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Autumn habitat selection of the harvest mouse (*Micromys minutus* Pallas, 1771) in a rural and fragmented landscape

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Abstract: The harvest mouse *Micromys minutus* has, through nest findings, been documented to live in wetlands in tall sedges and grasses in Central Europe. However, there is very little information on the type of habitat this species uses outside of nesting, because this rodent is difficult to capture in ordinary trapping set ups. In France and Switzerland, the harvest mouse populations have decreased strongly in the past two centuries due to the drastic reduction of its favored habitat. The present study used radiotracking to examine a small population in Eastern France living in a fragmented rural landscape. The aim was to learn more about the habitat and vegetation selection of this population during autumn. The results showed that the most favored habitats were in patches of stinging nettles (*Urtica dioica*) and American goldenrod (*Solidago gigantea*) rather than in their supposedly preferred vegetation type, which are tall grass wetlands. The results also presented migrating behavior in three out of the eight monitored individuals, which lead to the discovery of a possible wintering area in an unmown grassy site around a plant dump. These results suggest that disturbed, but unmown areas are important for the harvest mouse as wintering vegetation and should be available in the surrounding of a reproduction site. The results also showed that wetland management must take into account the affinity of this mammal for areas invaded by American goldenrod, in order to prevent the harvest mouse populations from decreasing in those secondary habitats.

Keywords: Harvest mouse - Radiotracking - American goldenrod - Stinging nettle - Habitat fragmentation.

INTRODUCTION

The harvest mouse *Micromys minutus* (Pallas, 1771) is the smallest rodent living in Europe. The ecology of this inconspicuous animal, like its dietary and habitat preferences, is poorly understood, due to the difficulty to trap and observe it in nature. However, a well-known behavior in harvest mice is their ability to build above-ground nests by tearing up the top part of tall grasses into strings, and by weaving them together. These nests are constructed to be used as a shelter and to litter their offspring. Several pioneer articles studying habitat selection of the harvest mouse (Trout, 1978a; Harris, 1979; Dickman, 1986), describe the presence of this species by the means of nest searching, which has the consequence of mostly disclosing the habitat chosen by the mice during the reproductive period. This means that the preferred foraging habitat of the harvest mouse is not necessarily known and might not be the same as the habitat chosen for resting or reproduction.

The conclusions of studies investigating the vegetation type favored by the harvest mice seem to vary depending on regions. For instance, several authors state that this species is mainly connected to wetlands (Trout, 1978a; Hata, 2011), while others point out its ability to live in a wider range of habitats, including hedgerow, shrubs, dry meadows and disturbed areas (Dickman, 1986; Harris, 1979; Bence *et al.*, 2003; Wijnhoven *et al.*, 2005). However, this rodent is usually not associated with woody areas, stinging nettles, and wastelands (Wijnhoven *et al.*, 2005).

In Central Europe, the harvest mouse is mostly known from marshes and wetlands dominated by tall grasses (*Molinion*, *Phragmition*), or tall sedges (*Caricion*) (Rahm, 1995; Haberl & Kryštufek, 2003; Surmacki *et al.*, 2005; Blant *et al.*, 2012). Unfortunately, these types of vegetation have substantially decreased in France and Switzerland during the past two centuries (Brinson & Malvárez, 2002; Gimmi *et al.*, 2011). Fragmentation and habitat loss have a significant negative influence on wetland species in general (Nilsson & Grelsson, 1995; Lienert *et al.*, 2002). Furthermore, expansion of invasive species like the Japanese knotweed *Reynoutria japonica* (= *Fallopia japonica*) (Polygonaceae) or American goldenrods [*Solidago gigantea* and *Solidago canadensis* (Asteraceae)] also affects negatively those types of habitats (Nilsson & Grelsson, 1995; SSC, 2000; Zedler & Kercher, 2004).

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The main goal of the present study was to increase our knowledge regarding the ecology and behavior of the harvest mouse, in particular its habitat selection in a fragmented environment during the autumn period. This study focused on the vegetation associations selected by the harvest mouse by means of radiotracking. A fragmented tall sedge meadow (*Caricion elatae*) colonized by the exotic and invasive species American goldenrod (*Solidago gigantea*) has therefore been chosen as the study area. In addition to radiotracking, a Capture-Mark-Recapture event was set-up to better understand the overall living conditions of the studied harvest mouse population.

Based on the knowledge gathered on the habitats selected by harvest mice to construct their nests, certain types of vegetation are expected to be favored by this species. In particular, we asked whether:

i) Harvest mice favor the habitat type they are known to prefer during reproduction elsewhere in Central Europe, which are tall sedge (*Caricion*) and/or tall grass (*Phragmition*, *Molinion*).
ii) Harvest mice avoid patches of stinging nettle and American goldenrod, woody areas and anthropogenic areas.
iii) Harvest mice stay in the vicinity of the tall sedge meadow where they are captured.

MATERIAL AND METHODS

Study area: The study area was located in France near the village of Greny, in the municipality of Péron (Fig. 1). The size of the study area was 23.1 ha which could be divided into many different types of vegetation types and associations (Table 1, Fig. 2, Appendix 2). The sector where the trapping was set up was a tall sedge meadow (association *Caricetum acutiformis*) of 0.26 ha, growing along a stream named "ruisseau de Chanvière". This stream was dry during the entire field study period (from mid-August of 2017 to mid-November of 2017). Some smaller patches of the lesser-pond sedge *Carex acutiformis* were also present near the main meadow. Together, the *Caricetum acutiformis* represented around

Table 1. Surfaces of the different habitats present in the study area. The marsh vegetation and grassy areas are the type of vegetation expected to be preferred by harvest mice. Areas invaded by American goldenrods and by stinging nettles had an overall similar surface and availability than the previously mentioned habitat types. Woody areas were the most common type of vegetation in the study area.

Vegetation type	Proportion (%)	Association	Surface (ha)	Proportion (%)
Marsh Vegetation	5.5%	*Caricetum acutiformis*	0.48	2.06
		Phragmition communis	0.37	1.59
		Mentho-Juncion	0.24	1.06
		Molinion caeruleae	0.18	0.78
		Urtico-Calystegietum	0.36	1.56
		Solidagetum gigantae	1.19	5.14
Dry grassy area	0.54%	*Panico-Setarion*	0.12	0.54
Woody areas	63.8%	*Carpinion betuli*	10.69	46.29
		Alnion incanae	0.28	1.21
		Alnenion glutinoso-incanae	3.20	13.85
		Tree plantation	0.56	2.43
Mown areas	15.6%	*Molinion* (cut down)	0.80	3.47
		Mentho-Juncion (cut down)	1.93	8.36
		Caricetum acutiformis (cut down)	0.08	0.34
		Cynocurion (cut down)	0.79	3.43
Anthropogenic areas	7.89%	Path	0.45	1.96
		Road	1.37	5.93
		Total	**23.10**	**100.00**

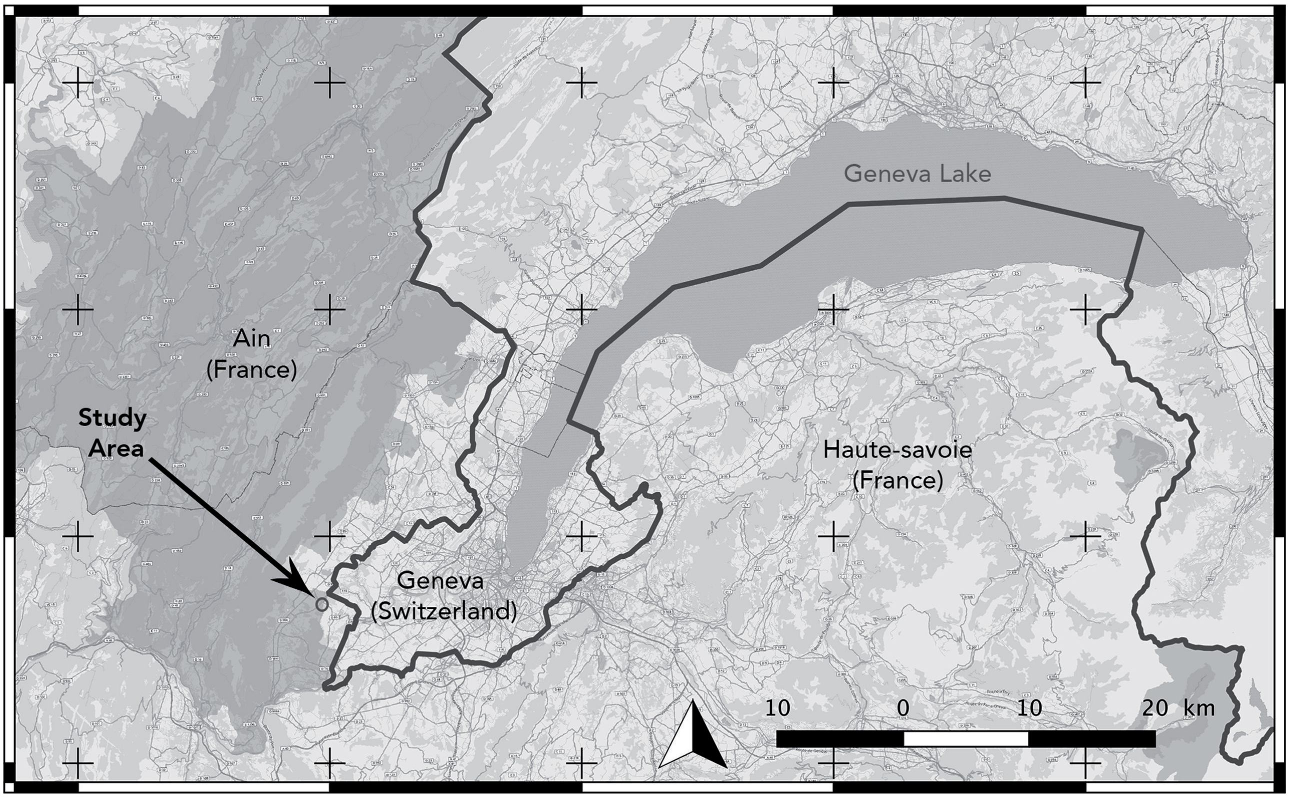

Fig. 1. Map representing the location of the study area. The middle of the main tall sedge meadow is found at the DMS coordinates 46°11'24.4"N 5°57'30.1"E. The study area is situated in the Department Ain, in Eastern France, near the French-Swiss border.

2% of the study area. The area had been shown to be inhabited by harvest mice in 2016, thanks to trapping and the discovery of nests (Gilliéron, 2017).

The habitats surrounding the main meadow included three types of deciduous forests [association *Carpinion betuli* (46.3% of the overall size of the study area), *Alnenion glutinoso-incanae* (13.9%), a tree plantation (2.4%), and an *Alnion incanae* (1.2%)]. In the marshy grasslands (associations *Mentho-Juncion* and *Cynosurion*) adjacent to the main tall sedge meadow, cattle were sometimes present. Some areas were invaded by American goldenrod (*Solidago gigantea*), and by stinging nettles [*Urtica dioica* (L., 1753)], described as characteristic of the alliance *Convolvulion* [associations were respectively *Solidagetum gigantae* (5.1%), and *Urtico-Calystegietum* (1.6%)].

Additional important habitats found in this site were patches of the association *Phragmition* (1.6%) and *Molinion* (0.8%), which are known to be ideal habitats for harvest mice in France and in Switzerland. A plant waste dump was also found near the tall sedge meadow, where a *Panico-Setarion* (0.5%) association thrived. The study area also included a large road constructed in 2001.

Trapping design: A capture-mark-recapture program (CMR) was set up. Trapping was conducted from the second week of August of 2017 to the first week of September of 2017. A total of 14 trapping nights were completed with 71 INRA traps aligned in 8 transects (Fig. 2, for more details, see below), resulting in 994 trap-nights.

The harvest mouse is a species known for its ability to climb, and has a higher inclination to be captured by traps placed above ground than on the ground (Nordvig, Reddersen & Jensen 2001; Vogel & Gander, 2015). Thus, to increase the probability of capturing the target species over other small mammals, the traps were placed on wooden platforms installed on 60 cm tall sticks (Fig. 3). They were baited with sunflower seeds.

The traps were installed in every substantial patch of tall sedge in and around the main tall sedge meadow. The traps were positioned in 8 line transects and spaced every 1.5 m until reaching the edge of the tall sedge vegetation. Four line transects were placed transversally in the main meadow, with a 10 m gap between each other. In narrower and elongated shaped sedge patches, the line transects were positioned longitudinally.

Initially, it was decided to carry out night-trapping only, with a first check of traps after dusk and a second check after dawn. Because of an overload of wood mice [*Apodemus sylvaticus* (Linnaeus, 1758)] and yellow-necked mice [*Apodemus flavicollis* (Melchior, 1834)], which are both nocturnal rodents, it was decided to

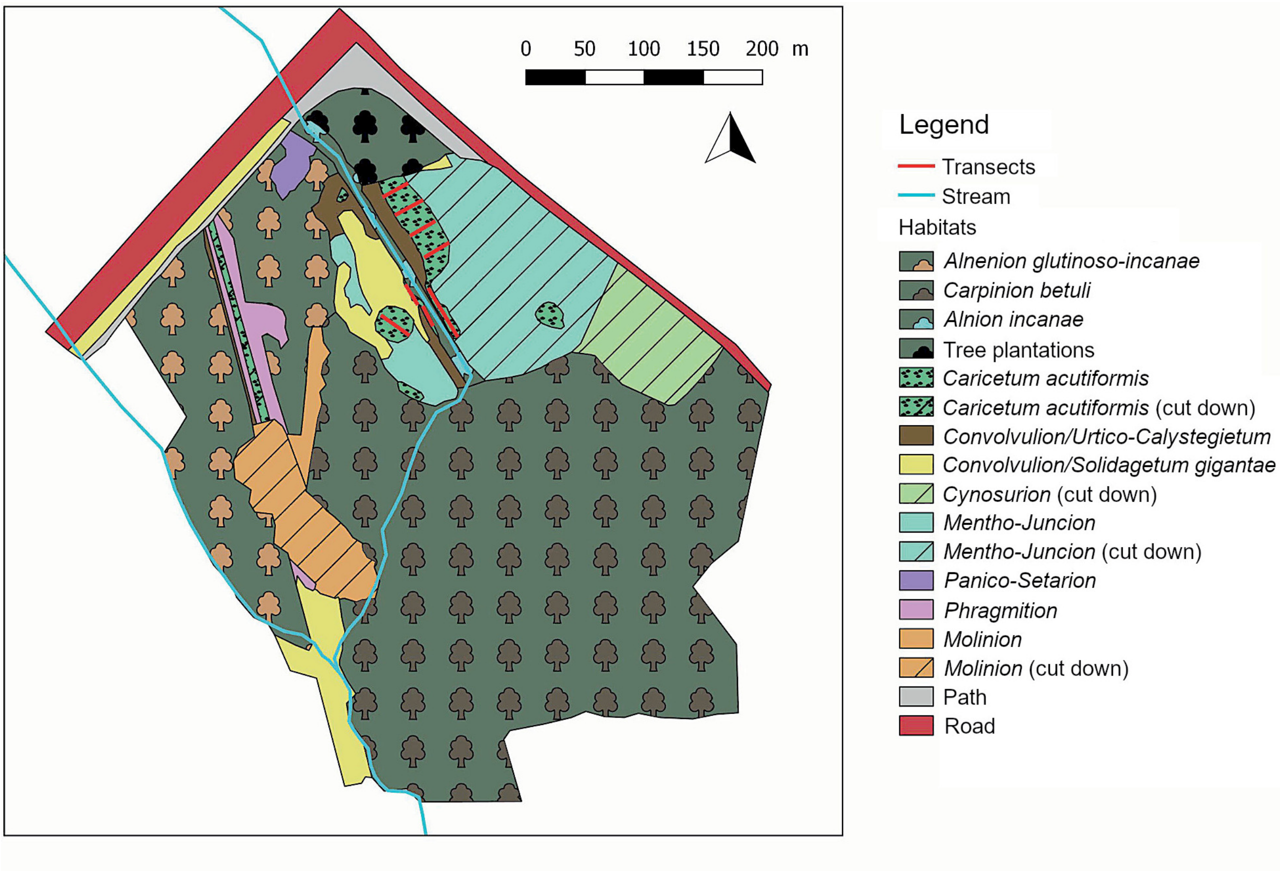

Fig. 2. Map representing the study area and the different habitat types present in it. The *Caricteum acutiformis* patch in the North is the main tall sedge meadow, where most of the study was conducted. The transects (red lines) shown on this map were the ones used for trapping (i.e., for the Capture, Mark and Release event).

activate the traps once during the afternoon for 4 h to capture mice active by day, and once during the evening for 4 h to intercept the nightfall movements.

The trapped harvest mice were marked by means of fur clipping with a small pair of scissors. Their age and sex were documented. The age is very difficult to determine on live harvest mice (Trout, 1978b; Harris, 1979). Therefore, it was decided that individuals weighting less than 6 g and with no apparent primary (testes) or secondary (nipples) reproductive organs were considered as subadults, while the other individuals were considered as adults. The other captured animals were only identified to the species level.

Radiotracking: The tags emitting the position of the tracked mice were glued without anesthesia between the shoulder blades of the captured individuals using veterinary glue. To facilitate the adhesion, the fur was first cut down with a pair of scissors at the implementation area. Among the captured mice, only those weighing at least 5.8 g were selected, for the tag not to exceed 5% of the weight of the equipped animal.

The "homing-in" method was applied to locate the tagged animals. It consists of getting as close as possible to the equipped individuals to know their location. The transmitters chosen for the radiotracking were 0.29 g PicoPip Tags from Biotrack©. These transmitters were relocated with an Australis 26k™ Titley© receiver, which was connected to a Yagi Three Element Antenna (151 MHz) from Titley©. The axis of the antenna was used to indicate the general position of the tag. The receiver was emitting a stronger signal when getting closer to the tags. This material had a maximum detecting range of 50 to 100 m depending on the vegetation density and humidity. The coordinates of the relocations were recorded with a Rugged, handheld Garmin GPSMAP 64®, which approximately had a 3-meter radius error.

The radio-telemetry was performed from mid-September to mid-October 2017. The tagged mice were released at the exact same spot where they had been trapped, defining their first coordinates. All the remaining traps present in the study area were closed to minimize their influence over the mice's wandering and foraging behavior. The location of the tagged animals was recorded every six hours – if the weather permitted – until the transmitter fell off. The vegetation association was documented on the spot at the same time as the radiotracking and paired with each relocation. The tag could sometimes fall short after the release of the animal or stay put for up to eight

Fig. 3. Set up of the INRA traps, installed in mid-August of 2017 on 60 cm tall sticks, and baited with sunflower seeds. The transect represented here was located in the sedge patch on the South side of the stream la Chanvière. The yellow flowers behind the *Caricion elatae* are the American goldenrod extending nearly to the edge of the forest.

days. Only the individuals that carried the transmitter long enough to be recorded for at least five relocations (which corresponds to at least 24 hours) were kept for the results.

Nest searching and supplementary trapping: A week of trapping was completed from late October to mid-November in the areas where monitored harvest mice were found to spend time (Appendix 1, secondary transects shown as red lines). Nest searching was also carried out in those areas (Appendix 1, shown in grey) to find evidence of long-term occurrence of harvest mice.

Analyses of location data:

CMR (capture-mark-recapture): The size of the harvest mouse population was assumed to be the same as total number of captured and marked individuals during the CMR event.

Radiotracking: The distance between recorded relocations was measured on the QGIS Geographic Information System (Open Source Geospatial Foundation Project) with the distance matrix analysis. The home range was calculated with RStudio with the package HabitatHR (Calenge, 2015) by combining the GPS coordinates recorded for each tracked individual, using the bandwidth href and including 50% and 80% of the relocations.

RESULTS

CMR: A total of 191 mammals were caught during the first Capture-Marking-Recapture session (Table 2). Despite the high amount of non-target species being caught in the traps by night (188 captures), the harvest mouse was trapped as many times by day (12 times) as by night (12 times). These 24 trapped harvest mice represented 12.6% of the 191 total captures.

Wood mice and yellow-necked mice (*Apodemus* spp.) were the most dominant species during the live-trapping event. They were caught a total of 87 times in eight days, exclusively during the night sessions. The next most dominant species was the bank vole *Myodes glareolus*

Table 2. Results of the CMR event (from the 27th August of 2017 to the 8th of September 2017) in a tall sedge meadow. This represents 8 trappings-nights with 71 above-ground INRA traps. The traps were open 4 hours (day trapping) during the day to capture diurnal activities of harvest mice while avoiding the activity of most other rodents and shrews. The night trapping consisted of 4 hours during the evening to capture nightfall movements.

Species	Day trapping	Night trapping	Total	Proportion
Apodemus spp.	0	87	87	45.5%
Myodes glareolus	6	61	67	35.1%
Micromys minutus	12	12	24	12.6%
Neomys fodiens	2	8	10	5.2%
Sorex minutus	0	3	3	1.6%
Total	**22** (10.5%)	**188** (89.5%)	**191** (100%)	

(Schreber, 1780). Found mostly during the night (61 times), this species was also caught by day (6 times). Two species of shrews were also trapped in the *Caricetum acutiformis*. The water shrew *Neomys fodiens* (Pennant, 1771) was captured 10 times, while the pygmy shrew *Sorex minutus* (Linnaeus, 1766) was captured three times. The 14-day CMR event showed 12 marked individuals (Fig. 4). Those harvest mice were represented by four adult males, three adult females, three subadult males, and two subadults females. All the adult females captured during the CMR event were either pregnant or lactating.

Radiotracking: Eight harvest mice out of the twelve present in the main meadow were heavy enough (5.8 g or above) to carry the transmitter, and kept it for a sufficient amount of time to generate at least five GPS relocations. The picoPip tags remained on the mice from one to eight days, with a mean of just above three days. The longest distance an individual has moved from its original release point was 350 m.

Wandering behaviors: F1, a pregnant female (12 g, 9 relocations in 54 h), had proportionally the smallest wandering area of all the tracked individuals (Fig. 5, top right). It stayed close to the main tall sedge meadow. Despite this individual being the most closely connected to the *Caricetum acutiformis* of all the tracked mice, only 44% (4 out of 9 points) of the relocations were found in tall sedge. The other relocations were found in the stinging nettle invaded parts of the *Caricion*, (*Urtico-Calystegietum*) and always near American goldenrods.

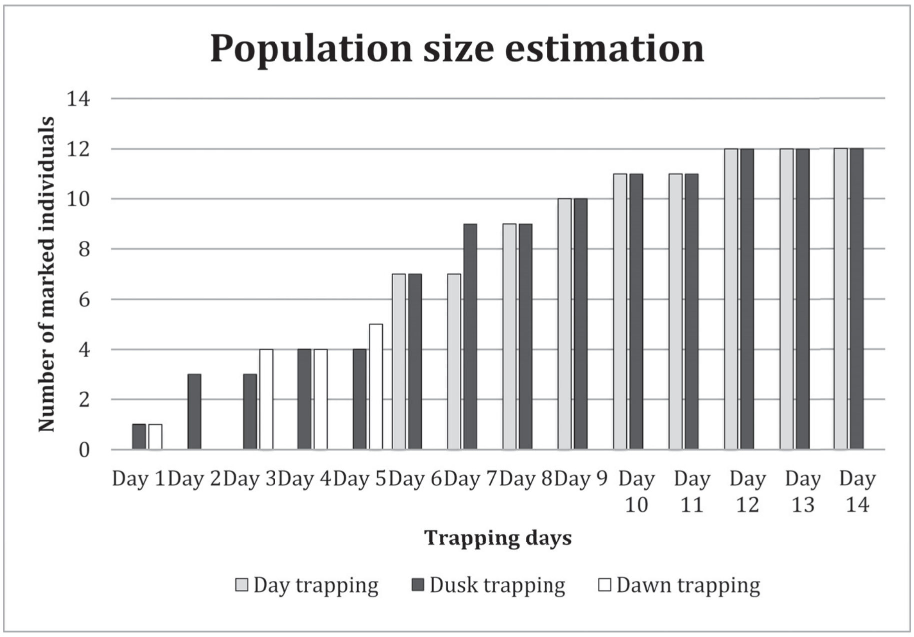

Fig. 4. Accumulated number of marked individuals captured during the CMR event. In the first 5 CMR days, the 71 traps were open 4 h in the evening during the dusk, and 4 hours in the morning during the dawn. The 8 following days (from day 6 to day 14), the traps were open 4 h during the day and 4 h at dusk. The population estimate levelled at 12 individuals, which corresponds to the total number of marked individuals captured during the 14 trapping days.

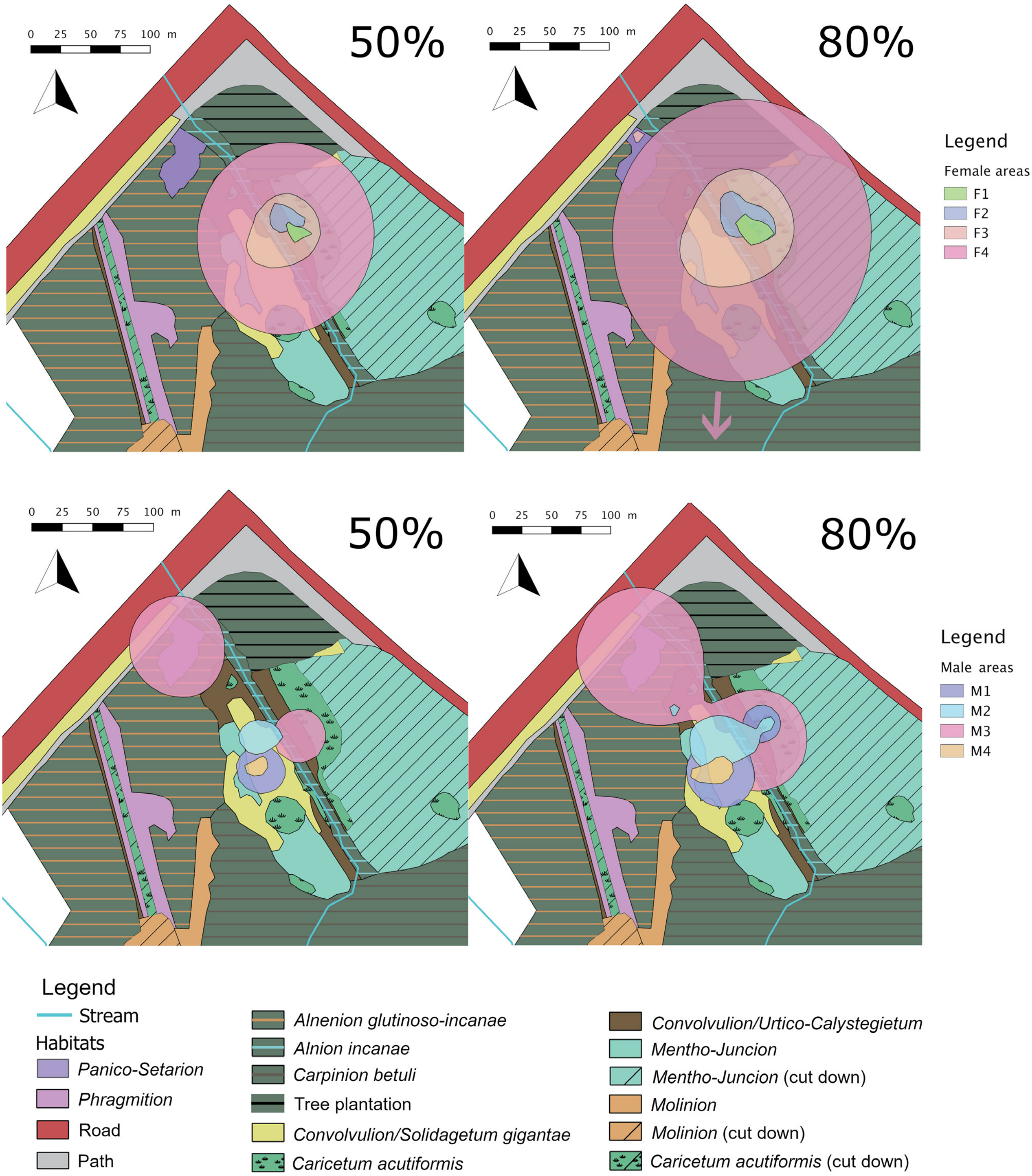

Fig. 5. Wandering areas of the four females (top) and four males (bottom) tracked from mid-September to mid-October of 2017. These ranges were calculated on RStudio with the package HabitatHR. The maps on the left were produced using 50% of the relocations, while the maps on right were produced using 80% of the relocations. These two territory sizes (50% and 80%) help picturing the possible wandering surfaces that may have been used by the tracked individuals. Their actual home ranges were probably between these two representations. Note that female F4 had an additional wandering area outside the presented map (indicated by the arrow on the bottom of the top-right image), when 80% of the relocations were included.

F2, a subadult non-reproductive female (5.8 g, 7 relocations in 40 h), was found equally in tall sedge vegetation and in nettle-invaded areas (43% for each of the habitats). American goldenrods were also consistently present in all the relocations, while not being the dominant plant species.
F3, a non-reproductive adult female (6.1 g, 12 relocations in 96 hours) was relocated near a plant dump, at around 130 meters away from its release point (Fig. 6, bottom left). F3 was located once out of 12 relocations in the *Panico-setarion* which corresponds to the main vegetation found around of the plant dump. It was its last relocation before losing its transmitter. Before moving to the disturbed area, F3 was found 50% in stinging nettles, 25% in goldenrods, and 17% in tall sedge.
F4, a subadult female (5.8 g, 26 relocations in 196 hours) moved the furthest from its releasing point of all the tagged mice (Fig. 6, bottom right). The tag of this female also stayed the longest on its back (eight days). This individual left the tall sedge area, and was found 355 m from its release point, in American goldenrods further south (Fig. 6, bottom right). The radiotracking yielded the same number of relocations in stinging nettles and in goldenrods (46% each), meaning that 92% of the relocations were found in the *Convolvulion* alliance.
M1, a sexually mature male (7.8 g, 5 relocations in 30 h), was mainly found in goldenrods (Fig. 7, top left).
M2, a non-reproductive male (6 g, 14 relocations in 9 hours) also favored the goldenrod habitat *Solidagetum gigantae* with 79% of its relocations (Fig. 7, top right).
M3, a sexually mature adult male (6.8 g, 16 relocations in 97 hours) was relocated in the same a disturbed area as F3 (Fig. 6, bottom left and Fig. 7, bottom left). M3 had 15% of its relocations in stinging nettles, including once in the plant dump area. It was never found in goldenrods. This individual had 56% of its relocations in the *Panico-Setarion*.
M4, a sexually mature adult male (7.8 g, 5 relocations in 26 h) was mainly found in the same area and habitat as M1 and M2 (Fig. 5, bottom).

Habitat selection: A total of 94 GPS points were recorded during the radiotracking survey of the eight harvest mice mentioned in the previous section. The vegetation type noted simultaneously with the relocations (Table 3) showed that 70% of the relocations were found in the plant alliance *Convolvulion*. This habitat either consisted of the association *Solidagetum giganteae* (American goldenrod patches, 36% of the relocations), or *Urtico-Calystegietum* (mostly represented by sedge patches invaded and dominated by stinging nettles, 34% of the relocations).
The next-preferred habitat used by the tagged harvest mice was the tall sedge meadow *Caricetum acutiformis* (16% of the relocations). It is important to acknowledge that about half of the points (7 relocations out of 15) representing this habitat corresponded to the trapping (and releasing) points of the tracked individuals. Two individuals out of eight moved from the tall sedge meadow to a grassy area with a *Panico-Setarion* thriving around a plant dump, which represents 10.6% of the overall relocations. Finally, three GPS relocations were found in the habitat *Mentho-Juncion*.

Nest searching and supplementary trapping: The nest searches revealed the establishment of harvest mice around the plant dump (*Panico-Setarion*), with a total of 7 green (i.e. fresh) nests found in an area of 1237 m^2. Yet, no harvest mouse was captured in that area in November during the secondary trapping session, even after eight trapping-nights.
No nest was found in the American goldenrods but a few individuals, including a pregnant female, were caught in the goldenrod patches near the tall sedge meadow, on the South-Western side of the stream. Furthermore, a small tall sedge patch was found on the same side, were at least three nests were found, and a juvenile harvest mouse was trapped.
One old nest (presumably from the year prior the study) was found in reeds (*Phragmition*), but no harvest mice were captured in the transects placed in this habitat.

DISCUSSION

The number of individuals estimated to be alive during the CMR event (12 individuals), showed that very few harvest mice live in the main meadow. This means that the majority of the mice alive (8 out of 12) were

Table 3. Summary of the vegetation associations found in relation to the 94 GPS relocations of the eight harvest mice tracked in October 2017. The *Solidagetum giganteae* association, representing American goldenrod patches, and the *Urtico-Calystegietum* association, representing stinging nettles-invaded sedge patches, were the most favored habitats. The *Caricetum acutiformis* association, which was expected to be the most preferred habitat, represented only 15.9%.

Alliance	Association	Number of relocations	Proportion
Convolvulion	*Solidagetum giganteae*	34	36.2%
Convolvulion	*Urtico-Calystegietum*	32	34.0%
Magnocaricion elatae	*Caricetum acutiformis*	15	15.9%
Panico-Setarion	–	10	10.7%
Mentho-Juncion	–	3	3.2%

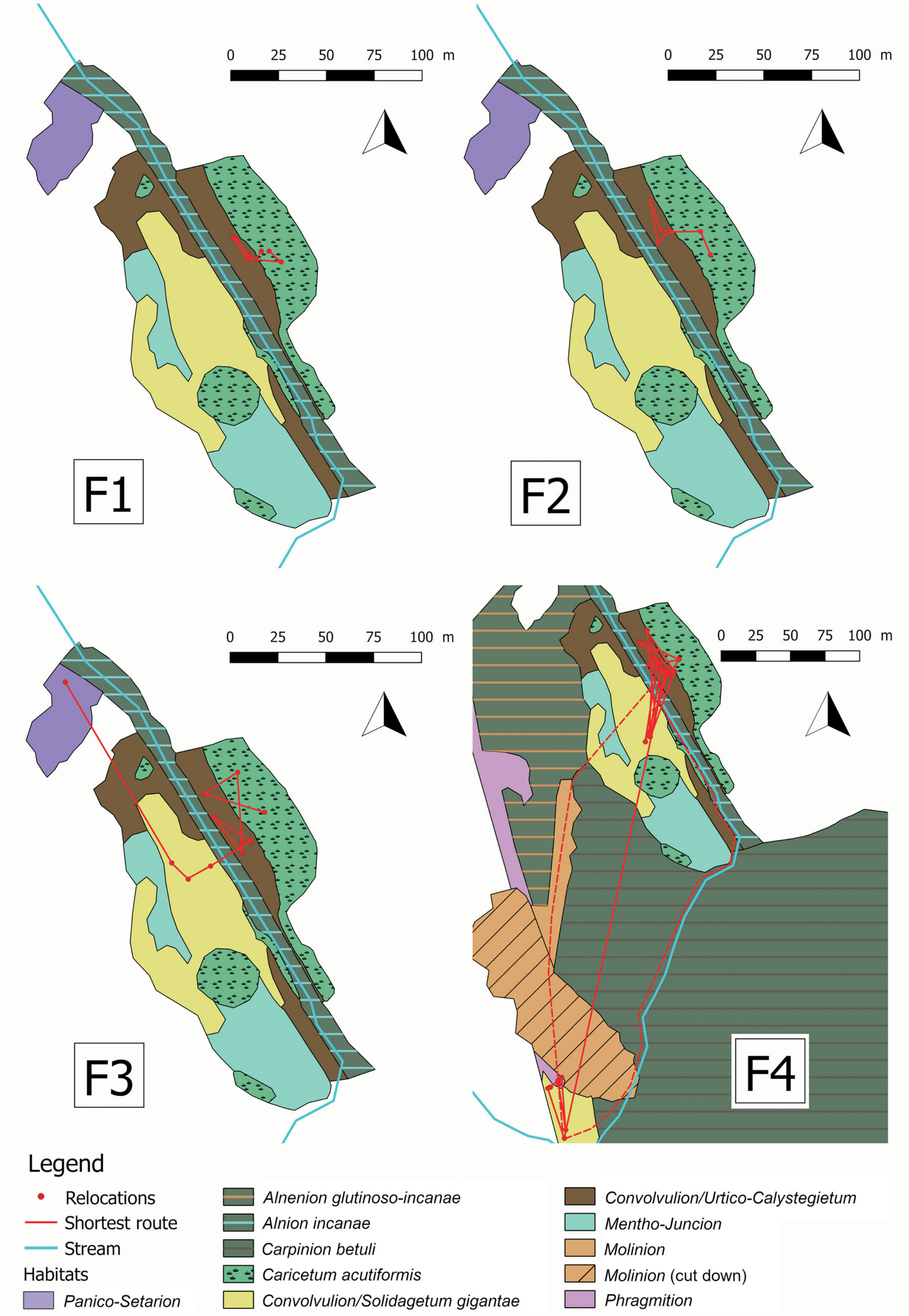

Fig. 6. Relocations of the four female individuals F1, F2, F3 and F4. F1 was tracked from the 17th to the 19th of September 2017. F2 was tracked from the 19th to the 21th of September 2017. F3 was tracked from the 24th to the 29th of September 2017. F4 was tracked from the 29th of September to the 2nd of October 2017. The dashed red line (F4) represents a possible migration route for the female F4.

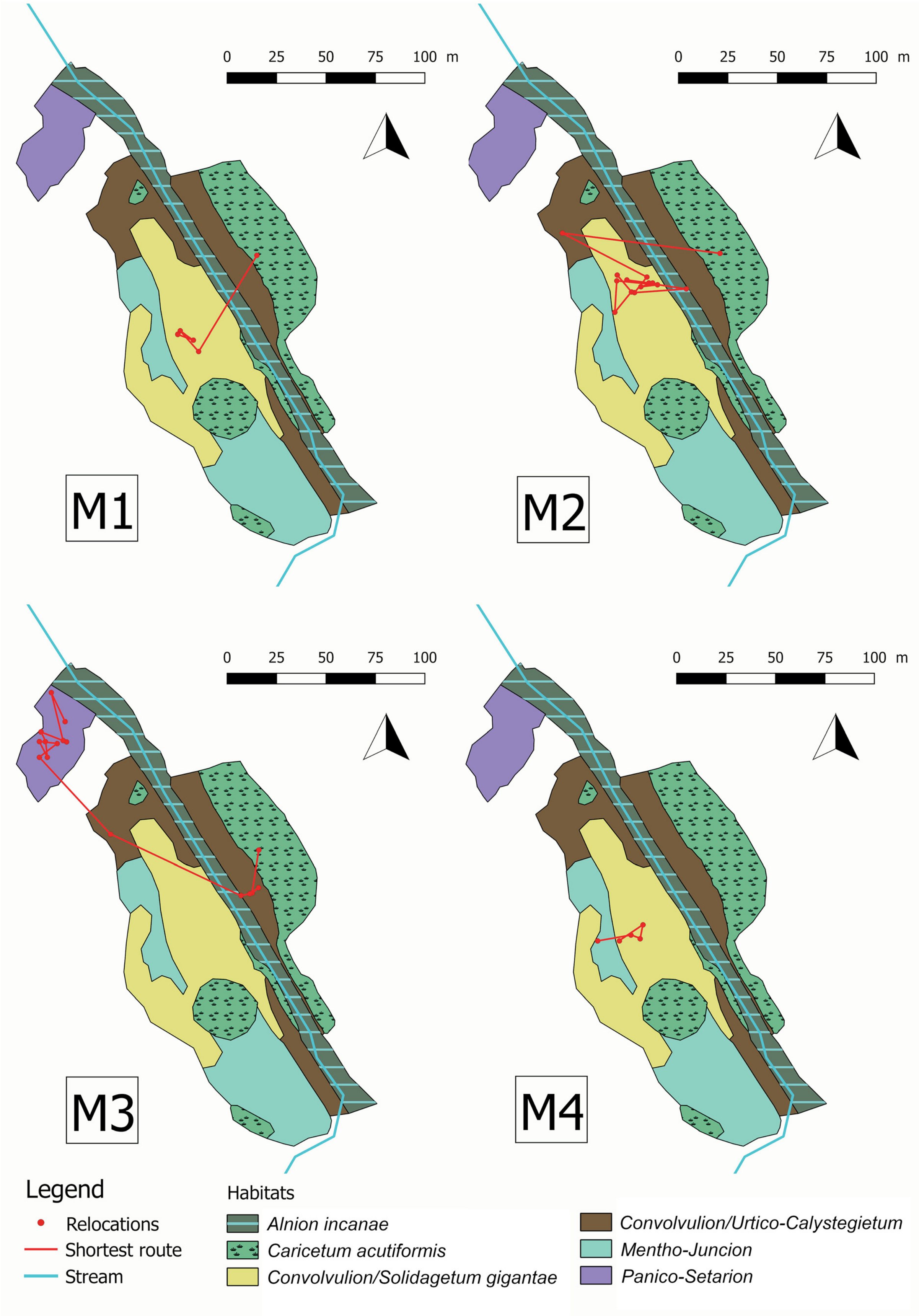

Fig. 7. Relocations of the four male individuals M1, M2, M3 and M4. M1 was tracked from the 19th to the 21th of September 2017. M2 was tracked from the 06th to the 10th of October 2017. M3 was tracked from the 15th to the 19th of October 2017. M4 was tracked from the 15th to the 17th of October 2017.

monitored during the radio-telemetry session. Because of the limited time during which these individuals were tracked (between two and eight days), the results only showed a glimpse of the habitat choices of the harvest mice in this area. Nevertheless, this can be assumed to be representative of the overall behavior of the harvest mice during this period of time.

Movements and habitat preference: The radiotracking revealed unexpected wandering behavior. The hypothesis that the tagged mice would stay within the main tall sedge meadow could be rejected. Indeed, three individuals out of eight showed a migration behavior, and three clearly preferred to stay in the goldenrods on the other side of the stream instead of inside of the *Caricion elatae*. Two individuals out of eight stayed near the main tall sedge meadow, but the majority of their relocations were not found in the lesser-pond sedge.

The calculated ranges (Fig. 5) show that the tracked harvest mice may have overlaying wandering areas according to their sex. Harvest mice tend to have overlapping ranges, but can have aggressive and territorial behaviors during the breeding season (Corbet & Harris, 1991). Aggression is usually characterized by tail biting, sometimes leading to partial tail loss, and this was observed in the two reproductive males, M1 and M4 that clearly had overlaying territories. This could indicate that the goldenrod habitat might be worth defending for male harvest mice.

Corbet & Harris (1991) also noted that harvest mice leave their breeding territory in the winter, and construct smaller, non-breeding nests low in grassy tussocks in their wintering area. Such nests correspond accurately to the nests (at least seven) found in the grasses growing around the plant dump, where two of the tracked individuals (F3 and M3) spent some time. This indicates that this area may very well be a wintering habitat for this population of harvest mice.

F4, the individual that left the main tall sedge meadow to travel more than 350 m in a day, might also have had a similar migration behavior to find a new habitat where to spend the winter. Since this individual was a subadult, this movement may also be explained by the dispersal and exploratory behavior observed on juveniles (Corbet & Harris, 1991).

The path taken by F4 to reach the Southern goldenrod patch is unknown, since the tag was found 25 hours after the previous point, which was located in the main tall sedge meadow. Only assumptions can be made, but two plausible routes might have been taken (see the dashed red lines on Fig. 6). F4 was close to the stream bed when found in the Southern goldenrod patch. This could indicate that F4 followed the stream to find the new habitat. However, harvest mice are not forest dwellers (Wijnhoven *et al.*, 2005). F4 would have had to go through the wooden area *Carpinion betuli* for at least 200 m, which is not very likely. The second way to reach the Southern goldenrod patch would be to go through the *Carpinion betuli* for 20 m only, on an area where the forest was the narrowest and were signs of other animal movements (Roe deer and fox) were visible. Furthermore, this path leads to a *Molinion*, which is a habitat known to be favored by harvest mice.

Either way, the harvest mouse is not known to be moving or living in wooden areas. Studies capturing a wide number of rodents in several habitats recorded few or no captures of this species in woodland or forests (Canova, 1992; Wijnhoven *et al.*, 2005; Paziewska *et al.*, 2010). Such movements through a forested zone are probably not common for the harvest mouse and is possibly only done during migration to new suitable areas.

After traveling, F4 stayed at least 72 hours in the Southern American goldenrod patch (the transmitter fell off before showing any further migration or wandering behavior), which implies that it was an adequate environment to stay in. This raises questions about why the *Convolvulion* habitat is so interesting for the majority of the tagged individuals. Indeed, all the tracked harvest mice favored this unexpected habitat. They showed a clear preference for stinging nettle and goldenrod invaded habitats (both being part of the *Convolvulion* plant alliance), while neglecting the lesser-pond sedge available nearby. The preference for stinging nettles observed during the radiotracking event is the opposite of what is known about habitat choices of this species in the literature. As a matter of fact, a negative correlation between stinging nettle presence and harvest mouse trapping has been shown (Wijnhoven *et al.*, 2005).

To our knowledge, no author described the relationship between habitats invaded by American goldenrods and the harvest mouse. This study is therefore the first to correlate the wandering behavior of harvest mice with this exotic plant. Several explanations can be hypothesized to explain the inclination of the harvest mice for stinging nettles and for American goldenrods.

The potential importance of stinging nettles: The radiotracking period was set from mid-September to mid-October, which corresponds to the last part of the breeding season for the harvest mouse (Corbet & Harris, 1991). One explanation for the harvest mice to select stinging nettles could therefore be linked to reproduction. Indeed, they might build nests in the stinging nettle-invaded parts, because in the study area, the under layer of the vegetation growing in the *Urtico-Calystegietum* association was mainly lesser-pond sedge. Surmacki *et al.* (2005), and Čanády (2013) noted the presence of harvest mouse nests in stinging nettles. Yet, both found that this plant is used as nest support in very low frequencies in comparison to other plants, like grasses or hedgerows. Stinging nettles might provide supplementary protection against predation thanks to the very dense layer it formed over the sedge, covering the aerial view of the invaded part of the meadow. Such affinity of the harvest mouse for dense vegetation cover was already observed by Trout (1978a). Furthermore, the trichomes of the stinging nettles can deter terrestrial predators to search into the vegetation.

Stinging nettles might simply constitute a better foraging habitat and vegetation for the harvest mouse. It has been shown by Dickman (1986) that the small rodent favors seeds, insects, and monocotyledon leaves as primary diet, but also includes dicotyledon leaves and fruits in variable proportions depending on the habitat it lives in. The areas that were largely dominated by lesser-pond sedges might have been neglected due to lower food availability in the form of seeds. Indeed, the monitoring took place in autumn, a period of the year when the sedges had neither flowers, nor seeds. Therefore, based on Dickman's study (1986), it can be hypothesized that this rodent was either interested in seeds or in insects that were present in the nettle invaded habitats.

The potential importance of American goldenrods: Because of its invasive nature, the American goldenrod was by far the dominant species in the *Solidagetum giganteae* association patches. Almost no other plant was observed growing on the same soil as the goldenrods. The only species that was found near it was the common hop *Humulus lupulus* that was climbing on the flowers of the exotic plant. Nearly no vascular plant was found on the ground. This implies that American goldenrods might have a direct relationship with the habitat preferences of the harvest mouse in the study area. Either the plant itself was interesting to the rodent, or it was a factor directly associated with the exotic species. During the radiotracking period, the American goldenrods were in their seed state. It can therefore be hypothesized that the mice preferred to wander into the *Solidagetum* patch for foraging reasons. They might be interested in the goldenrod seeds, or in insects living in that habitat.

It is unlikely that the harvest mice chose to breed in the goldenrod invaded habitats since there were neither grasses nor sedge growing under the invasive plant. Therefore, nests virtually could not be weaved against them in those areas. The absence of nests found during the nest-searching event supports this hypothesis.

The potential importance of unmown grassy areas: The third habitat that attracted two harvest mice out of eight was the *Panico-Setarion*. This habitat was located around a plant waste dump mainly colonized with grasses (Poaceae), in particular the barnyard grass *Echinochloa crus-galli*, that was forming dominant patches. This plant species seemed to be very appealing to the two harvest mice relocated in that area, since most of the relocations of the individuals found in this habitat were found in the barnyard grass clumps. This behavior can supposedly be explained by the fact that, at that time, the panicles of this species were full of seeds. The radiotracking session being performed in October, the lesser-pond sedge was in its vegetative state, meaning that if the harvest mice were searching for seeds, they had to travel to sites involving the presence of unmown grasses. Indeed, this area was the closest place where grasses were fully grown and unmanaged. The *Panico-Setarion* patch seemed to be very attractive for other harvest mice too, since at least 7 fresh nests were found in an area of 1237 m^2.

Generally, the radiotracking showed the tendency of females to stay closer to the main tall sedge meadow (three females out of four) and stinging nettles, while males (three out of four) tended to stay more in goldenrod invaded areas. The radiotracking data also showed probable winter migration (three individuals out of eight), with a complete change of habitat type for two out of eight individuals, reaching a dry grassy area, rich in seeds.

CONCLUSION

The present study indicates that the breeding sites of the harvest mouse, and therefore habitats where this species' breeding nest are found, might not correspond to its foraging and wintering habitats. This means that trapping and radiotracking procedures are important to add to nest searching when monitoring this species populations and habitat utilization. This is specifically important for wetlands and marshes that are invaded by exotic species and/or suffer from scrub encroachment if not managed regularly and when subjected to eutrophication. Management of site populated by harvest mice must take into account the fact that some unexpected habitats can be used as wintering areas (like the plant dump) or foraging areas (like the American goldenrod and the stinging nettle patches).

The present study showed that the harvest mouse is able to adapt, to some extent, to changes and alterations of its main breeding habitat, like fragmentation, eutrophication, and changes caused by invasion from exotic species, like the American goldenrod, or other nitrophilous species, like the stinging nettles. However, alien species jeopardize the long-term persistence of the tall sedge meadow, which is essential for the mice to weave nests and reproduce. Indeed, alien species have been shown to modify their environment by increasing biomass (Zedler & Kercher, 2004). If no management plan is set up, this increase of biomass may dry up the marshy meadow and create an unsuitable growth habitat for tall sedges. It is therefore important to manage the area in order to keep the tall sedge meadow as it is.

Exotic goldenrods are sometimes fought in a very extensive manner, with complete elimination of the plants, usually combined with the removal of the surface layer of the soil (Canton de Vaud, 2013; AGIN, 2014). This study showed that harvest mice use this type of habitat during autumn, and it is likely that they forage in this vegetation at other times of the year. Complete removal of the alien species and of the soil in one season are not advised for the study area. Nevertheless, it is highly recommended to keep the American goldenrods out of the main tall sedge meadow to support the population source area. Furthermore, it is advised to contain the spreading of exotic plant by mowing the highly invaded part once or twice a year before the flowering of the plants (Canton de Vaud, 2013; AGIN, 2014).

One should keep in mind that this study followed the tagged mice in a very small portion of the year. This represents only a fragment of the life of the studied individuals, meaning that the same mice might favor other types of vegetation during other periods of the year, depending on temperature, phenology of the plants, phenology of the insects, and their own phenology. Anthropogenic influence of the study area, like periodical mowing and presence of cattle, can also have a considerable impact on the harvest mice's behavior and survival.

Further investigations on the habitat selection of harvest mice in fragmented landscape during other times of the year may bring different knowledge regarding the ecology of this animal. Such information would show when and why the harvest mice have such an affinity for disturbed areas. Further radiotracking events during late autumn may also show what kind of wintering habitats are needed to be preserved to create sustainable vegetation for the harvest mice populations.

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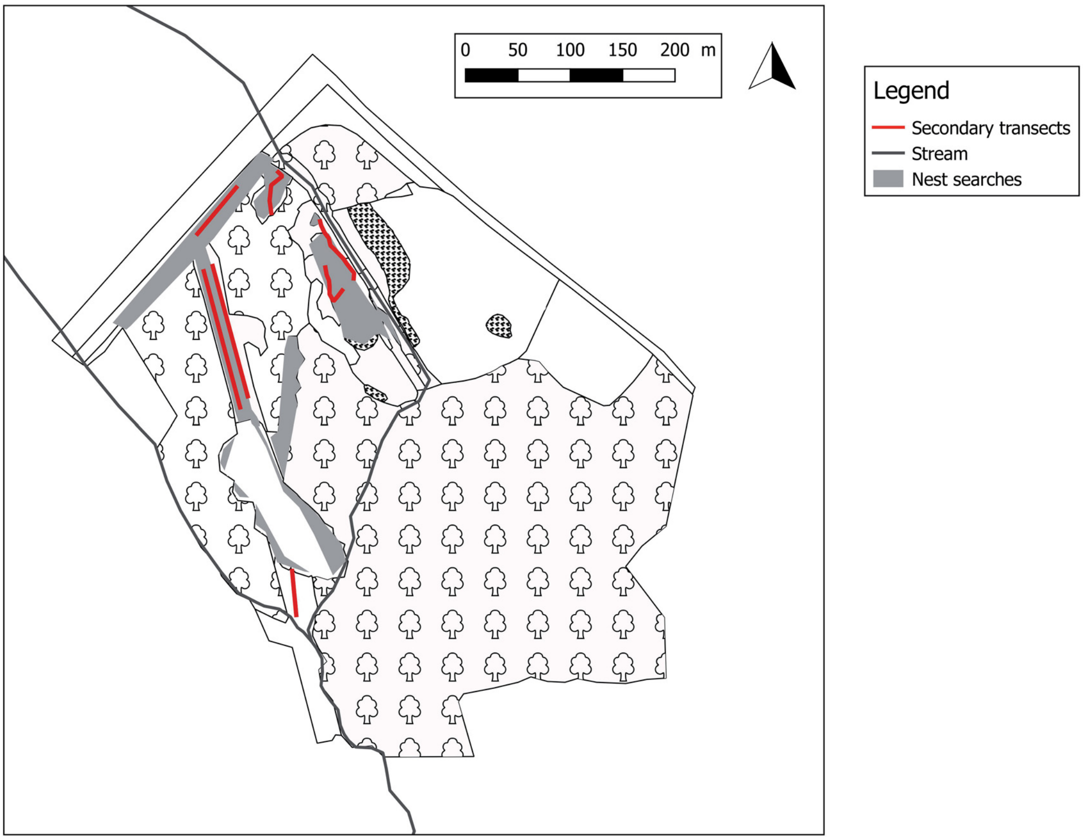
Appendix 1

Secondary transects (red lines) placed in late October to early November of 2017, after the radiotracking event. These transects were set up in areas to which harvest mice appeared to migrate to. Nest-searching was also done (grey areas). The aim was to know if other individuals were present or not in these areas.



Appendix 2

Names and references of plant associations used in this study:

Alnion incanae Pawłowski in Pawłowski, Sokołowski & Wallisch, 1928
Reference: Bardat *et al.* (2004).

Alnenion glutinoso-incanae Oberdorfer, 1953
Reference: Bardat *et al.* (2004).

Carpinion betuli Issler, 1931
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Reference: Devillers *et al.* (1991)

Cynosurion cristati Tüxen, 1947
Reference: Bardat *et al.* (2004).

Mentho longifoliae - Juncion inflexi Th. Müll. & Görs ex de Foucault, 2008
Reference: de Foucault & Catteau (2012)

Molinion caeruleae Koch, 1926
Reference: European Topic Centre on Biological Diversity (2008)

Solidagetum giganteae Robbe ex J.-M. Royer *et al.,* 2006
Reference: Bensettiti *et al.* (2002)

Urtico dioicae-Calystegietum sepium Görs & Müller, 1969
Reference: Bensettiti *et al.* (2002)

Panico-Setarion Sissingh in Westhoff *et al.,* 1946
Reference: European Topic Centre on Biological Diversity (2008)

Phragmition communis Koch, 1926
Reference: Bardat *et al.* (2004).

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