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The harvest mouse (*Micromys minutus* Pallas, 1771) as prey: a literature review

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Abstract. The harvest mouse is a prey item for numerous vertebrates in various habitats, ranging from marshes and farmland, to urbanized areas. It has no specialised avian or mammalian predator and it always represents a low proportion of their diet, except in some wetlands where its frequency can exceed 40 % of total mammals taken by owls, which confirms the harvest mouse preference for this kind of habitat. Conversely, it is a much less important prey in farmlands. In Europe, barn owl (*Tyto alba*), long-eared owl (*Asio otus*), tawny owl (*Strix aluco*) and to a lesser extent little owl (*Athene noctua*) are the major avian predators of harvest mouse. Among carnivores, polecat (*Mustela putorius*) seems to be the main predator for the harvest mouse, but the scarcity of literature does not allow definitive conclusions. The influence of snow cover on the availability of harvest mice for raptors is pointed out, since this mouse tends to move above snow and therefore becomes easier prey than other rodents. Moreover, it seems that carnivores may be more efficient than raptors for hunting *Micromys* mice, probably because of their way of foraging amongst tall vegetation that makes them more likely to discover harvest mice.

Key words: rodent, predation, habitat, winter

Introduction

The harvest mouse is a tiny and elusive mammal, widespread in the Palaearctic and Indomalayan regions, from Spain and Great Britain to Japanese islands (Wilson & Reeder 2005). Whereas IUCN has assigned the status "least concern" to this species (Aplin et al. 2008), the harvest mouse has the growing attention of scientists and naturalists in some countries like Switzerland and Great Britain where its populations have declined during recent decades (Harris et al. 1995, Perrow & Jowitt 1995, Blant et al. 2012). Recently, several programs of biological conservation survey and species management have been planned in these countries in order to restore the populations of harvest mouse (Macdonald et al. 2001, Kean 2006). Among important parameters in such restoration projects, the risk of predation needs to be assessed to assure the viability of reintroduced individuals. A lot of scientific articles have been published since the beginning of the 2000s which specify feeding habits of avian raptors and carnivores, particularly in central Europe, and which allow assessment of the importance of the harvest mouse as prey. Moreover, a large dataset of harvest mouse predation by raptors and mammals in France offers new information about the efficiency of each group of predators. It was thus interesting to re-assess the role of this little known species, almost forty years after Trout's report (1978) which is still the only review.

Material and Methods

Search strategy

A search was conducted to find references addressing topics related to predation of the harvest mouse in Europe. Firstly with Google Scholar and then three main electronic databases that cover international literature in environmental science: Web of Science, ScienceDirect and SpringerLink. Additionally, an internet search was conducted to find grey literature (i.e. literature that has not been published in peer-reviewed journals). The terms used for each search are "micromys" added to "diet" or "feed" or "foraging", and "diet" added to the predator's name. Secondly, the literature mentioned in these articles was screened to identify new references. Then searches were made of some references in books at the library of the Museum National d'Histoire Naturelle (Paris). It should be noted that a great proportion of pellets and scats surveys are made by naturalist societies which often publish in regional revues that are not easy to find. The search

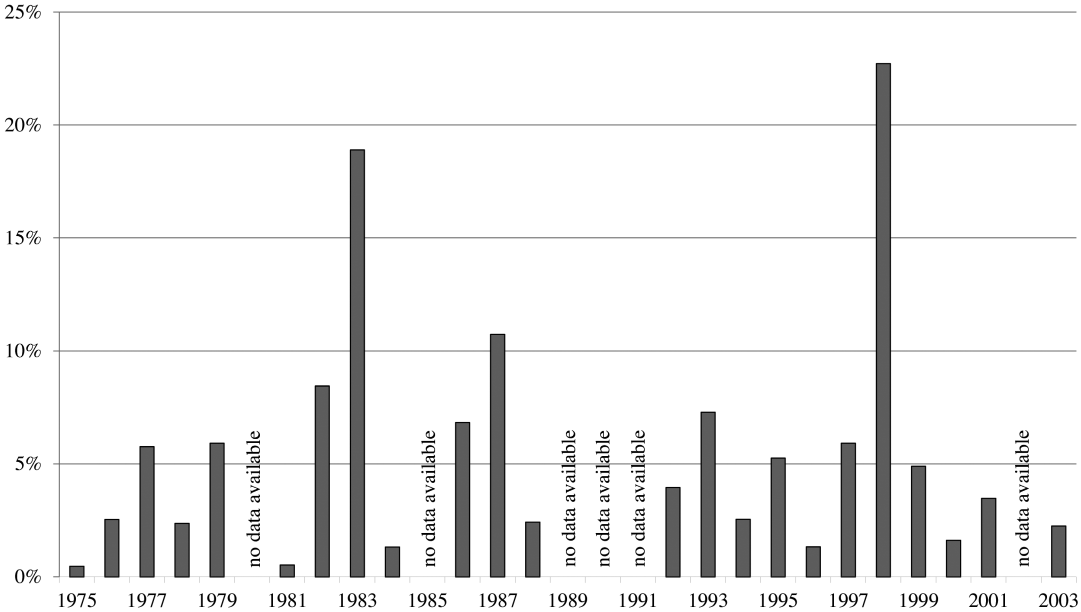

Fig. 1. Changes in the annual percentage of harvest mouse preyed by barn owl at Outines (Marne, France), from LPO dataset. See text page 127.

strategy did not have any language restriction but only papers published in English, French, Spanish, Italian and German could be used; others were only used when they contained a detailed abstract in English.

Reviewing

Studies were selected that met the two following criteria: (1) provided results from empirical research, (2) only quantitative results (total number of prey with number of specimens for each prey species or percentage of each prey). For each study site, the harvest mice frequency is calculated with the total number of mammals preyed, which is not necessarily the same as the total amount of prey, especially for primarily insectivorous birds of prey.

Additional data

The small mammal inventory that was conducted in the Champagne-Ardenne region (France) by the Ligue pour la Protection des Oiseaux (LPO) since 1970s provided 671067 prey items of 24 micromammal species, from several predators. This huge dataset has been generously made available by the LPO to the author in order to analyse specifically the harvest mouse contribution.

Results

The harvest mouse, a prey item for numerous avian raptors

In the whole of Europe, avian predators for harvest mouse include owls, harriers, falcons, buzzards, eagles, kites, shrikes, corvids, herons and even pheasants (Table 1); unfortunately, quantitative data are not available for each of these species. When it is present in their diet, the harvest mouse is always in low frequency and therefore surveys of avian raptor diet often do not quote *Micromys* as an item. Moreover, due to its low frequency in avian diet and to its small weight (6-8 g), harvest mouse usually represents a low biomass compared to other more frequent rodents like common vole (*Microtus arvalis*), bank vole (*Myodes glareolus*), field vole (*Microtus agrestis*) or wood mouse (*Apodemus sylvaticus*). Even when harvest mouse is an important prey by number, it never exceeds 10 % of the total biomass ingested by owls (Table 1). Caloric value of harvest mouse, equal to 23.78 kJ/g of dry weight, is rather high compared to other micromammals: 23.48 kJ/g for common vole, 21.68 kJ/g for wood mouse and 22.73 kJ/g for shrews (Soricidae) (Wijnandts 1984). However, according to this author, avian raptors seem to metabolize this energy with less efficiency than for other prey. For example, with long-eared owl, several tests tend to reveal that metabolizable energy coefficient, i.e. (kJ food intake – kJ rejecta)/kJ food intake, is the lowest for *Micromys* (0.61) compared to common vole (0.68), wood mouse (0.79) and shrews (0.62). Moreover, the weight percentage rejected in the pellets is high for the harvest mouse (25.4 %). As the compiling study is based on data gained with different methods from different people, their respective quality is not possible to judge. Due to the very delicate bones of

Table 1. European avian predators for the harvest mouse (*Micromys minutus*) according to the literature with available quantitative data. un. – unvailable data, * total prey (not only mammals) and unused for „Total“, ** on total prey (not only mammals).

	N (total mammals)	n (*Micromys minutus*)	%n range (on total mammals)	%n median (on total mammals)	% Biomass Range (on total prey)	Most frequent mammal prey by number (in quoted literature)	
barn owl *Tyto alba*	416832	9679	0.1-23.3	1.6	0.1-5.1	*Microtus arvalis*	Agnelli & Lazzeretti 2009, Alivizatos et al. 2005, Bon et al. 1992, 1997, Bosè & Guidali 2001, Buckley 1977, Buckley & Goldsmith 1975, Cserkész 2007, De Bruijn 1994, Godin 1975, Gonzales Oreja et al. 1993, Gotta & Pigozzi 1997, Hetmański et al. 2008, Indelicato 2000, Janžekovič & Ficko 2000, Kalivoda 2001, Karanović 1991, Kitowski 2013, Latková 2008, Lustrat 2002, Meek 2011, Millán de la Pena et al. 2003, Milchev et al. 2006, Miltschev et al. 2004, Obuch 2011, Pailley & Pailley 2000, Petrovici et al. 2013, Plass 2004, Purger 1990, 2014, Rolland 2011, Ružić et al. 2009, Sándor 2009, Sommer et al. 2009, Spitzenberger & Steiner 1975, Temme 2006, Uttendörfer 1952, Ważna et al. 2011, Wuntke & Ludwig 1998, Zabala 1973
long-eared owl *Asio otus*	100935	2464	0.09-27.6	3	0-5.4	*Microtus arvalis*	Balčiauskiene et al. 2006, Bencová et al. 2006, Benedek & Sîrbu 2010, Canova 1989, Dolenec & Kiš 2010, Dupal & Chernyshow 2013, Dziemian et al. 2012, Galeotti et al. 1997, Hetmański et al. 2008, Kafkaletou-Diez et al. 2008, Kopij et al. 2012, Nistreanu 2007, Petrovici et al. 2013, Pirovano et al. 2000, Roulin 1996, Rubolini et al. 2003, Stasiak et al. 2014, Ternois 1999, Tome 2000, 2009, Tulis 2011, Uttendörfer 1952, Wavrin et al. 1991, Wiącek et al. 2008, 2011
tawny owl *Strix aluco*	150432	1246	0.01-15.5	1.9	0-5.3	*Microtus arvalis* *Myodes glareolus*	Balčiauskas et al. 2011, Balčiauskiene et al. 2006, Baudvin & Jouaire 2006, Capizzi 2000, Gryz et al. 2008, Grzędzicka et al. 2013, Kuhar et al. 2006, Lesiński et al. 2009, 2013, Lesiński & Stolarz 2012, Obuch 2011, Poláček et al. 2012, Romanowski et al. 2013, Romanowski & Zmihorski 2009, Roulin et al. 2008, Tishechkin 1997, Uttendörfer 1952, Wiącek et al. 2008, 2009, Zalewski 1994, Żmihorski & Osojca 2006
common buzzard *Buteo buteo*	10603*	609	1.8**		un.	un.	LPO Champagne-Ardennes (unpublished)
little owl *Athene noctua*	6114	343	0.7-42	6.8	1-9.3	*Microtus arvalis*	Alivizatos et al. 2005, Bon et al. 2001, Gotta & Pigozzi 1997, Ławicki & Racławski 2006, Obuch 2011, Pocora et al. 2012, Romanowski et al. 2013, Schmitt & Hofer 2011, Šálek et al. 2010
Tengmalm's owl *Aegolius funereus*	17448	298	0.04-3.3	2.3	0.9-1.2	*Microtus arvalis*	Korpimäki 1986, 1988, Obuch 2011, Zárybnická et al. 2009
kestrel *Falco tinnunculus*	5458	174	0.3-2.5	2.4	0.1-1.1	*Microtus arvalis*	Boratyński & Kasprzyk 2005, Casagrande et al. 2008, Kečkéšová & Noga 2008, Kitowski 2014, Shrubb 1980, Skierczyński 2006, Żmihorski & Rejt 2007

red kite *Milvus milvus*	4230*	93	2.2**		un.	un.	LPO Champagne-Ardennes (unpublished)
Eurasian eagle owl *Bubo bubo*	30630	70	0.07-24.8	0.1	un.-0.5	*Microtus arvalis*	Mikkola & Tornberg 2014, Obuch 2011, Obuch & Karaska 2010
Montagu's harrier *Circus pygargus*	2035	59	0.6-3	1.9	0.2-un.	*Microtus arvalis*	Koks et al. 2007, Wiącek & Niedźwiedź 2005
Ural owl *Strix uralensis*	2604	37	0.4-12	0.8	0.1-3	*Apodemus flavicollis*	Kociuba 2012, Obuch et al. 2013, Vrezec 2001
great grey shrike *Lanius excubitor*	663	29	4.4		un.	*Microtus arvalis*	Brzeziński et al. 2010
pygmy owl *Glaucidium passerinum*	3014	28	0.6-15	0.8	0	*Microtus arvalis*	Halonen et al. 2007, Mikusek et al. 2001, Obuch 2011
hen harrier *Circus cyaneus*	297	23	1.8-14	7.5	un.	*Microtus arvalis*	Schipper 1973, Toffoli 1994
short-eared owl *Asio flammeus*	1244	23	1-5.8	1.9	0.5-un.	*Microtus arvalis*	Buckley 1973, Dupal & Chernyshow 2013, Noga & Dobry 2013, Szymański et al. 2010, Trnka & Obuch 2006, Uttendörfer 1952
Eurasian scops owl *Otus scops*	59	17	29		un.	*Microtus arvalis*	Bavoux et al. 2003
lesser spotted eagle *Aquila pomarina*	1601	4	0.2-1.9		0	*Microtus arvalis*	Meyburg 1970, Zub et al. 2010
hawk owl *Surnia ulula*	732	4	0.6		un.	*Myodes* sp.	Mikkola 1972
great gray owl *Strix nebulosa*	1517	3	0.7		un.	*Myodes glareolus*	Tishechkin 1997
imperial eagle *Aquila heliaca*	359	3	0.8		0.01	*Erinaceus roumanicus*	Demerdzhiev et al. 2014
greater spotted eagle *Aquila clanga*	322	2	0.6		un.	*Arvicola amphibius*	Dombrovski 2010
marsh harrier *Circus aeruginosus*	151	2	1.3		0.5	*Microtus arvalis*	Kitowski 2005
Total	742447	15209					

Table 2. Proportion of harvest mouse in the diet of the four main raptors. N – total mammal prey items, n – number of harvest mouse prey items in quoted literature (selection for n > 20), n% – percentage of harvest mouse prey items compared with total mammal prey items; Wet = wetland, Boc = bocage landscape, Wood = woodland, Farm = farmland, Urb = urbanized area, Mix = mixed habitats.

	Tyto alba barn owl			*Asio otus* long-eared owl			*Strix aluco* tawny owl			*Athene noctua* little owl				
	N	n	n%	N	n	n%	N	n	n%	N	n	n%	Habitat	
Austria	2670	39	1.5										Boc	Spitzenberger & Steiner 1975
Belarus							1517	30	2				Boc	Tishechkin 1997
Bulgaria	4842	66	1.4										Boc	Milchev et al. 2006
Bulgaria	23436	372	1.6										Boc	Miltschev et al. 2004
Czech republic				2701	40	1.5							Urb	Bencová et al. 2006
France	59109	233	0.4										Mix	Indelicato 2000
France	55515	783	1.4										Mix	Rolland 2011
France	6228	158	2.5										Boc	Millán de la Pena et al. 2003
France	52668	1495	2.8										Mix	Pailley & Pailley 2000
France							51734	28	0.05				Wood	Baudvin & Jouaire 2006
Germany	522	25	4.8										Farm	Wuntke & Ludwig 1998
Germany	794	77	9.7										Wet	Temme 2006
Great Britain	16481	226	1.4										Mix	Meek 2011
Greece				988	24	2.4							Farm	Kafkaletou-Diez et al. 2008
Greece										273	49	18	Wet	Alivizatos et al. 2005
Hungary	9693	152	1.6										Farm	Purger 2014
Hungary	23200	928	4										Boc	Cserkész 2007
Hungary	6131	313	5.1										Farm	Kalivoda 2001
Italy	4030	167	4.1										Farm	Bosè & Guidali 2001
Italy	4309	283	6.6										Farm	Bon et al. 1997
Italy	1233	100	8.1										Wet	Bon et al. 1992
Italy	200	24	12										Wet	Agnelli & Lazzeretti 2009
Italy										195	26	13	Farm	Bon et al. 2001
Italy	1472	270	23.3							348	78	25	Wet	Gotta & Pigozzi 1997
Italy				2511	132	5.3							Urb	Pirovano et al. 2000
Italy				2478	132	5.3							Farm	Rubolini et al. 2003
Italy				254	23, 88	9.4							Wet	Canova 1989
Italy				235	51, 94	22							Wet	Canova 1989

Italy				2247	620	27.6							Farm	Galeotti et al. 1997
Lithuania							1211	24	2				Mix	Balčiauskas et al. 2011
Moldova				4238	29	0.7							Urb	Nistreanu 2007
Netherlands				963	21, 19	2.2							Boc	Wijnandts 1984
Netherlands	9605	37	0.4										Wet-Farm	De Bruijn 1994
Poland				1976	97	4.9							Urb	Dziemian et al. 2012
Poland				3351	31	9							Farm	Wiącek et al. 2011
Poland				244	23	9.4							Urb	Kopij et al. 2012
Poland	30044	430	1.4										Boc	Ważna et al. 2011
Poland				1277	26	2							Urb	Wiącek et al. 2008
Poland										3090	22	0.7	Farm	Romanowski et al. 2013
Poland							3813	100	2.6				Farm	Kitowski & Pitucha 2007
Poland							7522	293	3.9				Boc	Lesiński et al. 2013
Poland							1038	64	6.2				Farm	Romanowski et al. 2013
Poland	1236	42	3.4										Farm	Kitowski 2013
Romania	1370	177	11.9										Wet	Sándor 2009
Romania				546	57	10.4							Urb	Benedek & Sîrbu 2010
Romania										60	25	42	Wet	Pocora et al. 2012
Serbia	2179	65	3										Farm	Ružić et al. 2009
Slovakia	9812	143	1.5										Boc	Latková 2008
Slovakia	49479	1028	2	49938	584	1.2	46743	360	0.8	1508	111	7.4	Mix	Obuch 2011
Slovakia				714	50	7							Farm	Tulis 2011
Slovakia							1237	99	8				Wet	Obuch 2011
Slovenia				3712	100	2.7							Mix	Tome 2000
Slovenia				10129	303	3							Farm	Tome 2009
Spain	1119	27	2.4										Farm	Zabala 1973
Total	377377	7660		88502	2345		114815	998		5474	311			
Median			2.8			5.1			2.3			15.6		

Micromys minutus, the portion of it in analyses maybe slightly underestimated in many studies except when these are based on crop or stomach analyses.

In the quoted literature, four raptors are the major predators of harvest mouse (Table 1): the barn owl (*Tyto alba*), the long-eared owl (*Asio otus*), the tawny owl (*Strix aluco*) and to a lesser extent the little owl (*Athene noctua*). Of 15209 specimens of harvest mice found in samples of the regurgitated pellets, 90 % were preyed upon by these owls and the barn owl is responsible for 64 % of the total. It seems that most of prey individuals are young animals: in a Great Britain survey, 74 % of the males were pubertal or prepubertal animals and 92 % of the females were low or nonparous specimens (Buckley 1977). These owls hunt out in the open but long-eared owls and tawny owls also hunt under tree canopies. Small mammals constitute their main food, with *M. arvalis* as the most important prey species and *M. minutus* as an occasional prey, rarely exceeding 5 % of the food intake. Nevertheless, it can constitute more than 20 % and exceptionally 42 % of the diet in particular conditions, related to the type of habitat where birds forage and to season. These owls can also breed in various urban environments, including suburban forests, cemeteries, city parks, roadsides and abandoned buildings (Petrovici et al. 2013) where the harvest mouse represents sometimes a prey as abundant as in the countryside (Table 2). The little owl (*A. noctua*) usually lives in open landscapes such as mixed farmland (bocage) and parks, but it is a fact that the number of individuals has declined in these appropriate habitats across Europe, due to new agricultural practices. Pocora et al. (2012) assume that marshes could offer new suitable hunting habitats for this owl, according to the huge percentage of harvest mouse hunted by the little owl in the Danube Delta, equal to 42 % of total mammal prey. Although mammals usually represent a small portion of its diet, the frequency of harvest mice is also very high in other wetlands such as rice fields and water meadows in the Sesia Natural Park (north Italy), reaching 24.8 % (Gotta & Pigozzi 1997) and 13 % (Bon et al. 2001) of total mammals preyed, or in the reedbeds and marshes of the Axios Delta (Greece), with 17.9 % (Alivizatos et al. 2005) and to a lesser extent in the Rhine alluvial marshes near Rheinberg (Germany), with 6.2 % (Schmitt & Hofer 2011).

The other owls are casual hunters of harvest mice, since the total number of individuals preyed on by all of them represents less than 6 % of the total *Micromys* items hunted, as quoted in literature. Among these raptors, there is the Eurasian eagle owl (*Bubo bubo*), the largest owl predator in Europe which mainly feeds on mammals weighing more than 200 g. In Finland, it has been shown that a high number of harvest mice in its diet may be an indication of food shortage or even starvation, when small prey specimens may be hunted as a last resort (Mikkola & Tornberg 2014). Thus, in 1990 and 2001 which were poor vole years, two eagle owls having nine harvest mice in their stomachs were discovered near the sea shore, where harvest mice live in the reed beds. Other owls live and hunt mostly in the forest: the pygmy owl (*Glaucidium passerinum*), the Tengmalm's owl (*Aegolius funereus*), the Ural owl (*Strix uralensis*), the great gray owl (*Strix nebulosa*) and the hawk owl (*Sturnia ulula*). Logically, as woody habitat is unsuitable for the harvest mouse, they constitute scarce prey for these owls with low percentages of prey (Table 2). For example, in Central Europe, in Slovakia (Choč Mts., Nízke Tatry Mts. and Oravská Mts.) and in the Czech Republic (Šumava Mountains), the harvest mouse is exceptionally hunted by pygmy owl (Mikusek et al. 2001, Obuch & Karaska 2010). In the same way, it is a rare prey for the hawk owl in Finland (Mikkola 1972) and the great gray owl in Belarus (Tishechkin 1997) which feed mainly on forest voles (*Myodes* sp.). However, in particular conditions, this proportion may considerably increase, reaching 11.8 % for a female Ural owl which was wintering in a small wood surrounded with wide grasslands, marshes and fields on Ljubljansko barje, in central Slovenia (Vrezec 2001). It is a fact that winter seems to make harvest mice more vulnerable to avian raptors. In Finland, the pygmy owl hoards prey in winter and it has been shown that the proportion of small mammals in the hoarded prey decreases dramatically after snow fall, except for the harvest mouse (Halonen et al. 2007). The reason is that it feeds and moves above the snow cover and therefore becomes more vulnerable to predation than voles and shrews, which move below the snow cover (Halonen et al. 2007). As for the scops owl (*Otus scops*) which is mainly insectivorous, it can surprisingly feed heavily on harvest mouse such as on Oléron Island (France), where five mice were brought back to the nest in 58 minutes; these serial catches may reveal the exploitation of a dense population of harvest mouse (Bavoux et al. 2003).

Low proportion of harvest mouse in the diet of some raptors is more surprising, particularly for birds hunting in suitable habitats for *Micromys*, such as harriers and short-eared owl (*Asio flammeus*). In reality, the low number of surveys of their feeding habits does not allow any reliable assessment. Among harriers, the hen harrier (*Circus cyaneus*) is known for breeding mainly in reedbeds. Some surveys do not mention any *Micromys* in its diet (Marquiss 1980, Roulin 1996, Millon et al. 2002) but one tends to show that it is a significant resource for hen harrier in the Netherlands, for 13.2 % of its diet (Schipper 1973): when voles become too scarce, the hen harrier turns to prey upon birds and harvest mouse. According to the few articles found, it is difficult to determine the importance of harvest mice in Montagu's harrier (*Circus pygargus*) and marsh harrier (*C. aeruginosus*) feeding. Some authors do not quote any *Micromys* in the diet of the marsh harrier (Underhill-Day 1985, Witrowski 1989). Nevertheless, the dataset from LPO Champagne-Ardenne (France) points out that Montagu's harrier is able to significantly hunt for harvest mouse, since the proportion of *Micromys* in its diet reaches 3.5 % in this region. We could also highlight the lesser spotted eagle (*Aquila pomarina*) and the greater spotted eagle (*Aquila clanga*) which live closed to wetlands and which are known to hunt small mammals: the harvest mouse seems again to represent a small part of their diet (Meyburg 1970, Dombrovski 2010, Zub et al. 2010). Unexpected data come from Thrace region (Turkey), where the imperial eagle (*Aquila heliaca*) preys on *Micromys* in low numbers, its main prey usually being much larger (Demerdzhiev et al. 2014). Surprisingly, very few feeding-habit surveys were found about common generalist raptors like crows (Holyoak 1968), common buzzard (*Buteo buteo*) (Jędrzejewski et al. 1994, Graham et al. 1995, Selås et al. 2007) and kites (Sergio & Boto 1999). Although no quote of harvest mouse was found in the diet of these birds, the dataset from LPO Champagne-Ardenne (France) shows that harvest mice are part of the common buzzard and the red kite (*Milvus milvus*) diet, in respective proportions of 1.8 % and 2.2 % of the total prey. Moreover, Sleptsov (1947) points out that crows and also magpies (*Pica pica*) can heavily hunt for harvest mice in winter: the stomach contents of 15 magpies and 46 crows caught in Russia contained 24 and 88 *Micromys* remains, respectively. As for the kestrel (*Falco tinnunculus*), it feeds mainly on common vole but the harvest mouse is also a frequent prey, even in suburban areas (Żmihorski & Rejt 2007, Kečkéšová & Noga 2008).

The great grey shrike (*Lanius excubitor*) is not a bird of prey but it has similar behaviour and feeding habits. This shrike feeds predominantly on orthopterans and beetles in southern Europe, where the abundance of invertebrates is high, but it also captures mammals and birds in northern and central Europe. Even if the main prey items are voles, shrikes often hunt for shrews and harvest mice. These seem to be small enough to be easily killed, and may become the main mammalian alternative prey if *Microtus* voles become scarce (Brzeziński et al. 2010). In south-west Finland, harvest mice are the most numerous prey items of shrikes in midwinter, when snow cover is thick, whereas the larger *Microtus* voles dominate in autumn and late winter. In December and January, harvest mouse can reach more than 50 % of all vertebrate prey of the great grey shrike when *Microtus* voles decrease to less than 20 % (Karlsson 2007). In the Champagne-Ardenne region, a great grey shrike has been seen impaling a harvest mouse upon a broken willow stalk. Moreover, three species of shrikes (*Lanius collurio*, *L. excubitor*, *L. sphenocercus*) have been reported to hunt for *Micromys* in Russia and Germany (Sleptsov 1947).

In spite of their attraction to wetlands and marshes, herons have provided very few data of predation upon harvest mouse. They are known to be predominantly fish and amphibian eaters, but small mammals are a part of their diet too. The only reference concerns the night heron (*Nycticorax nycticorax*) in the River Po region (Italy) which consumes an important proportion of harvest mice among a small number of mammals ingested: 4 *Micromys* for a total of 16 mammals (Fasola et al. 1981). Conversely, Jakubas & Mioduszewska (2005) found no remnants of harvest mouse in 1194 pellets of grey heron (*Ardea cinerea*) in large wetlands of northern Poland. No data was found about the Eurasian bittern (*Botaurus stellaris*) which yet shows a strong preference for reedbeds where the harvest mouse also lives. As for the common pheasant (*Phasianus colchicus*), it is able to eat young harvest mice, as observed by Sleptsov (1947) in cereal crops during autumn. Nowadays, in Europe, pheasants are widespread and common in the countryside due to frequent releases for hunting game (Hume 2014), and it may become a new predator for harvest mice in suitable habitats like marshy, reedy places and hedgerows.

A prey item for mammals

Surveys of diet for European carnivores are much scarcer than for avian raptors. These latter present the advantage of regurgitating pellets easy to find and to study, whereas for mammals it is necessary to examine scats, stomachs and guts. Nevertheless, this review yields some literature that reveals a great variety of mammal predators, mainly wild ones like red fox (*Vulpes vulpes*), stone marten (*Martes foina*), polecat (*Mustela putorius*), feral mink (*Mustela

Table 3. European mammalian predators for the harvest mouse (*Micromys minutus*) according to the literature with available quantitative data. N – total mammal prey items, n – number of harvest mouse prey items in quoted literature, n% – percentage of harvest mouse prey items compared with total mammal prey items, * on total prey (not only mammals) and unused for „Total".

	N	n	%n range	%n median	
domestic cat	6225	181	0.3 - 3.2	1.3	Borkenhagen 1978, Nelson et al. 2005, Woods et al. 2003
wild cat *Felis sylvestris*	2323*	66*	2.8*		LPO Champagne-Ardennes (unpublished)
red fox *Vulpes vulpes*	1405 + 5832*	18 + 92*	2.4-5.4	2.5	LPO Champagne-Ardennes (unpublished), Meisener et al. 2014, Prigioni & Tacchi 1991, Stiebling 1998
stone marten *Martes foina*	486 + 1012*	16 + 32*	2-3.9	3.2	Baghli & Engel 2001, 2002, Bakaloudis et al. 2012, Lanski & Széles 2006, LPO Champagne-Ardennes (unpublished)
pine marten *Martes martes*	5621*	141*	2.5*		LPO Champagne-Ardennes (unpublished)
polecat *Mustela putorius*	186	12	0.2-13	4.8	Baghli & Engel 2002, Baghli et al. 2005, Malecha & Antczak 2013
American mink *Mustela vison*	1198	6	0.4-1.2	0.8	Chanin & Linn 1980, Zschille et al. 2014
Total	9500	233			

vison), pine marten (*Martes martes*), wild cat (*Felis sylvestris*) and even golden jackal (*Canis aureus*). Sleptsov (1947) and Teagle (1964) also mention weasel (*Mustela nivalis*) as a serious predator of harvest mice. Furthermore, two domestic mammals are able to hunt for harvest mice: the domestic cat and the dog. All these wild species are likely to live in suitable habitat for *Micromys* but this represents a low proportion of their diet (Table 3). The only exception quoted in literature concerns the polecat for which the harvest mouse can reach 12.9 % of total mammals consumed in summer. Many authors regard the polecat as a generalist feeder (Blandford 1987, Hanski et al. 1991, Prigioni & De Marinis 1995), as an amphibian specialist (Jędrzejewski et al. 1989, Weber 1989, Jędrzejewski et al. 1993, Lodé 1996) or even a lagomorph specialist (Blandford 1987, Lodé 1997). In fact, its diet composition is strongly affected by habitat and in wetlands polecats principally feed on rodents and anurans (Lodé 1996, Malecha & Antczak 2013). Moreover, no effect of winter was found for polecat and stone marten as for avian raptors; the share of *Micromys* is even higher in summer in their scats (Baghli & Engel 2002, Baghli et al. 2005).

Predation upon harvest mouse is not clear concerning two others mustelids known to live in wetlands. In Poland, no *Micromys* were found in annual diet of otter (*Lutra lutra*) and feral mink in river valleys of Białowieża, although simultaneous live trapping revealed that it lives there with significant populations, up to 11 % of community of micromammals (Jędrzejewska et al. 2001). In the Mazurian and Brodnica lakelands (Poland), in spring, remnants of harvest mouse occur in 0.9 % of mink scats (Brzeziński & Żurowski 1992). In Devon (Great Britain), Wise et al. (1981) showed that mammals comprised only 1.2 % of the diet of otters and 29.5 % of that of mink, but harvest mouse was found only in scats of mink on rare occasions. Conversely, in the Słońsk Reserve (West Poland), in autumn-winter, only the harvest mouse occurs in mink scats with high frequency (10 %), which nevertheless makes less than 2 % of the biomass consumed (Bartoszewicz & Zalewski 2003). Red fox is a generalist predator which mainly preys on voles in western and northern Europe (Dell'Arte et al. 2007); harvest mouse never heavily occurs in its scats. No quantitative data were found in literature about harvest mice consumption by stoat (*Mustela erminea*) and pine marten. Nevertheless, some authors report that in Poland, pine marten occasionally feeds on *Micromys* in the Turew region (Goszczvnski 1976) and in Białowieża Forest (Zalewski 2007), whereas LPO dataset in Champagne-Ardenne region (France) reveals a significant share of harvest mouse in the diet of this mustelid (2.5 % of total prey). In western Finland, stoat (and also weasel) mainly feed on *Microtus* vole, but this mustelid is able to shift to alternative prey such as harvest mouse, house mouse (*Mus musculus*), bank vole (*Myodes glareolus*) and water vole (*Arvicola terrestris*) (Korpimäki et al. 1991). Others authors showed that *Micromys* mice may serve as alternative prey to many predators of rodents when abundant enough (Hanski & Henttonen 1996, Pekkarinen & Heikkila 1997).

As for the golden jackal, its distribution overlaps that of the harvest mouse in south-eastern Europe. It lives in semi-arid areas but also in shrublands, marshlands and cultivated areas. Its variable diet, resulting from opportunistic feeding habits leads the golden jackal to feed partially on *Micromys* in Hungary and Greece (Lanski et al. 2010).

Due to their abundance in many ecosystems, domestic and feral cats are major predators of wildlife. In Great Britain, Woods et al. (2003) demonstrated that mammals make up 69 % of the 14370 prey items brought home by 986 cats; among them, the harvest mouse represents 1.8 % of the prey. It is conceivable that predation by superabundant and well-fed predators such as domestic cats could lead to the decline of species, if only on a local or temporary basis. Thus, Baker et al. (2003) recorded a negative relationship between numbers of wood mice and the numbers of cats visiting suburban gardens. In an anecdotal way, it has been reported that hunting dogs can eat some harvest mice when they find an occupied nest during their search for game (Darinot F., pers. observ.).

And what about other vertebrate predators?

Snakes are real predators of *Micromys* and particularly for nestlings. In Great Britain, Prestt (1971) showed that 91 % of the prey of adult adders (*Vipera berus*) were mammals, including wood mice (*A. sylvaticus*), harvest mice, common shrews (*Sorex araneus*), pygmy shrews (*Sorex minutus*), water shrews (*Neomys fodiens*), and field voles (*M. agrestis*). In Japan, it has been shown that snakes directly attack the nests of harvest mice and consume the young mice in the nests (Hata 2011). In Lavours marsh (France), both grass-snake (*Natrix natrix*) and green whip snake (*Hierophis viridiflavus*) were found in trap boxes set on stacks at 60 cm above ground level, that were used for *Micromys* surveys in reedbeds: no doubt nestlings may offer a good feeding resource for these species (Darinot F., pers. observ.).

Comparison of mammal and avian predation

It seems that carnivores are more efficient than birds of prey for hunting harvest mouse. Indeed, in the Champagne-Ardenne region (France), remnants of *Micromys* represent 2.2 % of total mammal prey in faeces and stomachs of foxes, wild cats, pine martens and stone martens (of 13663 prey items), *versus* 1.2 % in pellets and crops of ten diurnal and nocturnal raptors (of 626340 prey items). In order to eliminate small samples that favour over-valuated frequencies of harvest mouse items, only faeces/stomach and pellet studies with total number of mammal prey higher than median value have been conserved (respectively equal to 337 and 43 prey items). The difference between these two percentages is significant (Mann-Whitney test for two unequal sample variance, $z = 5.998$ for $p < 0.001$) which means that faeces and stomachs contain more harvest mouse remnants than pellets and crops. Why are carnivores more efficient in foraging for harvest mouse? Trout (1978) assumes that the affinity of the mouse for dense cover vegetation reduces its availability for avian raptors. Conversely, carnivores that forage amongst tall vegetation may be more likely to encounter harvest mice.

Discussion

Critical view of data sets

Available data on *Micromys* prey items in the diet of raptors should be analysed regarding the size of pellet samples for each species of raptor, i.e. relative to the sampling effort. Numbers of pellets are often unspecified in studies or they are submitted aggregated in the form of sets, which is not useful to determine a sampling effort. However, total number of prey is generally provided and this gives a good estimation of the sampling value. Thus, we assume that median percentage of harvest mouse in the diet of barn owl, tawny owl, long-eared owl, eagle owl, common buzzard, Tengmalm's owl, little owl and kestrel is probably reliable due to the high number of total prey for each species (Table 1). Conversely, we should question the low proportion of harvest mice in the diet of avian raptors hunting in suitable habitats such as harriers and short-eared owl, due to the weakness of the prey sample: consequently, new surveys should be conducted to specify their feeding habits with a distinctive effort in wetlands. Secondly, the range of sampling area should be considered for analysing the proportion of harvest mouse in the diet of raptors. Large sampling areas, such as on a regional scale, lead to a smoothing of the average frequency of *Micromys* in predator diet because of a greater diversity of habitats, more or less suitable for the harvest mouse. For example, the average percentage of *Micromys* in the diet of barn owl equals to 1.4 % in the Rhône-Alpes region (France) for 55515 mammal prey on 43698 km² (Rolland 2011), into which it reaches 3 % in the Dombes plain, for 7183 mammal prey in a 1000 km² rich wetlands area (Aulagnier et al. 1980), into which it peaks at 24.2 % at Birieux, a small village surrounded by large ponds and reedbeds, for 434 mammal prey (Aulagnier et al. 1980). This remark particularly applies to some local surveys, for which the huge proportions of harvest mouse should be interpreted as a response of the mouse to a very suitable habitat. It is the case in the Danube Delta, where *Micromys* represents 42 % of mammal prey in the diet of little owl, with a survey that relies on a single site, the Letea village (Pocora et al. 2012). It also concerns the surveys conducted on Oléron island with 29 % of the diet of the Eurasian scops owl (Bavoux et al. 2003), in the Sesia Natural Park with 23.3 % of the diet of little owl (Gotta & Pigozzi 1997) and in the Monticchie Nature Reserve with 22.1 % of the diet of long-eared owl (Canova 1989). A lesser consideration should be devoted to bias due to annual fluctuations of harvest mouse population. Important density fluctuations have been observed in Russia (Sleptsov 1947) and in western Europe (Piechocki 1958, Migula et al. 1970, Trout 1978). In Britain, Trout (1978) has shown that annual densities may vary from 17 to 233 individuals/ha. Whereas these surveys were conducted with nests count or trapping, new results are given by owl pellets in the Champagne-Ardenne region (France), thanks to the Ligue pour la Protection des Oiseaux (LPO) (unpublished). This survey was conducted over 23 years between 1975 and 2003 in the village of Outines (Marne department) and yielded 565 *Micromys* items for 11690 mammal preyed by barn owl. In this single village, fluctuation of the percentage of harvest mouse in the diet of barn owl is significant over three decades (Fig. 1), ranging from 0.5 % to 22.7 %. Consequently, it is obvious that surveys of avian raptors diet habits, conducted in a restricted area, should rely on multiannual sampling or on an important amount of pellets which may correspond to several years of bird foraging.

Availability of prey

The proportion of remains of different mammal prey in pellets reflects their availability for raptors, which is linked with their population density in the birds' foraging areas and with their exposure to predation. This European review has shown that there is no specialised predator on harvest mouse, and moreover, that this species is almost always an occasional prey item. However, when main prey become scarce, i.e. their availability decreases, raptors are forced to hunt other prey such as the harvest mouse if present. Several authors describe this behaviour when the main mammal population density falls, due to interannual fluctuations (Schipper 1973, Kafkaletou-Diez et al. 2008, Brzeziński et al. 2010, Mikkola & Tornberg 2014). A less exposure to predation may be due to snow cover that hides small mammals and conversely, several surveys point out the influence of snow cover on the availability of harvest mice for raptors. In Finland, it was shown that Arvicolinae move rather under the snow cover, which makes them more difficult to hunt in case of the cover's larger thickness, whereas Murinae are being found rather above the snow, which usually makes them easier to hunt (Halonen et al. 2007). This was found also in Romania, where Benedek & Sîrbu (2010) showed that the share of common vole (*M. arvalis*), which is the main prey of the long-eared owl, decreases in January whereas harvest mouse becomes the dominant prey: although voles are also active during the cold season, they more frequently move under the snow, while mice prefer moving on the snow surface. In Italy, Canova (1989) also demonstrated that the proportion of harvest mice in the diet of long-eared owls increases with snow cover, from 4.5 % with no cover, to 9.4 % with less than 15 cm of snow and 22.1 % with more than 15 cm of snow. Moreover, in the riparian biotopes, large areas of ground remain free from snow and hygrophilous mammals like harvest mouse may become more available (Canova 1989). However, Stasiak et al. (2014) did not observe such an influence of snow cover in the Lublin region (Poland). Exposure to predators may be linked to the density of vegetation cover. During winter, harvest mice are more prone to owl predation, when vegetation cover is not so dense and the species needs to forage also during the night (Kopij et al. 2012). In some articles, seasonality is mentioned as an important aspect, without precise explanation of impacts on harvest mouse behaviour and vulnerability to raptors. Thus in Great Britain, the percentage of harvest mice in the barn owls' prey rises in the autumn and goes down in the spring: during the months of September to March this species forms more than 4 % of the prey, and after March falls steadily to a low of 1.2 % in late July/early August, rising again to over 4 % in September (Buckley 1977). The influence of winter can also be observed with the great grey shrike in Poland, for which the percentage of *Micromys* in its diet varies from 1.6 % in autumn to 4 % in winter and 0.6 % in spring (Brzeziński et al. 2010). Such increase of hunting on harvest mouse in winter is also recorded for the little owl in central Poland (Romanovski et al. 2013). In a farmland landscape in Italy, Rubolini et al. (2003) have assessed weather variables (mean monthly rainfall and temperatures) on the variation of individual prey categories of long-eared owls. These weather variables have no or limited effects on mammal prey. The only prey whose prevalence

in diet was consistently affected by temperature was the harvest mouse: it may reflect a higher availability of this prey with lower temperatures, when a fraction of the population may be forced to leave cultivated fields by habitat deterioration toward less suitable habitats but preferred by owls for hunting. More precisely, Romanowski & Żmihorski (2009) showed that the share of harvest mouse in the tawny owl diet increases in cold season *vs.* warm season in higher proportion in farmland than in forest (13.1 % *vs.* 0.6 % in farmland and 2.3 % *vs.* 1.2 % in forest). However, as for carnivores and specially the red fox, no increase of proportion of murids (*M. minutus* and *Rattus norvegicus*) in their winter diet has been shown in Finland (Dell'Arte et al. 2007).
Moreover, few reviews are interested in the influence of perturbations on small mammal predation. Among them, floodings are important natural perturbations for the harvest mouse that lives in wetlands. It has been shown that some individuals of *Micromys* find refuge on trees, willows and upper parts of reeds when flood arises (Darinot & Favier 2014) and indubitably this behaviour should enhance their exposure to avian raptors. Other perturbations are anthropogenic such as meadow-mowing and crop harvesting, which may lead to an increase of hunting of harvest mice by birds of prey as well as mammal predators, because of the destruction of vegetation cover.

Information about harvest mouse habitats

The harvest mouse is known to live in a wide variety of habitats (Harris 1979) from disturbed habitats with early vegetal succession, cultivated areas, urban environments, to marshes and wetlands. However, widespread changes in agricultural practice during recent decades have removed large areas of suitable habitat in which harvest mice appeared to be abundant (Harris et al. 1995). Nowadays, in several regions of Great Britain such as Suffolk and Norfolk, it is assumed that only wetland habitats harbour stable core populations of harvest mouse in lowland arable landscapes (Perrow & Jowitt 1995, Meek 2011). These wetland populations may have prevented the loss of the species from many intensive agricultural areas. The proportion of *Micromys* prey in the diet of avian raptors tends to confirm the preference of this species for wetlands. In northern Europe, in these habitats, the lowest quoted proportion (Table 2) is 9.7 % in the Weserinsel Strohauser Plate (Germany) while Uttendörfer (1952) had already found 12 % of *Micromys* remnants in long-eared owl pellets in the Sylt island (northern Germany). In the Netherlands, De Bruijn (1994) also found that the harvest mouse had a preference for river habitats in a farmland landscape, whereas Deuzeman et al. (2015) showed that *Micromys* represents 60 % of the mammals preyed by the great grey shrike in the Engbertsdijksvenen nature reserve peat bog (over 2314 pellets). For owls, the proportion can reach 42 % in the Danube Delta Biosphere Reserve (Romania), 24.8 % in rice fields and water meadows in the Sesia Natural Park (Italy), 22.1 % in wetlands of the Monticchie Nature Reserve, near the River Po (Italy), 17.9 % in the marshes of the Axios Delta (Greece). However, these figures could also result from the progression towards the south-east of the European range of the harvest mouse, where it is known to disappear from the less humid farmlands and is only found in moist primary biotopes (Böhme 1978). As regards the diet of barn owl, significant correlations have been established between the percentage cover of the wetlands in the hunting territory and the share of harvest mouse in the diet, as for other wet-loving species such as Miller's water shrew (*Neomys anomalus*) and water vole (*Arvicola terrestris*) (Milchev et al. 2006). Thus, the proportion of harvest mouse in the diet of barn owl is more important in valleys of large rivers with wetlands and along some water canals, with extensive grasslands (Stasiak et al. 2014). Similar results are found in other wetlands such as the Novosibirsk oblast and Lake Malye Chany (south-west Siberia), where the harvest mouse is an important prey for long-eared owl since it represents 7.6 % of the total number of vertebrate prey (Dupal & Chernyshow 2013).
The fact that current harvest mouse populations are lower in farmland than in wetlands is supported by our review: in agricultural landscape, the species is much less abundant in the diet of avian raptors than in wetlands, with percentage ranging from 0.1 % to 8.8 %. Although the decline of harvest mouse in agricultural areas is widely accepted, published data on former population densities in either farmland and wetland biotopes are lacking, as previously noted by Jüdes (1981). My review does not uncover new information on the trend of the harvest mouse, in spite of the huge amount of data on raptor diet, also collected by earlier authors, like Uttendörfer (1929, 1952). Nevertheless, the increasing rarity of the harvest mouse is now accepted and is known to have mixed causes linked to changes in agricultural practices. In crop habitat, mechanical harvesters that appeared in the middle of the twentieth century, cut down the nests woven in the stalks and kill the harvest mice in the field, whereas in earlier times grain crops were manually scythed and

the mice could escape to the margins of the field: in 1874, Gordon who was the vicar of the Harting parish, related that in west Sussex (Great Britain) "the harvest mouse…is not at all uncommon in our cornfields in the summer months, and our corn ricks in winter" (Gordon 1877). Nowadays, it has been shown that even arable field margins and rough grassland support very small numbers of harvest mice because of grass cutting practices and crop chemical use (Meek 2011). However, management of the margins to improve connectivity within a farm can increase the size of harvest mouse populations, especially when fields are surrounded by wet habitats (Jüdes 1981).

Unsurprisingly, this European survey reveals that the harvest mouse seems to be rarely attracted to woodlands, since this type of habitat is linked with the lowest proportions of *Micromys* in the diet of the four main raptor owls (Table 2). However, it is known that woodland borders and young plantations can provide to some extent suitable habitats for the species (Harris 1979). Results may be less predictable for urban environments since several surveys put forward a rather high percentage of harvest mouse in the diet of tawny owl and long-eared owls. For example, in the city of Milan (Italy), it represents 5.3 % for long-eared owls which hunt in the suburbs and the adjoining farmland (Pirovano et al. 2000). Several surveys quote harvest mouse in parks and cemeteries of big cities with shares in the diet of avian raptors often higher than in agricultural landscape. Thus, in Poland, *Micromys* represents 2 % and 4.9 % of the long-eared owl diet respectively in the Lublin and Rzeszów cemeteries (Wiącek et al. 2008, Dziemian et al. 2012) and 6.1 % of the tawny owl diet in the Toruń cemetery (Zalewski 1994). This proportion reaches 9.4 % for long-eared owls which roost in a cemetery of Wrocław, bordered with large water canal with mowed grassland, shrubs and trees along its bank (Kopij et al. 2012). In Romania, the proportion of harvest mouse reaches 10.4 % of long-eared owls diet which overwintered in a garden in the Satu Mare city (Benedek & Sîrbu 2010). In fact, percentages of harvest mouse depend on the urbanization level: a less urbanized locality means more *Micromys* items in the diet composition (Grzędzicka et al. 2013).

Conclusion and recommendations

A wide distribution range, a high diversity of habitats, a small size and a both nocturnal and diurnal activity rhythm make the harvest mouse available to a great variety of vertebrate predators; consequently, this review cannot claim to be exhaustive. Nevertheless, this study highlights a lack of data concerning the diet of some raptors as common buzzard, kites, hen and marsh harriers, as well as carnivores in general. Long multiannual mammal surveys appear to be rare too, in spite of their high interest for population ecology. In that respect, new studies should assess the impact of predation upon harvest mouse populations in wetlands where it may constitute the main prey for raptors, and also to quantify mechanisms of prey shift to *Micromys* when the main prey becomes scarce. At least, this survey confirms that nowadays wetlands are a very important habitat for the harvest mouse conservation, and in return this tiny and friendly rodent could be a useful flag-ship species for their protection in Europe.

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