

Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands

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Abstract

Nesting populations of Montagu's harrier (*Circus pygargus*) are declining in most parts of Europe; in France, western marshes remain the most important nesting sites in terms of breeding pairs. In this open field landscape dominated by grasslands, the common vole (*Microtus arvalis*) displays regular population outbreaks and constitutes a favourite prey of this raptor. Twelve years of field data indicate significant variations in nesting population size and young harriers produced, which correlate with yearly differences in vole densities. Up to 10 years ago, these marshes were traditionally used as extensive pastures but recent agricultural changes have resulted in almost 50% of the pastures being converted to drained agricultural production, as already observed in many localities of this region next to our study area. Our data, together with previous data collected from 1968 in this region, demonstrate that agricultural changes have resulted in a decrease of frequency and intensity of vole population peaks. A summer density of 100 voles/ha appears as a threshold value to support a good breeding success of harriers. These modifications of the vole fluctuation pattern suggest that nesting populations of Montagu's harrier from western French marshes could be endangered in future under these current trends in agricultural changes. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Recent developments in agriculture have considerably modified landscape and habitat structure (Baker, 1989; Turner et al., 1989). The most important and large-scale cause of habitat degradation and loss is the expansion and intensification of human land use (Burgess and Sharpe, 1981). The main consequence of landscape changes appears to be the fragmentation of habitats and, among the major components of habitat fragmentation, the loss of original habitats and the reduction of patch size seem to be the main causes of the decline in biological diversity (Wilcox and Murphy, 1985).

Montagu's harrier (*Circus pygargus*) has a scattered distribution in north-western, central and southern Europe. It breeds in open landscapes in places characterized by dense and tall herbaceous or chamaephytic plant communities including marshes, lowland heath, rough grassland, dunes, cereal fields and young conifer plantations (Leroux, 1989; Tucker and Heath, 1994).

About 75% of the European population can be found in Russia, with about 10% in France and smaller numbers in Spain (Tucker and Heath, 1994). Cramp and Simmons (1980) reported that Montagu's harrier populations decreased in many areas of Europe during the 19th century, they often increased again in the first half of the 20th century, but sharp declines occurred in some countries from the late 1950s. During the last few decades, the most marked decrease has been observed in Spain where population size declined from 6000 pairs to 3000 pairs. In France the population declined by over 50% between 1930 and 1980 (Cramp and Simmons, 1980) and has fluctuated since then (Tucker and Heath, 1994). In both cases, development of agriculture and extension of conifer plantations are suggested to explain the decline.

Up to now, the marshes of western France have supported the main part of the French nesting population of this raptor species (Leroux, 1987). The settlement of breeding pairs in these marshes is mainly governed by two factors: favourable nesting sites and higher vole availability than in more intensified drylands.

In this paper we report a 12-year analysis of common vole influence on Montagu's harrier reproduction in a

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marsh area and a long-term data analysis of vole density fluctuations in this region where rangeland conversion to agriculture has been observed. We also document the change in agricultural land use in our study site in the last decade. We finally develop hypotheses about the future patterns of both vole and raptor population dynamics in this region, which is still an important site for the conservation of Montagu's harrier in this western part of its range.

2. Study area

The study area (Fig. 1) is situated in the Saintongeais Marshes and is located at the north of the Charente river and the town of Rochefort (Charente-Maritime, France, 45°57' N, 0°55' W). The study area extends over 18 203 ha consisting of drained marshes and bounded by drylands devoted to crop production. Some small patches of drylands occur within these marshes. A ditch network delimits the parcels where, until the 1970s, extensive grazing represented the most common land use. During the last two decades agricultural fields have been considerably extended and intensified. Native grasslands have been converted to crop production by removing ditches and smoothing the surface of pastures. Buried drains are used to improve water drainage.

Pairs of Montagu's harriers breed mainly on natural sites represented by dense tall herbaceous communities (e.g. *Carex* spp., *Scirpus* spp.) and ungrazed or old abandoned pastures. Wheat fields sometimes constitute alternative nesting sites. The small mammal community is largely dominated by the common vole (*Microtus arvalis*). This rodent is characteristic of open field landscapes where the small mammal diversity is reduced (Butet and Leroux, 1994).

3. Methods

We evaluated the expansion of crop fields in our study site using censuses existing before 1987 and ones completed by ourselves in 1987 and 1994. The extent of crop fields between 1987 and 1994 was mapped from satellite pictures (SPOT 1990) and crop survey using Ordnance Survey Maps (National Geographic Institute 1:50 000).

The fluctuations of the vole population have been followed from 1986 to 1998 using a transect live-trapping method. Details of this method of vole density estimation are provided by Butet and Leroux (1993, 1994), and thus only a general outline is presented here. We used 20 trap lines randomly located on different parcels that represent the relative importance of agricultural land use within the study area. Three main habitats were sampled: abandoned pastures (four trap lines), grazed and mowed grasslands (12 trap lines), and

cereal crops (four trap lines). Abandoned pastures generally occur on very wet parcels. They are mowed every 3 or 4 years to limit the expansion of vegetation. All other grasslands were pooled together as they can alternatively be grazed (pastures) or mowed (hay cutting). Crops includes mainly wheat and maize fields. Trap lines were about 2 km apart to cover the entire study area, comprised 51 traps spaced at 2-m interval, and were opened for 48 h (equivalent to 2040 trap nights per trapping session).

Each year, sampling of voles was carried out in spring (April), at the arrival of harriers, and in summer (July), during the period of intensive provisioning of young harriers. For each sampled parcel, the relative abundance of

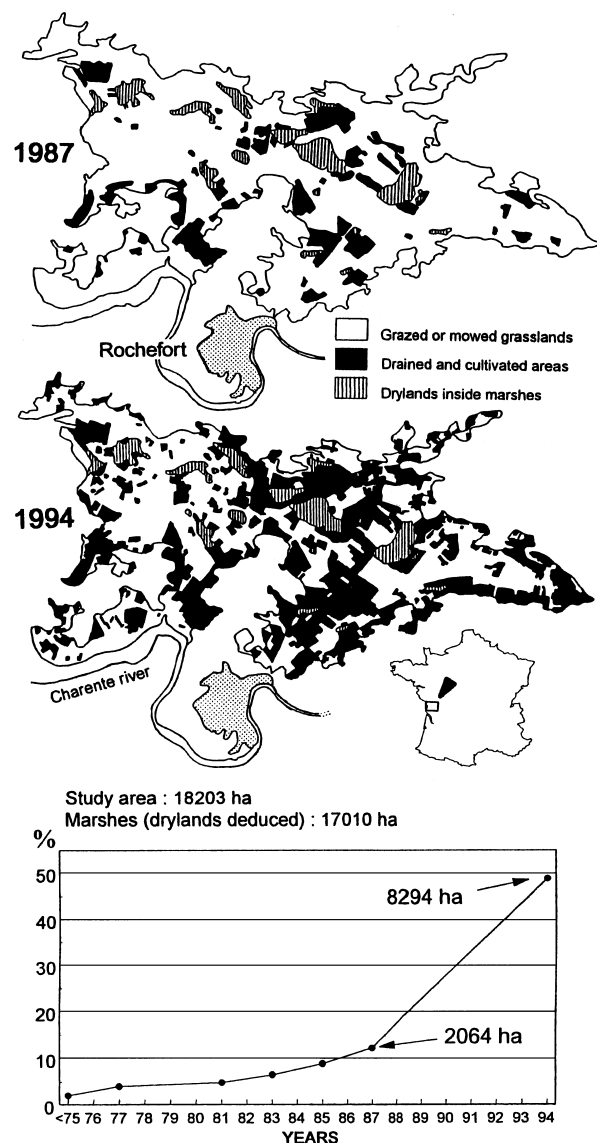
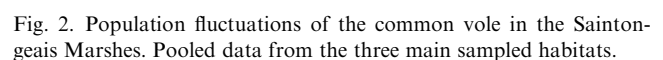


Fig. 1. Grasslands converted to cereal crops in the study area. Maps show their distribution in 1987 and 1994. The curve represents the change in areas from 1975 to 1994. The study site covers 18 203 ha, but marshes extend only over 17 010 ha when dryland patches are deduced from the whole area.

Data on fluctuations of the vole population over a 25-year period have been collected in this region including localities within a 30 km radius around our study area. We used them to support our hypotheses. Samples were collected in an agricultural zone where, as in our study area, grasslands have been progressively converted to crop production. These data were collected each year in winter (December) between 1968 and 1993 by crop

Fig. 2 shows the fluctuations of vole density between 1986 and 1998 (pooled values from the three main habitats). When harriers arrived in the study site in spring (end of April), the estimated mean vole densities ranged from 0.8 to 87.6 individuals/ha (Table 1). Summer vole densities ranged between 7.9 and 215/ha. The highest occurred in 1987 and 1993. In contrast, low vole densities were observed in 1986, 1988, 1989, 1991, 1994 and 1997, when densities ranged between 7.9 and 40 voles per hectare. We observed intermediate values in 1990, 1992, 1993, 1995 and 1996. These results indicate



that the vole population actually displays fluctuations with peak periods spreading over 2 years and being separated by 1 year of low population density. No peak exceeding 200 voles/ha has occurred since 1987 and the most recent population crash lasted 2 years. There was a significant correlation between vole density in spring and summer ($r_s = 0.78$, $P < 0.01$, $n = 10$) but increase rate varied between years.

We noted significant differences in vole densities between the three sampled habitats ($F = 4.02$, $P = 0.023$; Fig. 3). Highest densities were observed in abandoned pastures, the least disturbed habitat type. Average vole density in this habitat was of 102/ha with extreme values

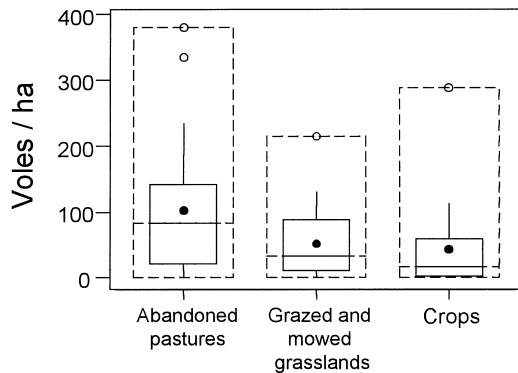


Fig. 3. Differences in vole densities between habitats (all years combined). Box plots with mean, median, quartiles, deviation and amplitude with abnormal values.

around 400/ha. Lowest values (43/ha) were observed in cultivated areas with many fields not being colonized during years with low overall vole density. Mean densities on grazed or mowed pastures were intermediate (51/ha). Densities in these latter habitats appeared to be partly dependent on grazing intensity, the less intensively grazed pastures sometimes supporting densities similar to those of abandoned pastures with tall herbaceous plant communities.

Fluctuations of the vole population in our study site indicate that high population densities seem to be less common compared with long-term data collected in this region between 1968 and 1992 (Fig. 4). For example very low densities occurred over five successive years between 1982 and 1986 and similar crashes were never observed before. Recent crashes (1994 and 1997) were very severe in our study area. Both ancient and our recent data were synchronised ($r_s = 0.72$, $P = 0.069$, $n = 7$) and peaks in 1987 and 1992 occurred simultaneously in the two population. This long time series shows clearly a trend of diminishing frequency and intensity of the population peaks. The shape of the curve is well fitted with a curvilinear (log) trend analysis.

4.3. Influence of vole fluctuations on harrier breeding parameters

Data on both vole and harrier variables are reported in Table 1. Clutch size, number of hatchlings and number

Table 1
Variation in harrier breeding variables and vole densities (nos/ha)^a

	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
Nests/10 km ²	1.3	2.5	1.8	2.2	3	0.6	1.8	2.7	0.4	1.9	2.9	0.8
Clutch size	3.43	3.80	3.48	3.61	3.80	2.81	4.05	4.39	2.80	3.67		
	0.16	0.15	0.17	0.14	0.21	0.40	0.18	0.15	0.37	0.26		
	(23)	(40)	(25)	(18)	(25)	(11)	(20)	(33)	(05)	(21)		
Mean no. of hatchlings (nests in which eggs hatched)	2.37	3.26	2.71	3.46	2.25	2.09	3.65	3.88	2.60	3.58		
	0.33	0.24	0.32	0.19	0.34	0.48	0.27	0.21	0.51	0.22		
	(27)	(38)	(24)	(15)	(20)	(11)	(20)	(33)	(05)	(19)		
Mean no. of young fledged												
Nests started	1.37	2.27	1.50	2.16	1.85	0.73	2.64	2.58	0.57	2.44		
	0.21	0.22	0.18	0.29	0.29	0.38	0.29	0.23	0.30	0.30		
	(35)	(60)	(42)	(18)	(26)	(11)	(25)	(41)	(07)	(27)		
Successful nests	2.18	3.09	2.03	2.60	2.82	2.00	3.14	3.21	1.33	3.14		
	0.17	0.17	0.16	0.21	0.20	0.70	0.20	0.15	0.33	0.20		
	(22)	(44)	(31)	(15)	(17)	(04)	(21)	(33)	(03)	(21)		
Hatching success	0.68	0.77	0.73	0.89	0.61	0.64	0.96	0.93	0.90	0.95		
	0.08	0.05	0.07	0.07	0.09	0.13	0.02	0.04	0.10	0.02		
	(24)	(43)	(29)	(15)	(18)	(11)	(18)	(27)	(05)	(19)		
Fledging success	0.63	0.79	0.55	0.70	0.96	0.31	0.81	0.81	0.20	0.82		
	0.10	0.05	0.07	0.09	0.03	0.12	0.06	0.03	0.20	0.05		
	(19)	(37)	(24)	(14)	(14)	(08)	(18)	(32)	(05)			
Breeding success	0.63	0.73	0.74	0.73	0.65	0.36	0.84	0.80	0.43	0.78		
Total young produced	30	96	46	81	94	7	81	118	4	79	105	15
Spring vole density	3.6	65.0	19.7	14.5	85.0	0.8	15.5	87.6	9.3	26.7	51.5	2.9
Summer vole density	15.5	215	37.6	40	99	16	116.7	140.9	7.9	104.2	109.0	8.3

^a Mean values (upper) with standard error (below) and sample size in brackets are furnished for harrier breeding data.

of fledglings are, of course, non-independent variables that are highly correlated. Only nest density, hatching success, fledging success and breeding success are independent variables.

There was a significant difference ($P < 0.01$, ANOVA, one-way, d.f. = 9) between years in all the breeding variables (clutch size, mean number of hatchlings and young fledged, hatching and fledging success).

The nesting density ranged between 0.4 and 3.0 nests/10 km² and was correlated with spring vole densities (Table 2). Clutch size ranged from 2.80 to 4.39 eggs and was also correlated with spring vole density. Differences in brood size at hatching between breeding seasons exceeded one hatched young per nest. It varied from 2.09 to 3.88 and was significantly related to summer but not to spring vole densities. Hatching success was neither correlated with spring nor summer vole densities. Fledging success showed a significant correlation with summer vole density. The difference in the mean

production of young birds reached two birds per nest between the worst and the best years. There was a significant relationship of this variable with summer vole densities. As a final result, breeding success was linked with summer vole density.

Spring and summer vole densities appear to be good predictors of the breeding productivity (Table 2). The relationship showed a higher r^2 value when fitted to a non-linear curve. Young harriers produced each year are plotted against summer vole density (Fig. 5). We may recognize very unsuccessful years with < 10 fledged birds for the whole study area when mean summer vole densities were around 10/ha. At the other extreme the production seems to reach a ceiling value (around 100 young birds) when density was ≥ 100 voles per hectare.

5. Discussion

From early works on Montagu's harrier, we already know that western French populations seem to be dependent on vole predation (Thiollay, 1968a, b). In a previous study (Butet and Leroux, 1993) we furnished the first data confirming this close relationship. Additional results from this 12-year study demonstrate that numbers of young harriers produced depends both on spring and summer vole availability. The spring vole densities influence the settlement of pairs of harriers that will decide to nest, whereas summer vole density will influence the number of young per nest that adults will be able to rear. Similar findings are reported for other raptor species including harriers. Newton (1979) cited several studies where breeding variables were affected by vole cycles. The influence of spring vole density on the settlement of nesting pairs in harrier species has already been observed (Hamerstrom, 1979; Simmons et al., 1986). Vole density effect on fledging

Table 2
Correlation (spearman) and regression (curvilinear) analysis, for the relationships between harrier breeding variables and vole densities^a

	Spring vole density	Summer vole density
Summer vole density	0.78**	
Nest density	0.87**	
Clutch size	0.81**	
Brood size at hatching	0.50 ns	0.67*
Brood size at fledging		
All nests		0.89**
Successful nests		0.89**
Hatching success	0.20 ns	0.41 ns
Fledging success		0.73*
Breeding success (%)		0.76*
Total young produced	$R^2 = 80.8, P < 0.001$	$R^2 = 88.8, P < 0.001$

^a ns = non significant, $n = 10$ (years).

* $P < 0.05$.

** $P < 0.01$.

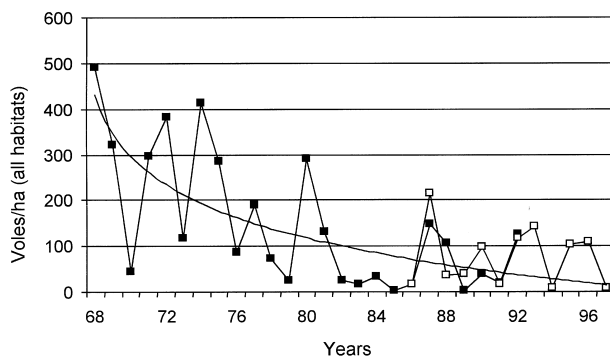


Fig. 4. Twenty nine years time-series showing diminishing peak intensity and frequency of the common vole population with best curvilinear (log.) adjustment. ■, changes over a 25-year period from this region (Toussaint, personal communication); □, present study. Time-series overlap between 1986 and 1992.

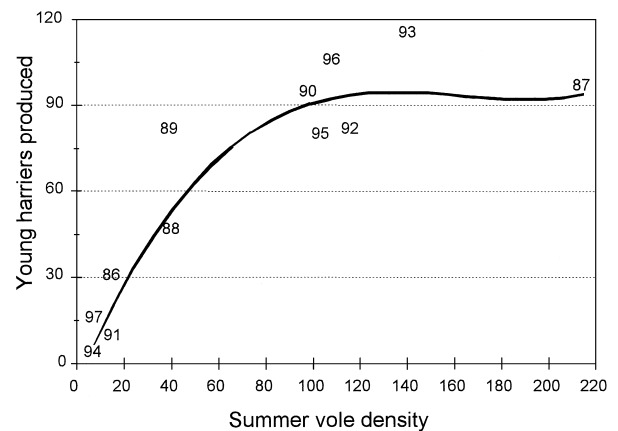


Fig. 5. Total young harriers produced versus summer vole density and best fitted curve (cubic adjustment). Yearly productivity of harriers is estimated by the mean number of fledglings per nest $\times$ total number of nests recorded on the whole study area (170 km²). Plots on figure represent the different years.

success has also been demonstrated in the case of the common buzzard (*Buteo buteo*) (Rockenbach, 1975) and kestrel (*Falco tinnunculus*; Village, 1979) but has been more rarely reported for harrier species (Simmons et al., 1986) because populations differ sometimes extremely in prey choice (Schipper, 1973).

In a recent paper (Salamolard et al., 2000), we postulated that the numerical response was mainly based on recruitment from the floating population defined as 'juvenile nomadism' by Andersson (1980). We also studied the diet of this species and demonstrated a 'type II' functional response curve as defined by Holling (1959). Finally we concluded that both numerical and functional responses were characteristic of a typical specialist raptor tracking vole abundance without time-lag and having no efficient alternative prey during years of vole crashes.

Our results show clear differences of vole densities between habitats. These results are similar to those observed by Ostfeld et al. (1985). For instance, old abandoned pastures appeared to be always the most populated areas and probably played the role of permanent source habitats. Vegetation is generally more diverse in this habitat and furnishes a good protection against predators. We may suppose that during favourable conditions a high reproductive rate in these places induces density-dependent dispersal towards less favourable habitats such as grazed and mowed grasslands and also non-permanent habitats like crops. Similar spatial dynamics have been demonstrated in other vole populations (Hansson, 1977).

The analysis of the population fluctuations of this rodent during the last 30 years reveals that changes in fluctuation patterns are linked to alterations in the landscape, in particular to the relative area occupied by permanent grasslands. In 1975 there were around 55% of land under permanent grass in this region compared with <30% in 1988 (Delattre et al., 1992).

A similar trend is actually observed in our study area where marshes have been drastically transformed during the last 10 years. Favourable habitats represented by lands under permanent grasslands have become more and more restricted and fragmented. This extension of ploughed lands has probably had severe effects on the winter survival of voles. Moreover progression of drained and cultivated areas has reduced favourable nesting sites for harriers.

Leptich (1994) analysed the influence of agricultural development on various raptor species in southern Idaho where large areas of native rangeland have been converted to agricultural production. Raptors exhibited lower abundance and diversity in areas highly developed for irrigated agriculture than in natural habitats. Two raptor communities have been studied by Howard and Slater-Blair (1983) along the Snake river canyon in Idaho. They found significantly lower nest densities in

agricultural areas and related them to lower prey abundance.

Nowadays, the largest French breeding populations are found in western coastal marshes (Leroux, 1989). As for heathland habitats, populations have already decreased or have tended to drop over the last few years. For example, in the 'Baie de l'Aiguillon', a reclaimed area, situated in the north of our study site, the breeding population was 100 pairs in 1967 (Thiollay, 1968a, b) and dropped to 14–30 pairs in 1990–1992 (Fonds d'Intervention pour les Rapaces, pers. commun.). In this latter place, the expansion of wheat cultures over grasslands and alfalfa fields appears as the main factor responsible for the decline.

Thus, at the landscape level, reduction and fragmentation of grassland habitats are probably the most important factors influencing vole outbreak frequency and intensity as has already been argued by Delattre et al. (1992). We observe that common vole densities fluctuate now with a 3-year time lag with peaks below 150 voles per hectare. Intensification of agriculture will certainly accentuate this trend with summer peak densities rarely reaching 100 voles per hectare, which appears to be the threshold value for optimal production of young harriers. This value is important as our study demonstrates that recent harrier breeding seasons were very successful when voles reached this density level and that higher vole availability did not significantly improve breeding success. But the main point to underline from our data is that such summer peaks were frequent in the past and sometimes much higher while they have been less frequent during the two last decades.

We may suppose that future progression of crops over grasslands will accentuate this trend leading to highly unpredictable breeding performance for harriers. This may lead to the decrease in total number of young harriers produced over several years on these areas and affects dispersal for sustaining peripheral populations. Thus, western French marshes which were semi-natural landscape but are now true agricultural landscapes will no longer act as a source habitat. This constitutes a real threat for this species in this region and probably in many other places in Europe that undergo similar changes.

Acknowledgements

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