Seasonal patterns in habitat use by the harvest mouse (*Micromys minutus*) and other small mammals.

Francesca Occhiuto[1], Eman Mohallal[2]; Geoffrey D. Gilfillan[3]; Andrew Lowe[4]; Tom Reader[1].

1. School of Life Sciences, University of Nottingham, Nottingham, NG7 2RD.

2. Desert Research Center, 1 Mathaf El Matarya St., Cairo, P.O. Box: 11753, El Matareya, Cairo, Egypt.

3. 89 Hillcrest, Bar Hill, Cambridgeshire, CB23 8TQ.

4. 159 Sherwood street, Market Warsop, Nottinghamshire, NG20 0JX.

Author for correspondence: Francesca Occhiuto: francesca.occhiuto12@gmail.com

Abstract

The ecology of the harvest mouse (*Micromys minutus*) is poorly understood, partly because it is a difficult species to monitor. It is commonly associated with reedbeds, where evidence suggests that it experiences strong seasonal fluctuations in abundance. However, it is unknown whether these fluctuations are caused by real changes in population size, or by movement between habitats. This study investigated seasonal changes in population size and habitat use by harvest mice, and other small mammal species, by trapping the reedbed and three associated habitat types: woodland, pasture and arable land. A sampling effort of 9,887 trap bouts across nine months, resulted in 70 captures of harvest mice, as well as wood mice (N=1,022), bank voles (N=252), field voles (N=9), common shrews (N=86) and pygmy shrews (N=7). The reedbed was the habitat with the most captures and highest diversity. Harvest mice were caught exclusively in the reedbed at the beginning of autumn. Wood mice and bank voles experienced fluctuations in population numbers and wood mice also showed seasonal variation in habitat use. Our study supports the idea that harvest mice undergo extreme seasonal fluctuations in abundance in reedbeds, but these do not appear to be related to changes in habitat use.

Key words: *Micromys minutus*, small mammal, reedbed, ecology, movement patterns

Introduction

Small mammals are important contributors to biodiversity, both directly and through interactions with other species. For example, they constitute important prey species for predators such as the barn owl (*Tyto alba*) (Bontzorlos et al. 2005; Frey et al. 2011), kestrel (*Falco tinnunculus*) (Korpimäki 1985) and badger (*Meles meles*) (Mortelliti and

Boitani 2008), making the study of small mammals crucial for the conservation of these species (Mortelliti and Boitani 2008).

Much of current knowledge about small mammal population dynamics comes from studies on some Arvicolinae species which show extreme and regular multiannual fluctuations in abundance, typically in Fennoscandia (Chitty 1952; Elton 1924; Krebs 1964; Norrdahl and Korpimäki 1995). The exact causes of these cycles are still debated, but among possible explanatory factors are predation, food quality, sociality and dispersal (Andreassen et al. 2013; Krebs et al. 1995; Radchuk et al. 2016). However, outside Fennoscandia, and for other small mammal species, changes in abundance across years are less dramatic and not very regular (Hanski et al. 1991; Jensen 1982). In small mammal species which do not show multiannual cycles, a yearly cycle of abundance is typically apparent (Crawley 1970; Flowerdew and Gardner 1978; Hansson and Henttonen 1985; Montgomery 1989; Trout 1978). Amongst these species, the wood mouse (*Apodemus sylvaticus*) is the best studied; this species typically shows a decrease in abundance in spring, followed by a stable phase in the early summer, and then an increase in the late summer and autumn (Crawley 1970; Fernandez et al. 1996; Montgomery 1989; Watts 1969).

Some studies of the ecology of small mammals suggest that habitat preference can change depending on the season (Ouin et al. 2000; Todd et al. 2000; Ylönen et al. 1991). If this is true then apparent fluctuations in abundance may at least partially result from the movement of individuals among habitats (Ouin et al. 2000). Wood mice have been reported to change habitat preference in different seasons, as they stay in woodlands and hedgerows in winter and move to arable fields in the summer as a result of the changes in resources available throughout the year (Ouin et al. 2000; Todd et al. 2000). In addition, the striped mouse (*Rhabdomys pumilio*) has also been found to move its home range in different seasons to reflect changes in availability of new plant growth (Schradin and Pillay 2006). However these movements have not previously been investigated in detail in the small mammal communities of the British wetlands, which are highly seasonal environments.

Wetlands, and in particular reedbeds, are known to be an extremely important habitat for several small mammal taxa, and many other species, but their significance is perhaps still not fully appreciated. Wetlands are usually patchy, meaning that the species that rely on them often occur in small and isolated populations, which makes them vulnerable to local extinction (Fahrig and Merriam 1994). In the UK wetlands are home to many native small mammal species, and there is evidence that mammal diversity is unusually high in wetlands, and in reedbeds in particular (Kettel et al. 2016; Marques et al. 2015). Although most studies of wetland mammals in the UK have concentrated on the water shrew (*Neomys fodiens*) and the water vole (*Arvicola amphibious*), because of their protected status and because they are wetland specialists (Churchfield et al. 2000; Carter and Bright, 2003), reedbeds are an important habitat for harvest mice (*Micromys minutus*), wood mice, bank voles (*Myodes glareolus*), and field voles (*Microtus agrestis*) (Kettel et al. 2016; Marques et al. 2015).

The harvest mouse is a native mammal in the UK and it is protected due to perceived declines in abundance (Harris 1979; Perrow and Jowitt 1995). This decline is believed to be caused by changes in agricultural activity and habitat loss (Perrow and Jowitt 1995), and has caused the species to be listed in the UK Biodiversity Action Plan (BAP)

(JNCC 2010). However data on the distribution and habitat use of harvest mice used to assess their status are very limited because of their scansorial lifestyle and preference for reedbeds (Harris 1979), which makes them difficult to monitor with traditional live-trapping methods, where traps are placed on the ground (Kettel et al. 2016; Poulton and Turner 2009). Nest searching has been used as an alternative method but with limited success (Kettel et al. 2016; Riordan et al. 2009). Recent studies by Kettel et al. (2016) and Darinot (2019b) showed that live-trapping using elevated traps in the stalk zone of tall vegetation is much more effective than other methods, and therefore it is possible that harvest mice are present in areas where they were previously not detected. Implementing this method might shed light on the ecology of this understudied species and could inform decisions about its conservation status in the UK.

The population numbers of harvest mice have been found to decrease considerably from April to August, followed by a large increase in September (Sleptsov 1947; Trout 1976; Trout 1978). The magnitude of these fluctuations has prompted the suggestion that this may be the result of a change in trappability of the species; a study conducted in Switzerland suggested a more pronounced preference for elevated traps in summer compared to autumn (Vogel and Gander 2020). Additionally or alternatively, it is possible that the perceived decline in numbers in any one habitat is caused by a seasonal change in habitat preference. Although harvest mice are found most reliably in reedbeds, they have also been found in other habitats with tall and dense vegetation, such as cereal fields, field margins, and woodlands (Bence et al. 2003; Haberl and Kryštufek 2003; Harris 1979; Juškaitis and Remeisis 2007). Hence, the disappearance of the species from core habitat in spring and summer could be the result of harvest mice moving to other habitats. A study conducted in northern Finland has shown evidence of a change of habitat between the summer and the winter months by documenting migration from fields to river banks in late September and early October, which followed the first frost of the year (Koskela and Viro 1976). However, the density recorded in the river banks after the migration was very low, so it is impossible to determine whether this habitat constituted the winter biotope or the mice were just travelling through it. Because this is the only indication of a migration in this species, and the study was conducted in a population at the northern edge of the species range, it is not known whether this behaviour is typical of harvest mice elsewhere.

Some recent evidence of seasonal fluctuations in harvest mouse abundance in reedbeds comes from a study on the effects of flooding on harvest mice in southern France (Darinot 2019a). The study found that, unlike other species which move to drier ground, the harvest mouse remains in reedbed habitat during winter flooding. If the flooding season was particularly harsh, this could lead to a delay in the growth of the reedbed population in spring, but nest searches and trapping on the periphery of the reedbed did not show any obvious evidence for subsequent seasonal changes in habitat preference.

The aim of this study was to determine the habitat preferences of small mammals in a habitat mosaic, with particular focus on the understudied harvest mouse. By including reedbeds, which are the habitats where harvest mice have been most frequently surveyed in recent years, and also adjacent areas of woodland, pasture and arable, the intent was to extend knowledge on the habitat requirements of this species and other small mammals. Following a pilot study in 2016, we trapped small mammals in four habitat types across nine months in 2018 using a method that includes elevated and ground traps. Because captured animals were individually marked before release, we were able to report on both capture rates, and individual movement of animals within and between habitats over time. The results shed light on seasonal fluctuations in abundance and changes in habitat use in harvest mice and other species.

Materials and methods

The study was carried in Nottinghamshire, UK. The main site surveyed was the Thoresby Estate, and four other sites were used to corroborate the findings: Clumber, Sherwood Pines, Bevercotes and Bestwood (Figure 1). All of the sites had at least one reedbed dominated by common reed (*Phragmites australis*). Thoresby Estate a private estate situated 20 miles north of Nottingham, was chosen as the focal study site because it has all four habitat types of interest, a harvest mouse population was known to be present in the reedbed, and the site was secure, minimising the risk of theft of traps. It is a Site of Special Scientific Interest (SSSI) and it includes Thoresby Lake, which has a reedbed at its western end. The reedbed surveyed contained both flooded and dry areas at all times, with the end closest to the open water being permanently flooded, and the end furthest from the water being permanently dry. It was overwhelmingly dominated by *Phragmites australis* but, especially along the dry margins of the habitat, it also had some sedges (*Carex* spp.), reed canary grass (*Phalaris arundinacea*) and other species less tolerant of inundation including occasional willow (*Salix* sp.) saplings. The surrounding land is covered by woodland, pasture and arable, habitat types which are known to support harvest mice in some circumstances, all in close proximity to the reedbed (see Figure S1 in supplementary material)

Pilot study

In 2016 a pilot study was conducted to confirm the presence of harvest mice in the reedbed at Thoresby. Traps were set for 6 - 7 days in each of four sessions (Sessions P1 to P4), at approximately monthly intervals, from late July to early November (Table 1). A total of 56 traps was used and arranged in a grid pattern. All traps were placed at elevation, taped onto bamboo canes at about 1 m above the ground. We used Longworth traps, which have been shown to be more effective than alternative traps and nest searching for the monitoring of harvest mice (Kettel et al. 2016). Parakeet and cockatiel food mixed with sunflower seeds was used as bait and casters (fly pupae) were added to ensure the survival of shrews. Cotton wool was used for bedding.

Main study

The main study commenced in February 2018, and focussed on providing a time-series describing seasonal changes in community composition and habitat use at Thoresby. One trapping session was conducted every month until October 2018 (Sessions 1 to 9), resulting in a total of nine trapping sessions. Four other sites were surveyed once or twice each, to provide spatial replication of the observations at Thoresby, and some corroboration of the observed seasonal patterns. Logistical constraints meant, however, that we could not visit all sites in all months.

Only at Thoresby were all four habitat types (reedbed, woodland, pasture and arable) present. Clumber had reedbed, woodland and arable land, and the remaining sites had only reedbed and woodland. At Thoresby, two habitats were surveyed in the first week of a trapping session in the main study, and the remaining two were surveyed in the second week. The pairs of habitats were alternated so that the two habitats that were surveyed first changed every time. Due to time constraints, in the last session only the reedbed and woodland were surveyed in Thoresby. In addition, trapping in the arable habitat had to be cut short in July and August (session 6 and 7) due to agricultural activities. The second time Sherwood Pines was surveyed the traps were stolen from the woodland at the beginning of the session and therefore data were collected only from the reedbed. Up to 30 traps were placed in each habitat type. It was not always possible to place all 30, due to the size of some of the habitats. In Clumber, where three habitats were surveyed in one week, a maximum of 20 traps were placed in each habitat (Table 1). When possible, the traps were placed at 10-metre intervals in a grid. In Sherwood Pines and Bevercotes the shape of the reedbed did not allow for a grid and in Clumber the farmer only allowed the traps on the field margin so they were placed in line transects.

Longworth traps were also used in the main study and the bedding and food used were the same as described for the pilot study. In each grid or transect at least half of the traps were placed on the ground. Where possible, every second trap was placed at elevation. The traps were only elevated if the vegetation was at least 1 m high at the designated point in the grid; otherwise they were placed on the ground. This meant that in the pasture, and also in the arable land when the crop was not fully gown, all traps were on the ground (Table 1). In the reedbeds, the ground was often flooded, in which case ground-level traps were taped onto a cane about 10 centimetres above the water level.

Trapping sessions lasted one week, with two habitats typically being sampled in each. The traps were left in the pre-bait position on the first day, for three days (one or two days in the pilot), to allow the animals to become familiar with them. At 8am on the fourth day, traps showing signs of use, such as movement of the bedding, feeding or faeces, were cleaned and food and bedding was replaced, and all traps were set to catch. At approximately 3pm all the traps were checked, and the species and sex of captured animals was recorded. Animals were given a unique fur clip using a pair of fine scissors allowing us to distinguish individuals from one another, and then released at the point of capture. Thereafter, traps were checked twice a day, at 8am and 3pm. On the morning of the eight day, traps were checked for the last time and removed.

Statistical analysis

Within a session, each occasion on which the traps were checked, which happened twice each day, once in the morning and once in the evening, was considered a "trapping bout". Detailed analysis was carried out for the three most commonly encountered species: harvest mice, wood mice and bank voles. Analysis was conducted using R version 3.5.1 (R Core team 2018). The catch per unit effort (CPUE) was calculated as a measure of the relative abundance of each species by dividing the number of individuals of a species caught by the number of trapping bouts. To account for the fact that a trap that has already sprung cannot catch any more animals, half of a trapping bout was subtracted from the trapping effort for each trap used using the following equation:

$$CPUE = A \times 100/(TU–S/2)$$

where CPUE = catch/effort (expressed in percentage trapping success or animals caught per 100 trapping units), A = number of captured animals of the target species, TU = number of trapping units and S = total traps closed by any species (Nelson and Clark 1973).

The effect of species and sex on the minimum distance travelled by individuals between consecutive captures, was analysed with a non-parametric two-way Analysis of Variance. It is important to note that this method measures the minimum distance moved by animals between trapping events, and can only describe movement within the trap grid; this is unlikely to include the full home range of these individuals, and the distances calculated assume a linear path between capture points which is likely to be shorter than the actual path taken by the animals. A Chi-squared test was used to assess whether wood mice, bank voles and harvest mice in Thoresby showed a preference for certain trap locations. Spatial avoidance between harvest mice and other species was tested using a Spearman Rank Correlation between the number of individuals of each species caught in each trap, excluding the traps in which neither species was caught. Recaptured individuals were excluded from this correlation to make sure that the pattern was not driven by the preference of specific individuals.

The effect of several variables on the probability of catching an animal at Thoresby was tested using generalised linear mixed effects models. The error structure was assumed to be binomial and models were fitted by Laplace approximation using the glmer function in R. The fixed effects were session, elevation, habitat and site. The random effects were the trap location within the grid and the trapping bout. Harvest mice were only found in the reedbed, and only in September and October, so the analysis for this species was restricted to this habitat type and these two sessions. For the other species two types of analysis were used, one in which all four habitat types were considered for the first eight trapping sessions of the study, and one which considered only the two habitat types (woodland and reedbed) which were sampled in all nine sessions. Since the results of the two analyses were very similar, the second analysis is presented in supplementary material.

Results

Pilot study

Across 1,176 trap-bouts in the reedbed at Thoresby, 27 individual harvest mice were caught on a total of 40 occasions. Only the bank vole (41 captures) was more commonly caught. Wood mice (15), field voles (*Microtus agrestis*; 12) and common shrew (*Sorex araneus*; 1) were also captured. Harvest mice were never recorded in the summer (July and August), but were the most numerous species caught in autumn (September/October and November).

Main study

The total sampling effort in Thoresby consisted of 7,837 trap-bouts and resulted in 1,262 captures (see Table S1 in supplementary material). The wood mouse was most commonly encountered species (944 captures). The second most frequently caught species was the bank vole (200 captures), followed by the common shrew (66), harvest mouse (38), field vole (7) and pygmy shrew (*Sorex minutus*; 7).

Overall the habitat with the highest catch per unit effort was the reedbed, followed by the woodland, pasture and arable (Figure 2). All species were caught more often in the reedbed, apart from the wood mouse, which was most frequently caught in woodland (Figure 2). The harvest mouse, field vole and pygmy shrew were caught exclusively in the reedbed (Figure 2). Wood mice and bank voles were caught in every session, with wood mice being the most frequently caught species in all sessions (Figure 3). Shrews were caught mostly from July onwards and field voles were only captured in September and October. Harvest mice were also caught exclusively in the last two months of the study (Figure 3).

Patterns of movement in harvest mice, wood mice and bank voles

Within habitats at Thoresby, the average distance travelled between consecutive recaptures was significantly different for the three species considered (ANOVA: F2,159 =10.640, P=0.005). Wood mice moved the furthest on average (mean = 13.7 m; SD = 12.2; maximum = 70 m; n = 112 individuals), followed by harvest mice (10.8 m   11.1; maximum = 31.6 m; n = 8), with bank voles moving the least (9.8 m   13.1; maximum = 44.7 m; n = 39). There was also a significant difference between the sexes across the three species (F1,160 =4.930, P=0.026), with females moving less far between recaptures (10.3 m   10.1; maximum = 44.7 m) than males (16.4 m   14.0; maximum = 70.0 m). The interaction between the effects of species and of sex was not significant (F2,159 =4.150, P=0.126

The two species which were found in multiple habitats at Thoresby were wood mouse and bank vole. Forty-three wood mice, 18 females and 25 males were trapped in at least two habitats at Thoresby and all possible combinations of habitats were represented in the trapping histories of individuals. Twelve individuals were trapped in at least three habitats (five females and seven males), and one male was caught in all four habitats. Eight bank voles were caught in two different habitats: two females and five males were caught in the reedbed and the woodland, while one male was caught in the pasture and the woodland (see Table S2 in supplementary material).

Spatial distribution within habitats at Thoresby

At Thoresby, harvest mice showed a significant preference for certain trapping locations within the reedbed (Chi-Squared test: $X^2_{(29)} = 80.421$, $P < 0.001$). They used mostly the central portion of the grid and the NE side (see Figure S6 in supplementary material). Wood mice used all the traps in the reedbed, but they showed a significant preference for those closer to the edge ($X^2_{(29)} = 80.421$, $P < 0.001$; Figure S7). In the woodland there was a significant preference for traps in the SW corner of the grid, close to the pasture ($X^2_{(29)} = 173.683$, $P < 0.001$; Figure S8); only two traps were never used. The captures in the pasture were significantly clustered on the edges of the grid ($X^2_{(29)} = 237.647$, $P < 0.001$, Figure S9), especially on the NE side, which constituted the border with the woodland, and most of the traps in the centre of the grid were never used. In the arable land there was no significant preference ($X^2_{(29)} = 31.479$, $P = 0.343$; Figure S10). Bank voles showed a significant preference for the western half of the reedbed trapping grid ($X^2_{(29)} = 142.158$, $P < 0.001$; Figure S11). In the woodland, captures for this species were significantly clustered in a few traps ($X^2_{(29)} = 324.864$, $P < 0.001$;

Figure S12). The two traps that had the most captures, located in the northern and central areas of the grid, accounted for 45% of all captures.

When testing for possible spatial avoidance between species in the reedbed, a negative correlation was found between new captures of harvest mice and wood mice ($r_{s(11)}$= -0.71, P=0.006), and between new captures of harvest mice and bank voles ($r_{s(12)}$= -0.74, P=0.003).

Factors affecting the probability of capture

At Thoresby, harvest mice were completely absent from all habitat types for most of the study and were only caught in the reedbed in September and October. The total number of captures was 38, with 13 unique individuals. When considering all captures in just September and October, the elevation of the trap and the trapping session both had a significant effect on the probability of catching a harvest mouse (GLM: Δ Dev_1 = 11.366, P < 0.001 and Δ Dev_1 = 3.871, P = 0.0491 respectively). In the elevated traps the probability of catching a harvest mouse was almost ten times higher than in ground traps, and in October it was close to double what it was in September (Figure 4). The only other site where harvest mice were caught was Bestwood, which was surveyed in July and October. Since harvest mice were only trapped in this site in October, the difference between the July and the October session is consistent with the seasonal trend shown at Thoresby.

The wood mouse was the only species caught in all four habitat types, with a total of 944 captures and 178 different individuals. The probability of catching a wood mouse was significantly affected by habitat type (Table 2). The highest probability of capture was in the woodland, followed by the reedbed, pasture and lastly the arable (Figure 5). There was a significant effect of elevation, as this species was more likely to be caught on the ground than in elevated traps in all months and habitats, apart from in August in the reedbed (Figure 5). There was also a significant effect of session, as wood mice were most likely to be caught in August and April, while in September the probability was particularly low. There was a significant interaction of the effects of habitat and session as the probability of catching a wood mouse in each habitat varied greatly with each session (Table 2). In most sessions the woodland had the highest probability of capture, apart from April and May. In April the highest probability was in the pasture, while in May it was in the reedbed, followed closely by the arable (Figure 5).

There was a significant effect of session, habitat and elevation on the probability of catching a bank vole (Figure 6). August had a very high capture probability, almost twice the that of the next highest session, which was October (Figure 6). The probability of capture was very similar between the reedbed and the woodland, but it was much lower in the pasture, and zero in the arable. In the ground traps the probability of capture was about twice what it was in the elevated traps (Figure 6). There was also a significant interaction between the effects of habitat and session, as until July there were no bank voles caught in the reedbed, but from that session onwards the probability of capture in the reedbed exceeded that in the woodland, except in August (Figure 6).

Discussion

The main aim of this study was to shed light on habitat preferences in small mammals, and seasonal changes in those preferences which might explain apparent fluctuations in abundance, especially in harvest mice. The results support the idea that habitat use by small mammals such as wood mice and bank voles varies seasonally, and confirm that reedbeds in particular support relatively high small mammal abundance and diversity. While our findings suggest that harvest mice are typically abundant in reedbeds in autumn, we found no support for the hypothesis that their disappearance in the spring and summer is explained by movement into other nearby habitats.

The results from Thoresby support the idea that habitat preferences of small mammals can change substantially across the year. Specifically, there were seasonal changes in the effect of habitat type on the probability of capture for wood mice and bank voles. Wood mice are known to undergo seasonal fluctuations in abundance and most studies that looked at their population dynamics agree that their numbers decrease in spring and increase in autumn (Crawley 1970; Fernandez et al. 1996; Montgomery 1989; Watts 1969). Our study did not register a dramatic decrease in the numbers of wood mice in early spring months, but there was a slight decrease in May, followed by a slight increase in June and July and a peak in August. The difference between this study and the literature could be caused by the fact that most previous studies only looked at one habitat and therefore could have failed to record that individuals move between habitats in late spring and summer. In our study there were several instances of marked individuals moving between different habitats. This, in addition to the steep decrease in captures in the woodland and pasture in May, coupled with an increase in captures in the arable, suggests seasonal movement of individuals between habitats, as previously reported by Ouin et al. (2000). The results of our study therefore support the idea that apparent fluctuations in wood mouse population size are at least partially caused by a change in habitat preference (Ouin et al. 2000; Todd et al. 2000; Ylönen et al. 1991).

The data for bank voles show very low numbers from February to July and a large increase in August, which mostly supports the previous evidence for seasonal fluctuations in the population size for this species (Lambin et al. 2000). In regards to habitat preference there was a sudden appearance of bank voles in the reedbed starting from July. The reedbed became much drier in the summer months, with most areas lacking standing water, and therefore might have become more suitable for this species, which is largely restricted to the ground owing to poor climbing abilities (Buesching et al. 2008). However, this happened in coincidence with a sharp increase in the woodland and therefore it is possible that the captures in the reedbed represent an overall growth in population density.

Our data suggest that harvest mice are most easily caught in reedbeds in autumn. In the main study there were no captures of harvest mice in the reedbed, and all other habitats, at Thoresby during spring and summer in 2018. Results from other sites, and from the pilot study in 2016, are consistent with those from the focal site in 2018. Although previous studies have shown that harvest mice become extremely scarce during the summer, their perceived absence in the late winter and spring at our sites was unexpected. However, a similar pattern was seen in a study in Switzerland, which found no harvest mice in the first of the two winters surveyed and only one individual in the second (Vogel and Gander 2020). In the literature there is evidence that extremely cold temperatures cause an increase in mortality (Darinot 2019a; Perrow and Jowitt 1995; Sleptsov 1947; Trout 1978), and our sites are close to the northern limit of the range of the species in the UK. The winter of 2017/18 was unusually prolonged at our field sites, with low temperatures and snowfall both early (December) and late (March), and this may have had a negative effect on population size, causing the species to be undetectable.

Another possible explanation for the lack of records of harvest mice in spring and summer is competitive exclusion between harvest mice and wood mice in the reedbed. During the study the density of wood mice in the reedbed was very high until August, and it decreased in September and October, which are the only months in which harvest mice were caught. We found a negative spatial correlation between the number of harvest mice and wood mice caught at each trap location, which could be caused by competitive exclusion between the two species. However, the correlation could be driven by the different characteristics of the trap locations and the preferences of each species for different microhabitats, and without stronger evidence we cannot prove competitive exclusion between the two species.

Overall the results confirm that recorded harvest mouse abundance can vary dramatically over a period of months, and seem to indicate that harvest mice have the ability to recover quickly from population numbers so low that they are undetectable. Alternatively, it is possible that there is a change in trappability of this species in the months when it is not recorded. It has been suggested that increased use of higher portions of the vegetation might cause reduced detection of this species in the summer (Vogel and Gander 2020), but our study included both ground and elevated traps, which seems to rule out this explanation. Indeed, Darinot (2019b) successfully detected harvest mice during the summer using a method of aerial trapping similar to ours, suggesting that if mice had been present they should have been captured. Changes in trappability are not therefore a compelling explanation for the seasonal absence of harvest mice in our study.

Reedbeds represent a refuge for small mammals and are a hotspot of biodiversity (Marques et al. 2015; Perrow and Jowitt 2003). At the focal study site (Thoresby) the reedbed was the habitat with the highest species richness and it supported populations of harvest mice, pygmy shrews and field voles, species that were not found elsewhere. This supports previous findings suggesting that reedbeds can be very important habitats for these species (Haberl and Kryštufek 2003; Harris 1979; Kettel et al. 2016; Marques et al. 2015). Reedbeds have a complex habitat structure, made up by tall reed stems and an underlayer of sedges and other herbaceous plans, which, combined with an abundance of food sources such as seeds and insects, provide ideal habitat for many small mammals (Canova and Fasola 1991; Marques et al. 2015).

Wood mice were the species that travelled furthest between consecutive recaptures, followed by harvest mice and then bank voles. This can be explained by the difference in size and ecology between the species. Wood mice are larger than harvest mice and this could increase their ability to travel longer distances. A relationship between body size and home range size has been demonstrated in mammals and could be a factor for these species too (Lindstedt et al. 1986). In addition, Bank voles tend to be more sedentary, while wood mice move between different habitats in search for food, which can explain the difference between these two species despite their similar body size (Bergstedt 1966). In all species, males travelled significantly further than females, which is consistent with the difference in size between the home ranges of males and females found in previous studies on small mammals (Korn 1986). This could be a result of the larger size of males but could also reflect the necessity for males to travel to look for mates.

We must be cautious in interpreting our data on individual movements, which are a measure of the minimum distance travelled between the trapping events, rather than the actual distance travelled. A more detailed study of individual movement that successfully employed radio-tracking of six individuals reported that harvest mice travel on average 90 m per day (Darinot 2019a). This study also seems to suggest that autumn is the time of year when harvest mice travel the shortest distance compared to the rest of the year, which might explain our results. However, the low number of individuals monitored both in our study and in the literature indicates the need for further research in this field.

Elevation had different effects on each species. Harvest mice were much more likely to be trapped in the elevated traps than on the ground. This reflects their scansorial habits (they forage and nest above ground, in the "canopy" of reedbeds and other habitats) and mirrors the results of the few successful live trapping studies for this species (Harris 1979; Hata 2011; Riordan et al. 2009; Surmacki et al. 2005). This result also further confirms that elevated traps are an effective tool for monitoring harvest mice, at least at some times of year, as shown in a previous study (Kettel et al. 2016). The probability of catching wood mice was higher in the ground traps, which confirms the findings of a previous study that wood mice spend most of their time close to the ground (Buesching et al. 2008). Interestingly, in the reedbed in Thoresby in August wood mice were found more often in elevated traps than on the ground. This happened in coincidence with an increase in the number of bank voles present, and therefore it could have been caused by an increase in competition for the ground traps. Wood mice are known to be more agile and be able to exploit the higher parts of the vegetation compared to bank voles (Buesching et al. 2008), which may be why they were the species that was displaced. Bank voles were much more likely to be captured in the ground traps than in the elevated ones, even compared with wood mice. In addition to being less agile than wood mice, they have smaller eyes and ears, which could mean that they are less able to detect predators in time and therefore they rely less on escaping from aerial predators and more on hiding from them (Buesching et al. 2008).

Conclusion

Overall, our results confirm that understanding habitat preferences is crucial in the study of small mammal communities, and they underscore the importance of reedbeds as a reservoir for small mammal diversity. We have provided evidence of seasonal changes in habitat use by wood mice and bank voles, demonstrating the need for trapping across multiple habitat types in studies of small mammal abundance in heterogeneous landscapes. Our study also contributes to a scarce literature on the ecology of harvest mice in the UK. Although we have found strong evidence of dramatic seasonal variation in the capture rate for this elusive species in reedbeds, further research is required to understand the relative importance of life history (i.e. seasonal patterns of mortality and fecundity), and changes in habitat preference and trappability, in explaining such variation. This research will be crucial to the development of a meaningful conservation strategy for the harvest mouse.

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Figures and Tables

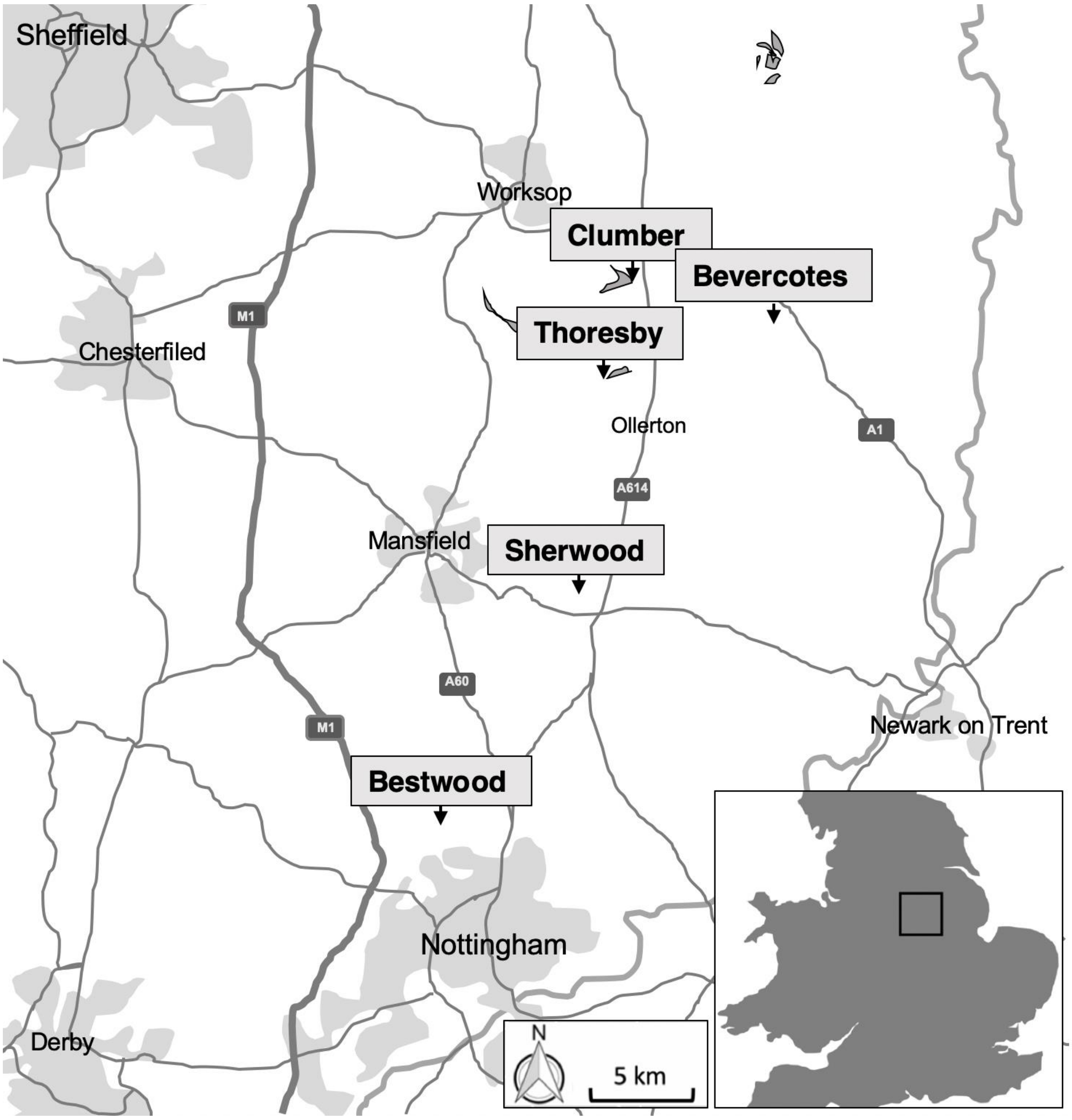

Figure 1 Location of the five sites surveyed: Thoresby Estate, Clumber, Sherwood, Bevercotes and Bestwood.

Table 1. Dates of trapping sessions, and number of elevated (E) and ground (G) traps used at each site, divided by habitat. Dashes indicate habitat types which did not exist, or were not available.

Session	Site	Date	Habitat type											
			Reedbed			Pasture			Woodland			Arable		
			E	G	**total**	E	G	**total**	E	G	**total**	E	G	**total**
P1	Thoresby	26/07/16 – 31/07/16	56	0	**56**	0	0	**0**	0	0	**0**	0	0	**0**
P2	Thoresby	23/08/16 – 28/08/16	56	0	**56**	0	0	**0**	0	0	**0**	0	0	**0**
P3	Thoresby	26/09/16 – 01/10/16	56	0	**56**	0	0	**0**	0	0	**0**	0	0	**0**
P4	Thoresby	07/11/16 – 13/11/16	56	0	**56**	0	0	**0**	0	0	**0**	0	0	**0**
1	Thoresby	09/02/18 – 23/02/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**
2	Thoresby	09/03/18 – 23/03/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**
3	Thoresby	06/04/18 – 20/04/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**
	Bevercotes	20/04/18 – 27/04/18	15	15	**30**	-	-	**-**	15	15	**30**	-	-	**-**
4	Thoresby	04/05/18 – 18/05/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**

	Sherwood pines	18/05/18 – 25/05/18	6	6	**12**	-	-	-	15	15	**30**	-	-	-
5	Thoresby	08/06/18 – 22/06/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**
	Clumber	22/06/18 – 29/06/18	8	8	**16**	-	-	-	10	10	**20**	0	20	**20**
6	Thoresby	06/07/18 – 20/07/18	15	15	**30**	0	30	**30**	15	15	**30**	12	18	**30**
	Bestwood	20/07/18 – 27/07/18	12	13	**25**	-	-	-	9	11	**20**	-	-	-
7	Thoresby	03/08/18 – 17/08/18	15	15	**30**	0	30	**30**	15	15	**30**	0	0	**0**
8	Thoresby	07/09/18 – 21/09/18	15	15	**30**	0	30	**30**	15	15	**30**	0	30	**30**
	Sherwood pines	21/09/18 – 28/09/18	9	4	**13**	-	-	-	-	-	-	-	-	-
9	Thoresby	05/10/18 – 12/10/18	15	15	**30**	-	-	-	15	15	**30**	-	-	-
	Bestwood	12/10/18 – 19/10/18	15	15	**30**	-	-	-	3	8	**11**	-	-	-

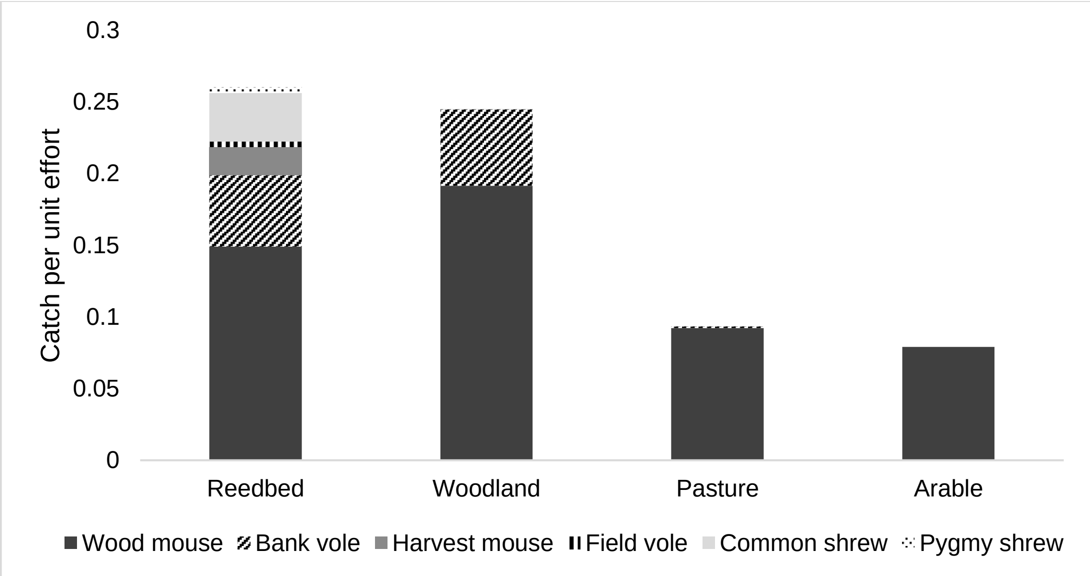

Figure 2 Catch per unit effort for six small mammal species caught in Thoresby across four different habitats over nine months.

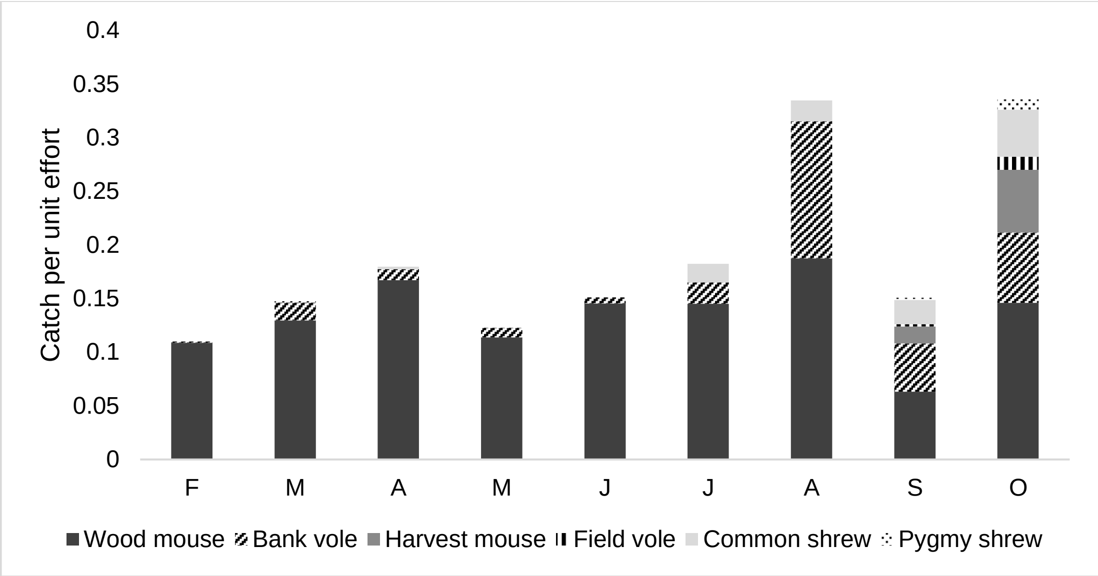

Figure 3 Catch per unit effort for six small mammal species caught in Thoresby each month, pooling data across four habitat types.

Table 2: Results from a generalised linear mixed effects model with binomial errors testing the effects of elevation, trapping session and habitat on the probability of catching wood mice and bank voles across eight trapping sessions in four habitat types at Thoresby. For this model the final trapping session was excluded because not all habitats were sampled in this session.

Term	Wood mice		Bank voles	
	Change in deviance $_{(df)}$	P	Change in deviance $_{(df)}$	P
Elevation	$5.390_{(1)}$	0.020 *	$19.733_{(1)}$	<0.001 ***
Session	$85.737_{(7)}$	<0.001 ***	$233.520_{(7)}$	<0.001 ***
Habitat	$46.421_{(3)}$	<0.001 ***	$47.201_{(3)}$	<0.001 ***
Habitat x session	$179.380_{(21)}$	<0.001 ***	$64.695_{(21)}$	<0.001 ***
Session x elevation	$63.663_{(7)}$	<0.001 ***	$9.540_{(7)}$	0.216
Habitat x elevation	$5.182_{(2)}$	0.075 .	$0.069_{(2)}$	0.966

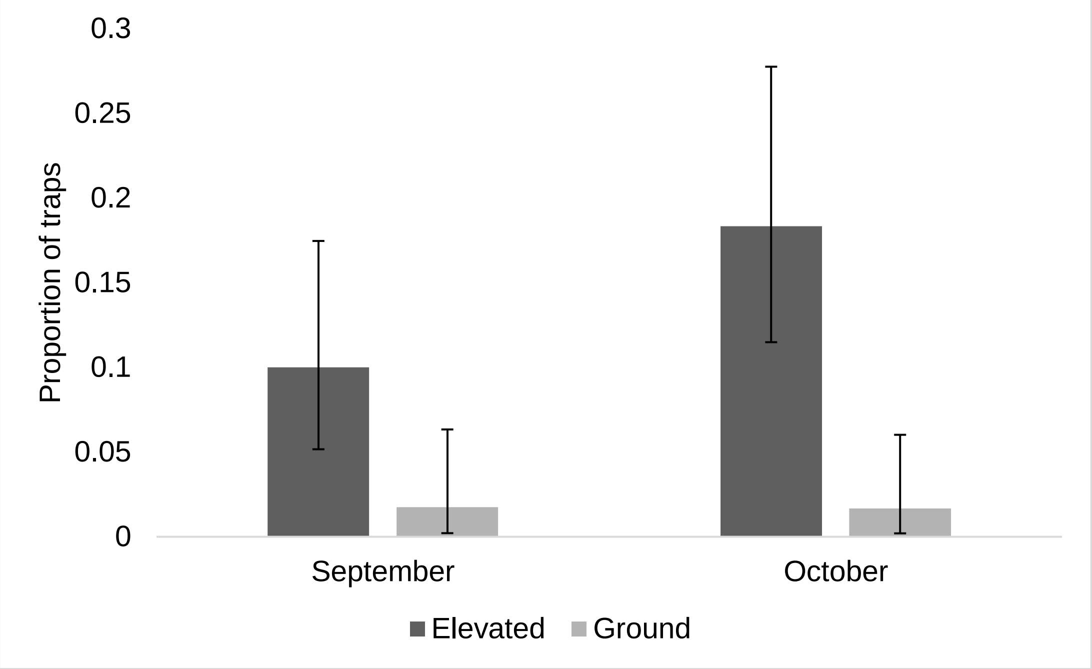

Figure 4 Proportion of elevated and ground traps which caught a harvest mouse during the September and October sessions in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

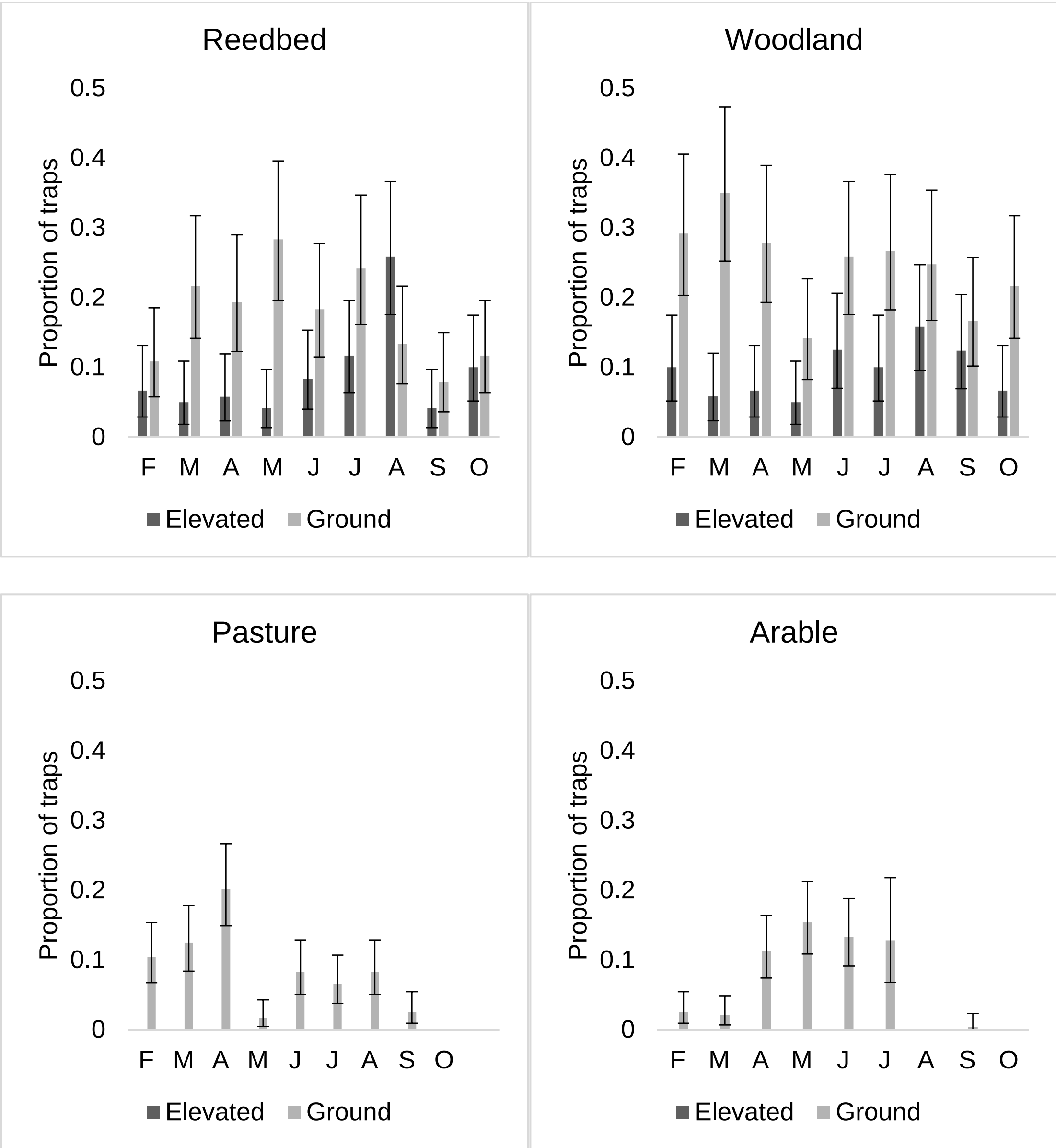

Figure 5 Proportion of elevated and ground traps which caught a wood mouse during each session and in each of the four habitat types in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

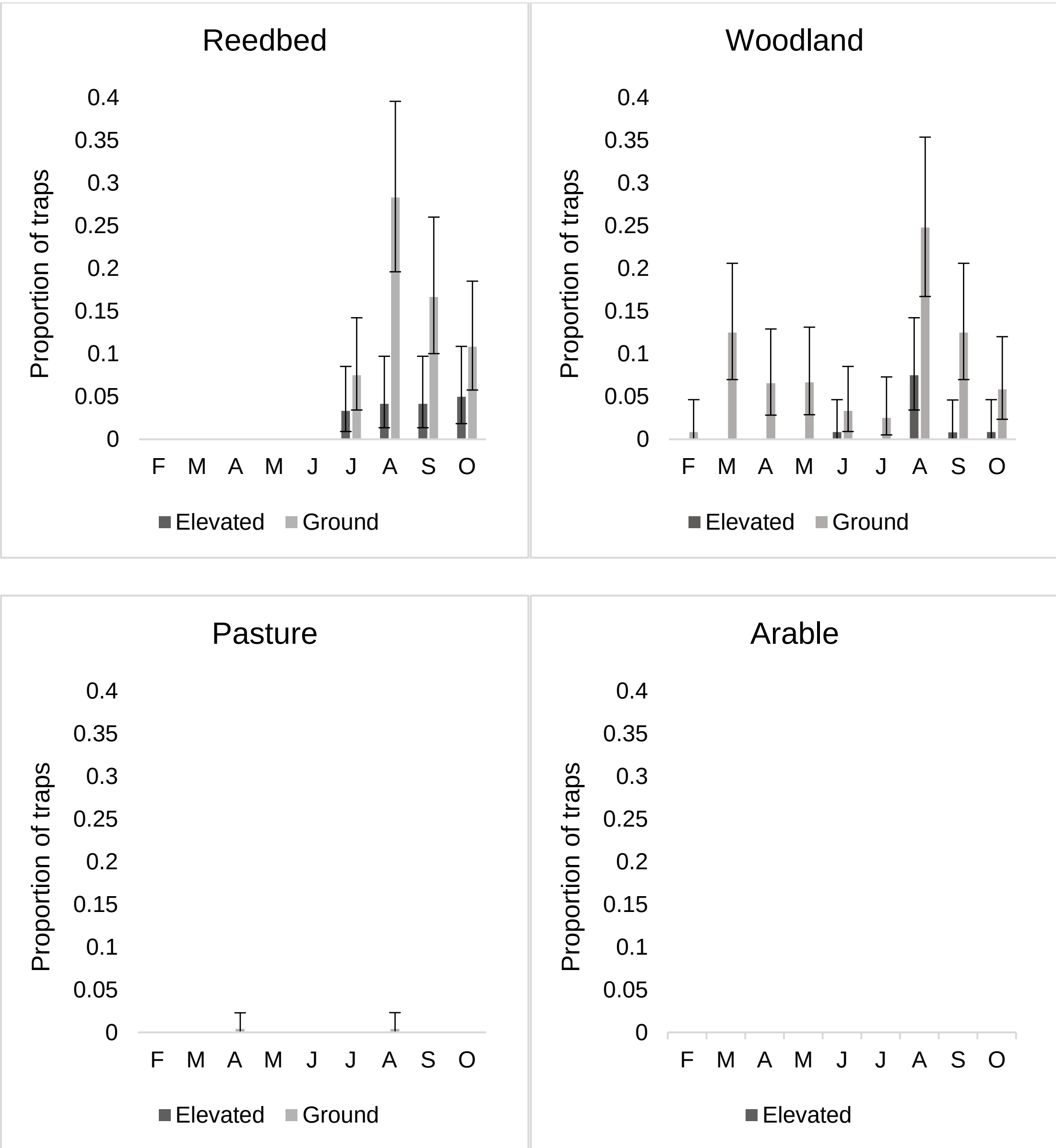

Figure 6 Proportion of elevated and ground traps which caught a bank vole during the different sessions in the reedbed, woodland and pasture in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.