



How the common vole copes with modern farming: Insights from a capture–mark–recapture experiment



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ABSTRACT

In this study, using capture–mark–recapture (CMR), a common vole population was monitored for one year in an experimental study site dominated by meadows, in which field management followed a gradient of intensiveness. The aim was to estimate the demographic response to agricultural practices of the common vole. During the spring, the numbers captured were highest in the most intensively managed plots. After cereal harvesting, they were higher in meadows with the highest nitrogen input. No difference in survival was found among treatments. However, the pattern of transitions suggested that high mobility explained this result. Also, mechanical interventions like ploughing appeared to have powerful consequences for common vole survival. These results underline the critical role of dispersal and refuge habitats in the maintenance of populations of voles in agroecosystems.

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1. Introduction

Although the use of synthetic fertilizers, and particularly of nitrogen, has been sometimes found to be beneficial for herbivorous vertebrates (e.g. voles: Morilhat et al., 2007; geese: Patterson and Fuchs, 2001) or agricultural pests (e.g. sap feeding insects: Awmack and Leather, 2002), the negative consequences of agricultural intensification for biodiversity are now widely documented (Benton et al., 2003; Krebs et al., 1999; Robinson and Sutherland, 2002). At the field spatial scale, mechanical interventions like ploughing and harvesting disturb communities and are known to be highly destructive of particular groups of animals, such as ground nesting birds (Bretagnolle et al., 2011), arthropods (Garratt et al., 2001) or small mammals (Jacob, 2003). At the landscape scale, agricultural intensification reduces the amount of semi-natural habitats (e.g. meadows) and increases annual crops and field size (Benton et al., 2003; Concepción et al., 2008). Overall, agricultural landscapes nowadays form a patchwork of habitats with

different levels and timing of perturbation due to farming practices, which could make survival difficult for the remaining wild populations. Perturbations act as ecological filters selecting rather ruderal (Grime, 1977) or “fugitive” species, i.e. species able to colonize and reproduce fast enough to renew populations before a new perturbation occurs (Ronce et al., 2000). Highly mobile species, like small mammals, can respond to habitat perturbation by re-locating their daily activities among different habitats within their individual home ranges (Jorgensen, 2004) or by shifting to another habitat.

A recent study (Fischer et al., 2011) has shown that a single small mammal species out of seven, the common vole (*Microtus arvalis*), is able to survive the ecological filter of intensive agriculture: common voles increase with the area covered by arable, field size, amount of nitrogen fertilizers and wheat cover (Fischer et al., 2011). These results are however contradictory with previous studies (e.g. Butet and Leroux, 2001; Delattre et al., 1992) which concluded that this species is not adapted to intensive agriculture. Despite low dispersal ability (Boyce and Boyce, 1988a), small scale mobility is intense (Gauffre et al., 2009) and results in the common vole being a good colonizer (Louarn and Quéré, 2003) in highly disturbed landscapes (Lambin et al., 2006; Tkadlec and Stenseth, 2001). Moreover, despite the intensive perturbation regime in agroecosystems, common voles can show high density outbreaks and

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sometimes cause damage to crops, in most of their distribution area, including central western France (Lambin et al., 2006) where about 90% of the landscape is ploughed annually.

At a small scale, the negative effects of agricultural practices have been documented: mechanical work impacts vole populations through direct killing, habitat destruction and/or a decrease in food availability (Jacob and Hempel, 2003). Ploughing is likely to be the worst hazard for common vole because it destroys burrow network (Brügger et al., 2010). Harvesting and mowing also directly increase vole mortality (Jacob, 2003). In addition, indirect effects occur, such as increased exposure to predation or decreased home-range size, owing to sudden reductions in vegetation height (Jacob, 2003; Jacob and Hempel, 2003).

The aims of this study were to measure the demographic responses of a natural common vole population to agricultural practices with a focus on adult survival and mobility. The agricultural practices considered here were nitrogen fertilizer use, ploughing and harvesting: the study therefore covered a wide range of the most used practices. An accurate monitoring survey of a common vole population was carried out in natural conditions, during a complete calendar year of agricultural practices, in an experimental site where interconnected plots of culture follow a gradient of intensification and mimic a real farmland landscape, though reduced in size.

2. Materials and methods

The study was conducted in an experimental station, the *Observatoire de Recherche en Environnement* (ORE, Lusignan; 46°24'48" N, 00°07'20" E), belonging to the INRA (*Institut National de Recherche Agronomique*), in central western France. The study site size was 8 ha, surrounded by an intensive agricultural plain, partly open-field with some pastures, edges and a wood 1 km away. The ORE consisted of 20 plots organized in four blocks replicating five treatments that differed in the intensiveness of their agricultural practices, each block with one plot of each treatment (hence 20 fields in total). Plots were 72 m × 54 m (3888 m²) in blocks 1 and 2 and 90 m × 44 m (3960 m²) in blocks 3 and 4.

In 2010, the most intensive treatment (T1) was an annual crop (winter barley) sown in October 2009 after ploughing and fertilized in 2010 with 83 nitrogen units. The barley was harvested in the beginning of July, and the plots ploughed again in March 2011. The four other treatments were all meadows, mowed simultaneously three times in 2010 (April 26th, June 2nd and July 19th), but characterized by decreasing level of intensiveness. The most intensive meadow treatment (T2) was sown in 2008 and fertilized with 160 nitrogen units in 2010. Two meadow treatments (T3 and T4) were identical at the time of the study, sown in 2005 and fertilized as well with 160 nitrogen units in 2010. Lastly, the less intensive meadow treatment (T5) was sown in 2005 and fertilized with 30 nitrogen units only in 2010. Except for the treatment T4 planned to last 25 years, all the ORE plots were ploughed in March 2011. One week before ploughing, meadows were mulched.

2.1. Common vole trapping

Common voles were trapped with Ugglan traps (GRAHNAB, Sweden) in four grids matching the four blocks. Traps were 15 m spaced and each field had 15 traps (thus, a total of 300 traps were set). The blocks 1 and 2 were sampled from May 2010 to May 2011, whereas the blocks 3 and 4 were only sampled from January to May 2011 for logistical reasons. In the two days preceding the beginning of a capture session, the traps were baited with wheat grains, and remained open. A total of 11 trapping sessions was carried out, each session lasting from two to four consecutive days (see Table 1). Early

Table 1

Time schedule of the capture–recapture operations for blocks 1 and 2 and blocks 3 and 4, with the number of individuals caught over all plots (and number of captures in brackets).

Trapping session	Dates	Individuals (captures)	
		Blocks 1 and 2	Blocks 3 and 4
Spring			
1	19–21 May 2010	19 (25)	–
2	10–11 June 2010	32 (40)	–
3	15–18 June 2010	78 (124)	–
4	30 June–2 July 2010	89 (116)	–
Summer			
5	7–9 July 2010	96 (119)	–
6	18–20 August 2010	13 (23)	–
7	21–24 September 2010	16 (27)	–
Winter			
8	9–12 December 2010	82 (92)	–
9 ^b	4–6 January 2011 ^b	–	47 (66)
9 ^a	12–14 January 2011 ^a	104 (190)	–
10 ^c	9–11 February 2011 ^c	–	67 (120)
10 ^a	16–18 February 2011 ^a	72 (140)	–
11 ^c	9–11 March 2011 ^c	–	67 (113)

^a Trapping carried out with a time lag of one week in block 2 compared to block 1, dates refer to block 1.

^b No trapping session was carried out at block 3.

^c Trapping carried out with a time lag of one week in block 4 compared to block 3, dates refer to block 3.

in the morning of the first day, traps were closed, still baited. The first capture occurred during the first day afternoon. Then the other captures occurred the morning and the afternoon of the following days. During the last capture, the traps were opened again until the next session. Each time a trap had been visited, wheat grains were added. Captured animals were examined and measured to determine species, sex, reproductive status and mass (g). Captured individuals heavier than 14 g were uniquely marked with an under-skin passive transponder (Trovan) on their first capture. It was our experience that smaller individuals may be excessively stressed by the tagging operations. Thus, only a piece of ear was clipped for the latter to identify previously captured individuals. A small fraction (5.2% of the total captures, $n = 63$ individuals) died during the trapping, most of them (40) during a heat wave that occurred in the early summer.

2.2. Measuring vole movements and survival at ploughing

In order to evaluate the consequence of ploughing on common vole survival, survival was quantified by intercepting escaping individuals. For logistical reasons, this dedicated survey was restricted on the four T2 plots where common vole densities were the highest in order to maximize sample sizes.

The trapping device consisted of a 35 cm high and 15 cm deep buried tarpaulin circling the entire plot. In each corner and every 10 m, 30 cm deep buckets were buried at ground level, embracing the tarpaulin. Voles trying to flee the plot were stopped by the tarpaulin, and following it, they fell into buckets. The device was previously tested on ten animals with success. Even the biggest individuals were unable to jump out of the buckets. For two plots (B1P3 and B2P2), the design was set up the day before ploughing, providing a 24 h capture control, and was dismantled 24 h after ploughing. For the two other plots (B3P4 and B4P3), the devices were set up two days before ploughing and dismantled 72 h after ploughing. The weight, sex, reproductive status, tag number and bucket position of each individual was noted.

In addition, diurnal predation and scavenging by avian predators were observed on the whole 8 ha of the study site. To that aim, focal sampling was used, noting every single avian predator present on the study site and detected by the observer visually. All avian

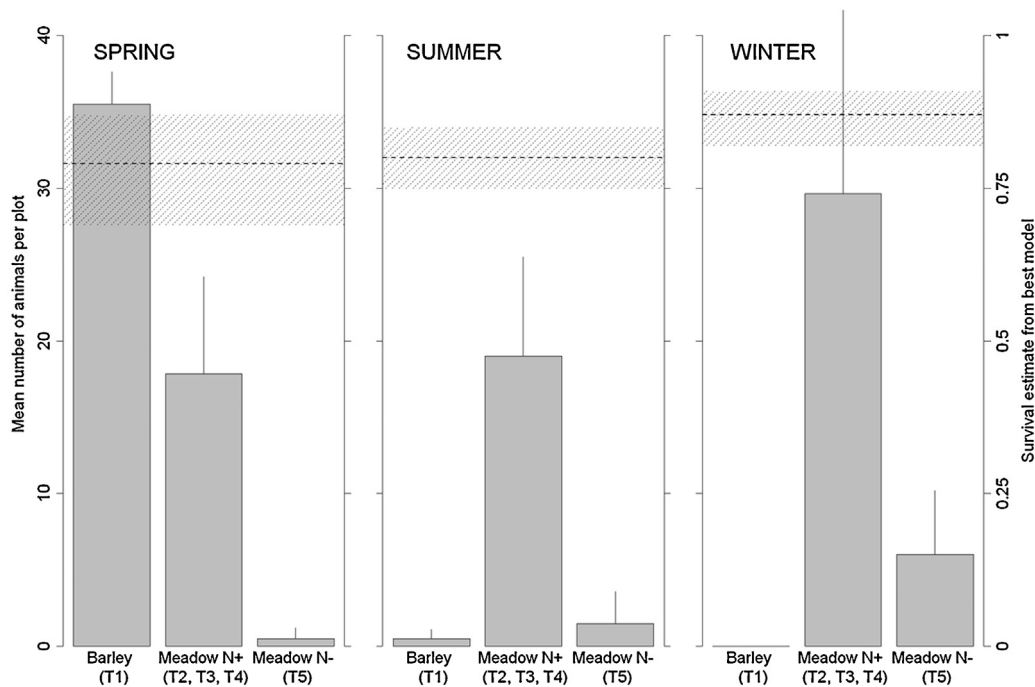


Fig. 1. Mean number of animals captured per plot (SD) for each nitrogen input category and season (left axis) and seasonal survival estimate from the best model with 95% confidence interval (right axis).

predators, once detected, were monitored for any capture attempt, as long as they remained visible. This was done 2h25 before ploughing in three sequences, 2h50 during ploughing in two sequences and 4h30 after ploughing in five sequences. Potential vole consumers present in the vicinity were hen harriers (*Circus cyaneus*), common buzzards (*Buteo buteo*), common kestrels (*Falco tinnunculus*), gray herons (*Ardea cinerea*), rooks (*Corvus frugilegus*) and carrion crows (*Corvus corone*).

2.3. Survival analysis

The CMR data included only tagged animals. Because the trapping occasions were different between blocks 1 and 2 and blocks 3 and 4, all statistical analyses were carried out separately among blocks. However, given that more data were collected over a longer period in blocks 1 and 2, the survival analyses for blocks 3 and 4 were used to confirm or reject conclusions from the survival analyses in blocks 1 and 2, rather than constituting an equally powerful test of the biological hypotheses investigated and are therefore presented in Appendix A2.

In order to estimate survival and given that voles were observed moving between plots and even between blocks, multistate models with each plot being a different state were used (Hestbeck et al., 1994; Nichols et al., 1992) because these models allow movements of individuals among states. Multistate models however required that all movements occurred between trapping sessions. Because some of the observed movements (ten) happened within trapping sessions, trapping sessions two to five were further split to allow these movements to occur between newly split trapping sessions. Time intervals between trapping sessions were adjusted consequently to this splitting.

Following Lebreton et al. (1992), the analysis of CMR data started by determining the goodness of fit of a general model to the data and then, from this general model, carried out model selection from a set of candidate models. The goodness of fit of the general model to the data was assessed by running first the four classical tests and then their multistate equivalents (see Pradel et al., 2005 for further

explanation). The program U-Care was used to perform goodness of fit tests (Choquet et al., 2009a). GOF tests indicated the presence of heterogeneity of catchability (HC) in the data (see below, goodness of fit tests) so to accommodate this, multievent models, a generalization of multistate models (Pradel, 2005), were used. The probability of survival, denoted S , was expressed on a seven-day basis to account for different time intervals between consecutive primary trapping sessions (from one to 11 weeks). The probability of transition between states, denoted TM , was included in the modeling to allow voles to move among plots. Three other parameters were introduced in the modeling to cope with HC (see Crespin et al., 2008 for further details). The probability of recapture, that allowed to cope with incomplete detection of voles, was split into a low and high catchability classes (denoted $P(\text{catch})$). A second probability of transition denoted THC was estimated to allow the individuals to switch between the two catchability classes. Finally, initial state probabilities (denoted p_i) were estimated as required in multievent models.

Multievents models were fit with the program ESURGE (Choquet et al., 2009b). However, the program ESURGE in its current version could not handle mixed hierarchical models that appeared adapted to our study site where plots were nested into treatments. Therefore, in order to determine the importance of plot effect, a preliminary analysis was first carried out. This analysis showed that this effect was small (see Appendix A1) and then a model selection was run among HC models.

As recommended by Anderson et al. (1998), model selection was performed with the Akaike's Information Criterion corrected for small sample sizes (hereafter AIC_c). For each model, the difference in AIC_c (noted ΔAIC_c) from the model with the lowest AIC_c score and the Akaike weight of the model (that can be interpreted as a relative degree of support for a given model within the set of candidate models, see Link and Barker, 2006) were calculated.

For survival and recapture probabilities, sex or age differences were not included in the analysis because of the relatively small sample size (see below, goodness of fit tests) but two sources of variation were modeled: difference between states (*plots* and

Table 2
Observed transitions grouped by nitrogen input categories and season. A total of three transitions occurred in blocks 3 and 4 in winter.

From	To	N transition
Spring		
Barley	Barley	1
Barley	Meadow N+	5
Meadow N+	Barley	5
Meadow N+	Meadow N+	8
From spring to summer		
Barley	Meadow N+	3
Meadow N+	Meadow N+	1
Meadow N+	Meadow N–	1
From spring or summer to winter		
Barley	Meadow N+	1
Meadow N+	Meadow N+	2
Winter		
Meadow N+	Meadow N+	4
Meadow N+	Meadow N–	1
Meadow N–	Meadow N+	1

treatments) and time (time and season). The variable *plot* had a different value for each plot but, given the low numbers of transitions and captures observed in T5 plots (see Fig. 1), these plots were pooled to increase the power of the analysis. The variable *plot* had nine levels. The variable *treatment* had a different parameter value for each treatment (and therefore five levels). The variable *Ninput* (three levels) was used only for survival probabilities and represented the differences in survival with regard to the amount of nitrogen input. The variable *time* (ten levels) meant a fully time-dependent model with a different parameter value for each time interval. The variable *season* had three levels depending on the crop phenology and the breeding intensity in the vole population: the first one (spring) matched the period when all crops were favorable and to the breeding season, the second one (summer) started after the barley harvest and corresponded to the end of the breeding season and the last one (winter) to the season without breeding. To keep the number of parameters reasonable in the modeling, no two-way interactions between variables were included, except the one crossing *treatment* × *season* (nine levels) in the probability of survival.

For THC transition, models with a single parameter were used (intercept-only models referred to as *THC(.)*). For TM transition probabilities following Nichols et al. (1992), only the transitions between plots observed in the data were modeled (see Table 2); other TM transitions were set at zero. TM transitions were pooled over their arrival and departure states to keep only three different transitions. First two TM transition parameters were about the movements between barley and other plots. The barley plots were thought to be good habitats until they were harvested; therefore, TM transitions from any meadow to barley plots were expected to be high and from barley to any meadow plots to be low. After harvesting, barley became a lower condition habitat and so we expected the TM transition from barley to any meadow plots to be high (and the reverse transition, from any meadow to barley plots to be low). The third TM transition parameter pooled all movements among the four types of meadow. This parameter was expected to be lower than the TM transitions from/to barley plots. Models for the TM transitions will be denoted as *TM(mod)* in the text. In the same vein, initial state probabilities were modeled as different among catchability classes and plots for all models and denoted *pi(mod)*.

To sum up, for blocks 1 and 2, the set of candidate models included the crossing of seven models for survival (*S(time)*, *S(seas)*, *S(.)*, *S(Ninput)*, *S(seas × Ninput)*, *S(treatment)*, *S(plot)*) and five models for recapture (*P(catch)*, *P(catch + seas)*, *P(catch × seas)*, *P(plot)* and *P(treatment)*), defined above, plus a model with no

variation or full time variation in both recapture and survival probabilities, i.e. 37 models in all.

2.4. Estimation of population size and apparent mortality due to ploughing

Population sizes were estimated at the trapping session immediately preceding the ploughing (from two to four weeks before) in T2 meadows (plots B1P3, B2P2, B3P4 and B4P3) from data over three days of trapping. Also, for this trapping session, several individuals less than 14 g were trapped (respectively one, one, zero and five individuals at plots B1P3, B2P2, B3P4 and B4P3) which allowed to work out the population size for the whole common vole population. To estimate population sizes, model M_{th} including heterogeneity in recapture probabilities was used with the Jackknife estimator because it has been shown to be robust to departures from model assumptions (Boulanger and Krebs, 1996; Burnham and Overton, 1978). The program DENSITY was used to work out the estimates from this model (Efford et al., 2004). Assuming that the trapping device set up at ploughing allowed to catch all the common voles alive after ploughing and given (1) the population size at the trapping session immediately preceding the ploughing (N_{ind}) and (2) the weekly survival estimate in winter from the CMR data (S_w), an expected number of voles alive may be computed as $S_w^{(N_{weeks})} \times N_{ind}$ and compared to the number of voles trapped after the ploughing (N_{surv}).

3. Results

Over all trapping sessions, a total of 1195 captures of 575 individuals were observed. Blocks 3 and 4 had less captures (299 of 134 individuals) than blocks 1 and 2 (896 of 441 individuals), partly because trapping in these two blocks only started at the 9th trapping session (Table 1). Among the 512 individuals alive at their first capture 298 were recaptured at least once (two captures: 143 individuals, three: 70, four: 40, five: 22, six: 13, seven: 7, eight: 2 and nine: 1).

During spring, the total number of individuals captured increased with time (Table 1) and there were more individuals caught in barley plots than in meadows (Fig. 1). The number of individuals decreased strongly in summer, especially between sessions five and six; barley harvesting corresponding to session five. Then, the population increased again in autumn (sessions six to eight), reaching similar numbers as those in spring. After barley harvesting only one single individual was captured in barley plot in summer, and none in winter. Less intensively fertilized meadow (T5) had fewer captures than any other meadow, whatever the season (Fig. 1).

In blocks 1 and 2, the transitions to and from barley constituted 15 out of the 30 movements recorded (Table 2). Most transitions occurred between the second and fifth trapping session. Among the six transitions observed in winter, three occurred in blocks 3 and 4. There was no sex bias in the individuals involved in transitions (11 females, nine males and three individuals for which sex was unknown). Most of the transitions occurred in the same block ($N=23$) rather than between two different blocks ($N=10$). No transitions between blocks 1 and 2 and blocks 3 and 4 were observed.

3.1. Survival analysis

For blocks 1 and 2, with unistate data (i.e. all states pooled together), strong transience (TEST 3G.SR: $z=2.42$, one-sided $p=0.008$) and trap-happiness effects (TEST 2.CT: $z=-4.30$, $p=1.72 \times 10^{-5}$) were detected while other components were not significant. Taken together, these results indicated a strong heterogeneity of catchability (HC) in the data (see Crespin et al., 2008). With multistate data, however, the transience effect was no longer significant (TEST 3G.SR: $\chi^2=48.85$, $df=51$, $p=0.56$). Although no test of trap-dependence could be carried out because of small numbers of recaptures in the data, TEST 3G.SR suggested that HC had been greatly reduced when the states were added into the model. To sum up, results of goodness of fit tests indicated heterogeneity of catchability and model selection was therefore carried out on HC models.

HC models improved indeed very much the fit over 'classic' multistate models. The difference in AIC_c between simple models $S(.)P(.)$ and $S(.)P(catch)$ was large (~ 55 , see Appendix A3). Out of the 37 models run, the best model was a model with seasonal variation in survival probabilities and additive seasonal variation over the two classes of catchability in recapture probabilities (model $S(seas)P(catch+seas)TM(mod)THC(.)pi(mod)$, $K=23$, $AIC_c=3068.98$, see Appendix A3) since the second best model was distant of more than two units of AIC_c with two extra parameters. There were three models with variable *Ninput* in survival for which $\Delta AIC_c < 10$;

Table 3Total number of individuals caught, average probability of capture (p -hat), population size (N), with 95% confidence intervals based on the sampling preceding ploughing.

Plot – treatment	B1P3 – T2	B2P2 – T2	B3P4 – T2	B4P3 – T2
Trapping session preceding the ploughing experiment				
Individuals (captures)	14 (26)	14 (29)	11 (16)	27 (49)
p -hat	0.39	0.49	0.38	0.35
N [95% CI]	16.8 [14.5–28.9]	14.8 [14–29.2]	11.3 [11–25]	35.2 [29.9–49.7]
Expected numbers alive at the time of ploughing				
Interceptions during the ploughing experiment	10	10	8	29
First 24 h after ploughing				
From 24 to 72 h after ploughing	3	3	2	5
	NA	NA	1 (48 h)	1 (72 h)

evidence for the inclusion of *Ninput* in survival was however weak as the first ranked model was more than five units of AIC_c from the score of best model ($\Delta AIC_c = 5.27$). Variables *treatment* or *plot* were respectively almost not or not supported by the data (with ΔAIC_c respectively of 9.47 and 12.91) suggesting that there was no difference among the plots and treatments in survival probabilities.

3.2. Inferences from best model

The difference in weekly survival estimates between the spring and summer taken together (respectively 0.79 [0.69; 0.87] and 0.80 [0.75; 0.85]) versus winter (0.87 [0.82; 0.91]) was large in terms of population dynamics (see Fig. 1). Differences among seasons in recapture probability were strong also with estimates for the high catchability class being respectively in spring, summer and winter: 0.60 [0.48; 0.71], 0.80 [0.61; 0.91] and 0.97 [0.86; 1.00]. Estimates for the low catchability class were respectively: 0.03 [0.01; 0.09], 0.07 [0.02; 0.20] and 0.41 [0.17; 0.69]. The proportion of individuals in the high catchability class was estimated to 0.52 [0.39; 0.65] and the proportion of individuals first caught ranged from 0.07 [0.05; 0.10] to 0.19 [0.16; 0.23] among plots. The transition between catchability classes was estimated to 0.03 [0.00; 0.26]. Transition estimates matched well the hypotheses of poor vs. good conditions we made about the barley plots. As expected, the transition from any meadow plots to the barley plots was high (0.07 [0.03; 0.16]) before the harvest of the barley and low after (estimated as zero as no transition occurred from any meadow plots to the barley plots). Also, reverse transition estimates from barley plots to any meadows were low before harvest (0.03 [0.01; 0.06]) and high after (0.14 [0.02; 0.61]). The standard error of this last estimate was high because most individuals having made this transition had not been recaptured for a long time and therefore the exact moment when they made the transition was uncertain. For the rest of transitions, estimates seemed slightly higher at the beginning, until the fifth trapping session (0.04 [0.02; 0.09]) than at the end of the study (0.03 [0.01; 0.06]).

3.3. Common vole demographic parameters at ploughing

A total of 24 common voles were trapped in the buckets before ploughing and 15 after ploughing (Table 3). Unfortunately, not all voles trapped were weighted for logistic reasons; however, among the 24 common voles trapped before ploughing, 20 were weighed, among which eight were <14 g. Among the 15 common voles caught after ploughing, four were recaptures, six were weighted, among which four were juveniles. This higher proportion of juveniles in the interception devices compared to Ugglan traps (seven out of 66 at the trapping session preceding ploughing) suggested that the interception devices were characterized by a better catchability because juveniles are notoriously difficult to capture in small mammals. During the two first trapping sessions after ploughing no common voles were caught on ploughed plots. The first capture on ploughs occurred four weeks after ploughing. In addition, no animal formerly tagged on the ploughed plots was recaptured later on the ORE. Therefore, most, if not all the dispersing individuals were intercepted.

About the importance of predation, no diurnal predation event was observed and only one scavenging behavior was reported on all plots after ploughing. Further, there was no evidence of the presence of vole predators during the whole experiment and, when dismantling the experimental devices, no burrows were observed under or through the tarpaulins.

Average probabilities of capture estimates were similar over all four plots (from 0.35 to 0.49; see Table 3). Moreover the estimated population sizes at the trapping session preceding ploughing were quite homogenous (between 11 and 17 individuals per plot) except for plot B4P3 where the population size was estimated as twice the others (35 individuals). The estimate of weekly survival in winter (S_w) was 0.874 in blocks 1 and 2 and 0.907 in blocks 3 and 4 and trapping occurred four, three, three and two weeks before ploughing for plots B1P3, B2P2, B3P4 and B4P3 respectively. Therefore, from the estimate of population size at the last trapping session, one would expect ten, ten, eight and 29 individuals alive for plots B1P3, B2P2, B2P4 and B4P3 respectively. Since the number of common voles intercepted was 15 (three, three, three and six for B1P3, B2P2, B2P4 and B4P3 respectively, see Table 3), i.e. markedly lower than the expected number of common voles alive (57), it was clear that a strong mortality or emigration took place between the last trapping session and three days after the ploughing.

4. Discussion

Survival rates were higher in winter than in spring and summer. This seasonal variation was consistent with previous estimates found in literature for small mammals. For example, in a study over three years on a closely related species, the field vole *Microtus agrestis*, monitored at several clear-cut sites in spruce forests, survival rates were generally highest in the late autumn and over winter, and then decreased in spring to reach a seasonal low between May and July before increasing again (Graham and Lambin, 2002). Also, the same work yielded estimates of adult survival per 28 days from 0.15 to 0.93 which were comparable to the present study, calculated over the same 28 days period, from 0.39 to 0.68. It was however more difficult to compare the estimates of recapture from the models used in this study to the ones found in the literature because HC models with two catchability classes were employed in this study while other works typically used a single parameter of recapture. Nevertheless, the HC models highlighted that the probability of recapture was seasonal and increased from the spring to the winter. Graham and Lambin (2002) also reported seasonal variation in the probability of recapture and provided site-specific probability of recapture equaling 85.8%, 88.5% and 91.7%, i.e. estimates close to the ones from the high catchability classes. Bryja et al. (2001) monitored a high density population of *M. arvalis* and reported an arithmetic average of recapture probability of 0.61, which was very close to the smallest estimate of recapture for the high catchability class.

4.1. Seasonal patterns in abundance and demographic rates

The studied common vole population showed marked differences in abundance between treatments; in particular, abundance was related to crop type as well as the level of nitrogen input (Fig. 1). In 2010, the total harvested dry biomass was three times higher in the N+ than in the N– meadows (5.5 and 1.7 t/ha respectively, X. Charrier, pers. comm.) and the vegetation height measured at each sampling session was on average twice in the N+ than in the N– meadows (data not shown). Hence, greater food availability as well as the presence of a better cover against predators could explain the difference in abundance between N+ and N– meadows. Furthermore, nitrogen is generally considered to be the primary limiting nutrient among terrestrial herbivores (Mattson, 1980) and many examples exist of increases in key population parameters such as growth, reproduction and survival in response to higher nitrogen availability in the plants (Morilhat et al., 2007; Parsons et al., 2005; Patterson and Fuchs, 2001). Hence, cereals harbored the highest abundance in spring which was in accordance with previous observations in Central European agricultural landscapes (Janova et al., 2011). The week following barley harvesting, no capture was made in the four barley plots and only one individual was captured in the five subsequent trapping sessions. These results demonstrated that cereal harvesting made a field almost unsuitable for voles, as previously suggested (Aschwanden et al., 2007). This might be due to the disappearance of cover against predation (Jacob and Brown, 2000)

since harvesting shortened vegetation height from 90 to 0 cm on average. Harvesting could probably be deadly itself as suggested by Jacob and Hempel (2003) who found three of their 14 radio tracked common voles dead after wheat harvesting. In the present study, the common vole abundance in barley was halved the week before harvesting (from 48 individuals captured at the 3rd session to 24 at the 4th session) which might be explained by a decline in food quality, especially of water content, when barley gets ripe. Also high transition rates from barley to meadows (0.14) were estimated in summer, just following harvesting. These observations were consistent with a previous study on a Southern American rodent (Cavia et al., 2005) and suggested that vole disappearance after harvesting was mainly due to emigration rather than death. In addition, the highest survival rate estimated in summer was inconsistent with an additional mortality due to barley harvesting.

While abundance strongly differed according to plot, treatment or nitrogen input, no such effects were found on survival rates using CMR modeling. This apparent discrepancy could be partly due to the small amount of data in the less favorable treatments that drastically reduced the statistical power of the CMR modeling. However, there were also good arguments to believe that survival was actually not different between treatments since variations in abundance might be explained by differences in reproduction and directional movements between treatments as suggested by the observed pattern of transition.

4.2. Common vole population response to ploughing

In this study, the number of common voles that survived ploughing through emigration was estimated at the population level (15 out of 57). The negative consequences of ploughing for common vole survival have already been discussed (Jug et al., 2008), but the single quantitative estimation of mortality due to ploughing available in the literature was based on four dead and two lost out of six radio-tracked animals (Jacob and Hempel, 2003). The reliability of the estimates presented in this paper depends however on an accurate and unbiased estimate of survival yielded from capture mark recapture multievent models taking into account the HC observed in the population. Further it is likely that no common vole remained alive and dispersed after the interception design was dismantled since no individual was captured after ploughing and no tagged animal from the monitored fields was subsequently recaptured (which suggests that no surviving resident had dispersed after the device was removed). Finally, the estimates of numbers that survived ploughing depended also on the estimates of population size made at last trapping session. These estimates came from a closed-population model known to be robust (Boulanger and Krebs, 1996; Burnham and Overton, 1978). The higher proportion of juveniles intercepted (40%) compared to the previous CMR trapping session (11%, $N=66$ animals) suggested that the population size before ploughing and thus the mortality due to ploughing were underestimated. Therefore, 74% (42 missing out of 57 voles estimated in the population) could be considered as a minimal estimate at the population level of vole mortality due to ploughing.

The ploughed environment appeared unsuitable for common voles, as demonstrated by the absence of captures in the following weeks, very likely because most burrows were destroyed (Brügger et al., 2010), vegetation was nonexistent and food resources were very much reduced. The present study showed that it was possible for a common vole to remain alive at least 72 h on a ploughed field. However, this was based on only one individual while 13 out of the 15 intercepted common voles tried to leave the plot in the first 24 h. Perhaps the two other intercepted individuals could remain alive in the plots thanks to the 30–50 cm wide unploughed strips along the interception devices. Hence, these emigrants were considered to be the only survivors of the population. The observations carried

out on predators suggested that predation was negligible, at least in this study, despite numerous raptors and gulls observed on freshly ploughed fields (pers. obs.). Such absence of bird predators could be due to the fact that the experiment occurred in March, when the breeding season of these birds has not yet started, and summer resident raptors were still absent.

4.3. Common vole dynamics in real farming landscapes

One major question was whether demographic parameters estimated in the present study, in particular with such small fields, could be translated into real farming landscapes. Plot size was obviously the major limitation of the present survey: about 0.4 ha, in comparison to about 4 ha in the study site where previous common vole field studies had been conducted in Western France (Gauffre et al., 2008; Inchausti et al., 2009; Salamolard et al., 2000). Their small size could have artificially enhanced edge effects and facilitated animal movements among plots. However, common vole home ranges are known to be small with respect to the ORE plot size, about 125 m² in wildflower strip, 145 m² in alfalfa and pastures (Briner et al., 2005) and 200 m² before farming practices in the Jacob and Hempel (2003) study.

Numbers of common voles having survived ploughing were low in this experimental study. Therefore, one may wonder how common vole populations persist when annual crops are the major land use (often 90% of land use), and are ploughed annually. The resolution of this paradox lies in the fact that common voles disappear from cereal crops rapidly after harvesting, i.e. much before ploughing occurs in these crops, and therefore the number of common voles remaining in the ploughed plots at the time of ploughing is minimal. Habitat heterogeneity and the presence of perennial habitats appear to be critical factors favorable to the common vole, underlying the crucial role played by grasslands which act as refuge habitats that remain undisturbed in the landscape, without any ploughing for several successive years, while annual crops become temporarily completely unsuitable (Heroldova et al., 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.05.005>.

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