freshly mown grassland were more accessible than in wild flower and herbaceous strips, despite their 8-times lower density. On freshly mown grassland, a much larger surface can be scanned for prey, and prey is probably detected from a greater distance, because there is no protective plant cover for small mammals and because the grassland surfaces were much larger than the small wild flower and herbaceous strips. Moreover, plant stems do not interfere with catching the prey. The densest vegetation occurred on wild flower and herbaceous strips and consisted of different species of herbaceous plants (e.g. *Cirsium* spp., *Dipsacus sylvestris*, *Hypericum perforatum*, *Malva sylvestris*, *Verbascum* spp.). During the summer, these plants dry out and become an inflexible, bristly and dense plant cover, which greatly reduces the accessibility to prey. Therefore, vegetation structure seems to have been the dominant factor for selecting hunting sites by both bird species. Similarly, in the raptor studies mentioned above the density of vegetation was assumed to be of greater importance for the choice of hunting sites than prey density.

Because kestrels and long-eared owls preferred freshly mown artificial grassland and low-intensity meadows, it might be expected that hunting was more successful there than on unmown surfaces. Interestingly, the success rate of hunting attempts of kestrels did not differ between habitat types and vegetation heights of grassland. Long-eared owls made 14.4 hunting attempts per h, but only about 8% were successful, whereas kestrels only made 5 hunting attempts per h, but 33% of the hunting attempts were successful. Thus, both species arrived at about 1–2 successful hunts per h. The difference in the frequency of hunting attempts is probably due to differences in prey detectability. Kestrels are visually hunting diurnal raptors, which are able to discover a beetle from 50 m and a bird from 300 m (Kostrzewa and Kostrzewa 1993). In contrast, nocturnally hunting long-eared owls use mainly their sense of hearing (Mebs and Scherzinger 2000). Therefore, long-eared owls usually hunt by flying low (1.5 m) above the vegetation (Voous and Cameron 1988). A short attack distance probably reduces the time to react and to decide whether a hunting attempt will be successful or not. Thus, every potential noise or movement of a small mammal requires a fast reaction from the owl. In contrast, kestrels usually fly high above their territory and are additionally able to

hover. As a consequence, they have ample time to observe prey and to wait (by hovering) for the right moment to attack.

We do not have data on the rate of prey catching in different habitat types, because the small plots did not allow us to observe hunting birds long enough in one type of habitat. It seems likely that hunting on freshly mown grassland was more profitable, because kestrels could more quickly find a relatively exposed prey to catch. The few successful hunts observed in long-eared owls do not allow further interpretations. One interesting point is the observation that kestrels used low-intensity meadows only after they were freshly mown (Fig. 4). Compared to kestrels, long-eared owls already hunted on low-intensity meadows before mowing, but had no success.

Although kestrels and long-eared owls did not prefer the habitat types with the highest prey density, wild flower and herbaceous strips apparently still had an influence on hunting. Kestrels and long-eared owls preferred freshly mown low-intensity meadows and artificial grassland bordering a wild flower or herbaceous strip. Presumably, small mammals from the high-density wild flower and herbaceous strips invaded the adjacent freshly mown grassland and became an easy prey for kestrels and owls.

In contrast to the situation in summer in our study, wild flower and herbaceous strips are the preferred hunting places for kestrels during winter and early spring (Buner 1998) when vegetation is shorter and less dense. These areas have higher densities of small mammals than the surrounding agricultural fields (Baumann 1996; Buner 1998; Aschwanden et al., in preparation). There is no winter study on the hunting behaviour of long-eared owls in relation to ecological compensation areas, but it is likely that they also benefit directly from these strips in winter.

In conclusion, in intensively farmed regions, ecological compensation areas, particularly those not mown each year, are an important refuge for small mammals. Therefore, these areas have positive effects on the two predator species studied, and possibly other vole hunters, by providing food. This food source can be accessed during winter when vegetation is less dense. During summer, however, when vegetation in wild flower and herbaceous strips is dense, accessibility is apparently higher on nearby freshly mown grassland and kestrels and long-eared owls prefer to hunt there. Hence, a mosaic of different habitat types with grassland mown at different times of the year together with undisturbed strips is best suited to provide a year-round supply of accessible food for vole hunters.

Zusammenfassung

Sind ökologische Ausgleichsflächen attraktive Jagdgebiete für Turmfalken (*Falco tinnunculus*) und Waldohreulen (*Asio otus*)?

Die Bestände von Turmfalken *Falco tinnunculus* und Waldohreulen *Asio otus* haben in landwirtschaftlich intensiv bewirtschafteten Regionen abgenommen. Ein Grund für diese Entwicklung sind sinkende Wühlmauspopulationen der Gattung *Microtus*. Gegen den zunehmenden Verlust an Biodiversität in intensiv bewirtschafteten Regionen fordert das Schweizer Gesetz, dass 7% der Betriebsfläche eines Landwirtes als ökologische Ausgleichsfläche bewirtschaftet wird. Zu diesen Flächen gehören Buntbrachen und Krautsäume, welche nicht jedes Jahr gemäht werden und daher zum Teil eine bis zu acht Mal höhere Kleinsäugerdichte aufweisen, als intensiv bewirtschaftete Flächen. Diese Studie untersucht ob Turmfalken und Waldohreulen ökologische Ausgleichsflächen als Jagdhabitat bevorzugen und ob die Präferenz vom Kleinsäugerangebot oder von der Vegetationsdichte und Höhe abhängig ist. Beide Arten jagten trotz geringer Kleinsäugerdichten hauptsächlich auf frisch gemähten Extensiv- und Kunstwiesen. Folglich war die Struktur der Vegetation für die Auswahl der Jagdhabitate wichtiger als das Beuteangebot. Allerdings wurden Kunst- und Extensivwiesen bevorzugt, welche an Buntbrachen oder Krautsäume direkt angrenzten. Wahrscheinlich wurden Wühlmäuse, welche diese Flächen verliessen, zur leichten Beute auf den angrenzenden frisch gemähten Wiesen. In intensiv bewirtschafteten Regionen sind ökologische Ausgleichsflächen, die nicht jedes Jahr gemäht werden, ein wichtiges Rückzugsgebiet für Kleinsäuger. Im Sommer sind diese für jagende Vögel jedoch nicht direkt erreichbar. Ein Mosaik aus verschiedenen Habitattypen mit abwechselnd gemähten Wiesen und ungestört belassenen Landstreifen kann das ganze Jahr hindurch erreichbare Nahrung für Turmfalken und Waldohreulen bieten.

Acknowledgments We thank the arsenal of Sursee for providing the ambient light intensifier, the Wauwiler Moos prison and local farmers for information about work planned on their fields (mowing and harvesting dates) and for allowing access to their farmland, Karl Langenstein for information about the birds and their nesting sites, Verena Keller, Reto Spaar and Niklaus Zbinden 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 Reyher for his supervision and comments on the thesis.

References

- Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325
- Baker JA, Brooks JR (1981) Distribution patterns of raptors in relation to density of Meadow Voles. *Condor* 83:42–47
- Baumann L (1996) The influence of field margins on populations of small mammals—a study of the population ecology of the common vole *Microtus arvalis* in sown weed strips. MSc Thesis, University of Berne, Switzerland
- Bechard MJ (1982) Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84:153–159
- Birrer S (1993) Bestand und Bruterfolg der Waldohreule *Asio otus* im Luzerner Mittelland, 1989–1992. *Ornithol Beob* 90:189–200
- Birrer S (2003) Bestandsentwicklung der Waldohreule *Asio otus* in der Schweiz. *Vogelwelt* 124:255–260
- Buner F (1998) Habitat use of wintering Kestrels (*Falco tinnunculus*) in relation to perch availability, vole abundance and spatial distribution. MSc Thesis, University of Basel, Swiss Ornithological Institute Sempach, Switzerland
- Butet A, Leroux ABA (2001) Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biol Conserv* 100:289–295
- Graf R (1999) Vom Reservat in die Fläche—Ein Revitalisierungs- und Informationsprojekt für die Wauwiler Ebene. *Mitt Naturf Ges Luzern* 36:347–357
- Hagemeyer WJM, Blair MJ (1997) The EBCC atlas of european breeding birds: their distribution and abundance. Poyser, London
- Hämker S, Borstel K (2003) Langzeituntersuchung über den Zusammenhang zwischen Kleinsäugerbestand und Anzahl der Greifvögel auf dem Flughafen Bremen unter Berücksichtigung der veränderten Grünlandbewirtschaftung. *Vogel Luftverkehr* 23:31–32
- Harder W (1998) Parlament verabschiedet "Agrarpolitik 2002". *Agrarforschung* 5:229–232
- Henrioux F (1999) *Écologie d'une population de Hibou moyen-duc Asio otus en zone d'agriculture intensive*. PhD Thesis, University of Neuchâtel, Switzerland
- Illner H (1988) Langfristiger Rückgang von Schleiereule *Tyto alba*, Waldohreule *Asio otus*, Steinkauz *Athene noctua* und Waldkauz *Strix aluco* in der Agrarlandschaft Mittelwestfalens 1974–1986. *Vogelwelt* 109:145–151
- Korpimäki E (1984) Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. *Ann Zool Fenn* 21:287–293
- Korpimäki E, Norrdahl K (1991) Numerical and functional responses of Kestrels, short eared owls, and long eared owls to vole densities. *Ecology* 72:814–826
- Kostrzewska R, Kostrzewa A (1993) Der Turmfalke. Sammlung Vogelkunde im AULA-Verlag. AULA-Verlag, Wiesbaden
- Leban (1999) Resource Selection for Windows, Version 1.00 Beta 8.4: www.msu.edu/course/fw/424/Fred%20Leban/
- Mebis T, Scherzinger W (2000) Die Eulen Europas. Kosmos, Stuttgart
- Oppermann R, Gujer HU (2003) Artenreiches Grünland bewerten und fördern—MEKA und ÖQV in der Praxis. Ulmer, Stuttgart
- Schmid H (1990) Die Bestandsentwicklung des Turmfalken *Falco tinnunculus* in der Schweiz. *Ornithol Beob* 87:327–349
- Schmid H, Burkhardt M, Keller V, Knaus P, Volet B, Zbinden N (2001) Die Entwicklung der Vogelwelt in der Schweiz. Avifauna Report Sempach 1, Annex. Schweiz. Vogelwarte Sempach
- Sheffield LM, Craik JR, Edge WD, Wang GN (2001) Response of American kestrels and gray-tailed voles to vegetation height and supplemental perches. *Can J Zool* 79:380–385
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton
- Tattersall FH, MacDonald DW, Manley WJ, Gates S, Feber R, Hart BJ (1997) Small mammals on one-year set-aside. *Acta Theriol* 42:329–334
- Village A (1998) *Falco tinnunculus* Kestrel. BWP Update 2:121–136
- Voous KH, Cameron A (1988) Owls of the northern hemisphere. Collins, London
- Wakeley J (1978) Factors affecting the use of hunting sites by Ferruginous Hawks. *Condor* 80:316–326
- White GC, Garrott RA (1990) Habitat analysis. In: Analysis of wildlife radio-tracking data. Academic Press, San Diego London, pp183–205
- Wijnandts H (1984) Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* 72:1–92
- Ziesemer F (1973) Siedlungsdichte und Brutbiologie von Waldohreule, *Asio otus*, und Turmfalk, *Falco tinnunculus*, nach Probeflächenuntersuchungen. *Corax* 4:79–92