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

by

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Abstract

Small mammals are an important group due to their multiple roles in the ecosystem: they act as prey species for raptors and larger mammals, as predators of invertebrates and seeds and they can also facilitate dispersal for some plants and fungi. They have some very interesting population dynamics as they experience strong fluctuations in numbers. Due to their unusual patterns, most studies have focused on the multiannual cycles observed only in voles and lemmings in the arctic region, while there are fewer studies on the more common annual cycles. Recently there have been studies that suggest that small mammals change habitat preference in different seasons but not much supporting evidence has followed. The harvest mouse (*Micromys minutus*) is a particularly understudied species because of its small size and scansorial lifestyle, which make it difficult to trap using the conventional live-trapping technique that consists of placing the traps on the ground. There is some evidence of an extreme reduction in the numbers of harvest mice present in the reedbeds in the summer months, but due to the difficulties in monitoring them, it is unknown whether this is caused by mortality or movement to other habitats. A new technique of live-trapping at an elevation has been much more successful than previous methods and therefore it is now possible to monitor this species more effectively.

This study has attempted to monitor the presence of harvest mice and other small mammals by live trapping both on the ground and at an elevation in habitat mosaics in Nottinghamshire. The focal site was surveyed every month

from February to October 2018 and additional sites were surveyed either once or twice throughout the study. The four habitat types surveyed were: reedbed, woodland, pasture and arable. The presence of the reedbed is crucial as this habitat is known to have the highest biodiversity of small mammals but has not yet been the focus of many studies. The total sampling effort consisted of 9,887 trap bouts and resulted in 1,446 trapping events, which included harvest mice (N=70), 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 biodiversity. Harvest mice were only caught in the reedbed of two sites at the beginning of autumn. Wood mice were the dominant species in all habitats and showed seasonal variation in their habitat preference, as in late spring their numbers decreased in the woodland and the pasture and increased in the arable. Bank voles did not show a clear change in habitat preference throughout the course of the study but experienced a sharp increase in numbers in August, after a long period of very low numbers.

Although this study was not successful at shedding light on the population dynamics and seasonal habitat preference of the harvest mouse, it provided records for this very understudied species and others. It also confirmed the fact that harvest mice prefer the wet areas of the reedbed. The evidence collected seems to support the idea that this species undergoes extreme reductions in numbers for part of the year and then it is able to make a fast recovery. However further research is necessary to prove that this is a repeated trend and not the result of a harsh winter.

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1.

Introduction

1.1. Introduction

In agricultural contexts small mammals are often considered nothing more than pests, because of their impact on crops, but they are often important in shaping the community through their interactions with other species, some of which are of conservation interest. They constitute the majority of the prey species for some predators such as the barn owl (*Tyto alba*) (Bontzorlos *et al.*, 2005; Frey *et al.*, 2011), the kestrel (*Falco tinnunculus*) (Korpimäki, 1985) and the badger (*Meles meles*) (Mortelliti and Boitani, 2008) and can affect their abundance and distribution, making the study of small mammals crucial for the conservation of these species (Mortelliti and Boitani, 2008) (Plesnik and Dusik, 1994). In addition small mammals can affect their habitat by feeding on invertebrates, fruits, seeds, other plant material and fungi (Watts, 1968; Dickman, 1986; Butet and Delettre, 2011). In some cases this can facilitate the dispersal of plants and fungi (Maser, Trappe and Nussbaum, 1978; Miyaki and Kikuzawa, 1988) but voraciously granivorous *Apodemus* mice can also reduce the number of successful tree seedlings (Sone *et al.*, 2002; Takahashi, Sato and Washitani, 2006).

Some species of small mammals are protected in the UK due to perceived declines in their numbers. The harvest mouse (*Micromys minutus*) for example is a native mammal in the UK and is believed to be declining, probably due to increased agricultural activity and changes in the landscape (Perrow and Jowitt, 1995). This has caused this species to become the subject of conservation plans and it has been listed in the Biodiversity Action

Plan (BAP) (JNCC, 2010). However the data on the distribution and habitat use of harvest mice used to assess their status are very limited because of their scansorial lifestyle (Harris, 1979b), which makes it very difficult to monitor them with traditional live-trapping methods (Poulton and Turner, 2009; Kettel, Perrow and Reader, 2016). Nest searching has been used as an alternative method but with very limited success (Riordan, Lloyd and Macdonald, 2009; Kettel, Perrow and Reader, 2016). A recent study by Kettel, Perrow and Reader (2016) has found that live-trapping in the stalk zone of tall vegetation is much more effective than any previously reported method, 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 very understudied species and could inform decisions about its conservation status in the UK (Kettel, Perrow and Reader, 2016).

Much of current knowledge about small mammal population dynamics comes from studies on some Arvicolinae species which showed extreme and regular multiannual fluctuations in their abundance (Elton, 1924; Chitty, 1952; Krebs, 1964; Norrdahl and Korpimäki, 1995). Although these cycles are very interesting they only apply to some species and arguably only appear in the Fennoscandia region (Jensen, 1982; Hanski, Hansson and Henttonen, 1991). In all other cases the changes in abundance still exist but they follow a yearly cycle (Crawley, 1970; Flowerdew and Gardner, 1978; Trout, 1978b; Montgomery, 1989). This cycle might in part be the result of a dilution effect, meaning that the perceived changes in abundance in a specific habitat might be caused by the dispersal of individuals into other habitats, rather than a

decrease in the population numbers (Ouin *et al.*, 2000). Changes in habitat preference in different seasons have been reported in the wood mouse (*Apodemus sylvaticus*) but have not previously investigated in most other small mammals (Kikkawa, 1964; Ouin *et al.*, 2000; Todd, Tew and Macdonald, 2000).

The aim of this study was to determine the habitat preference 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 areas of woodland, pasture and arable, the intent was to extend the knowledge on the habitat requirements of this species and others. The study spanned nine with the aim of beginning to distinguish seasonal fluctuations in abundance from seasonal changes in habitat use in harvest mice and other small mammals.

1.2. Population dynamics

Rodent population dynamics first captured the attention of the scientific community when the dramatic and regular cyclical changes in the abundance of some species in the Arvicolinae subfamily, such as voles and lemmings, were first described (Elton, 1924; Chitty, 1952; Krebs, 1964). Since then small mammal population dynamics and their interaction with their biotic environment have been very extensively researched in order to determine which regulatory processes cause these multiannual cycles (Krebs, 1964, 1966; Tapper, 1979; Hanski, Hansson and Henttonen, 1991; Norrdahl and

Korpimäki, 1995; Korpimäki and Krebs, 1996; Turchin *et al.*, 2000; Bierman *et al.*, 2006; Radchuk, Ims and Andreassen, 2016).

The exact causes of these cycles are still debated but among possible explanatory factors the most debated are predation, food availability, sociality and dispersal (Krebs *et al.*, 1995; Andreassen *et al.*, 2013; Radchuk, Ims and Andreassen, 2016). Krebs *et al.* (1995) found that the cycles of snowshoe hares (*Lepus americanus*) are caused by an interaction between predation and food availability. The analyses done by Andreassen *et al.* (2013) (Andreassen *et al.*, 2013) and Radchuk *et al.* (2016) (Radchuk, Ims and Andreassen, 2016) on vole populations revealed that dispersal must also be included into the model in order to explain the fluctuations observed in the wild. Although studying these cycles has taught us a lot about the factors which determine observed population dynamics in wild populations, outside Fennoscandia and for other small mammals species the changes in abundance across several years are less dramatic and not regular (Jensen, 1982; Hanski, Hansson and Henttonen, 1991). There is evidence of a gradient in the multiannual cycles of the Arvicolinae, which causes the dampening and increased irregularity of the cycles from North to South (Hansson and Henttonen, 1985; Hanski, Hansson and Henttonen, 1991; Lambin, Petty and Mackinnon, 2000). The causes of this pattern are not clear but one of the plausible explanations is the interaction between specialist predation and generalist predation, as the first is constant across the whole range and the latter increases as the latitude decreases (Hanski, Hansson and Henttonen, 1991).

In small mammal species which do not show multiannual cycles, a yearly cycle of abundance is typically apparent (Crawley, 1970; Flowerdew and Gardner, 1978; Trout, 1978b; Hansson and Henttonen, 1985; Montgomery, 1989). Amongst these species, the wood mouse is the most well studied species, with studies on its ecology spanning several decades (Crawley, 1970; Montgomery, 1989; Fernandez, Dunstone and Evans, 1996; Liu *et al.*, 2013). The wood mouse is a generalist species widespread across Europe and very successful in most habitat types, including different types of woodland, arable fields and wetlands (Canova and Fasola, 1991; Michel *et al.*, 2007; Mortelliti *et al.*, 2009; Marques *et al.*, 2015). Studies of the population dynamics of wood mice in woodlands and hedgerows have shown a decrease in population numbers in spring, followed by a stable phase in the early summer and then an increase in the late summer and autumn (Watts, 1969; Crawley, 1970; Montgomery, 1989; Fernandez, Dunstone and Evans, 1996). Voles seem to have different dynamics depending on the species and on the geographical location. A study on field voles (*Microtus agrestis*) in a woodland in northern England found that they have a very similar seasonal fluctuation in population numbers to wood mice, as they showed a population decline in spring (Lambin, Petty and Mackinnon, 2000).

Food availability was found to have some effect on the abundance of wood mice in a deciduous forest in England (Watts, 1969). A correlation was found between the overwintering success and the acorn (*Quercus spp.*) crop in the previous autumn but food availability cannot explain the drop in numbers in

spring, which coincides with the start of the breeding season, nor the increase in autumn (Watts, 1969; Flowerdew and Gardner, 1978). These changes have been explained by the demographic processes as the new young enter the population in early autumn but they also experience a high mortality late in winter (Watts, 1969). Density dependence was also cited by Watts (1969) as an explanation for these changes in abundance but the analysis that led to this conclusion was later criticised by Krebs and Boonstra (1978) (Krebs and Boonstra, 1978). A review of data coming from published sources confirmed that there is some density dependence involved in the population dynamics of wood mice but it only affects the increase in numbers in autumn, while the other changes are caused mainly by food availability (Montgomery, 1989).

1.3. Seasonal movement

More recent studies of the ecology of small mammals suggest that habitat preference can change depending on the season (Kikkawa, 1964; Ylönen, Altner and Stubbe, 1991; Ouin *et al.*, 2000; Todd, Tew and Macdonald, 2000). If this is true then the apparent fluctuation in abundance is at least partially the result of a dilution effect (Ouin *et al.*, 2000). Because wood mice are able to exploit several habitat types, their habitat use has been studied in habitat mosaics that include different habitats. There is overwhelming consensus that while the number of wood mice in woodland and hedgerows peaks in winter and decreases in spring, simultaneously their numbers increase in neighbouring arable fields (Kikkawa, 1964; Ylönen, Altner and Stubbe, 1991; Ouin *et al.*, 2000). This suggests that in the colder months wood mice prefer

the protection and food guaranteed by woodland or hedgerows, and then they move to the arable habitat when the crops start growing (Kikkawa, 1964; Ylönen, Altner and Stubbe, 1991; Ouin *et al.*, 2000). Kikkawa (1964) looked at the habitat use of bank voles (*Myodes glareolus*) as well as of the wood mouse and found that voles showed much less movement between different habitats and mostly stayed within their habitat range. However, this is only one study and more evidence is necessary to be sure of the spatial dynamics of this species.

1.4. Wetlands

Wetlands 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. These types of habitats 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). Gibbs (1993) predicted that the disappearance of the small wetlands present in his study area, which in the USA were not legally protected, would have caused an extinction of the local populations of small mammals, birds and turtles. In the UK reedbeds are considered important for the conservation of some rare bird species (e. g. the bittern (*Botaurus stellaris*) (Gilbert *et al.*, 2005)) as well as providing a valuable habitat for waterfowl and migrating passerines (Bibby and Lunn, 1982; Gilbert *et al.*, 2005). They are also important foraging grounds for bats (Stahlschmidt *et al.*, 2012). Wetlands are home to most the native small mammal species, but most UK studies 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, Barber and Quinn, 2000; Carter and Bright, 2003). In the case of the water vole it was evident that reedbeds are crucial for the survival of this species as they provide protection from predation by mink (*Mustela vison*) and this habitat needs to be protected in order to mitigate or reverse the decline of water voles in the UK (Carter and Bright, 2003).

Wetlands are also used by several species of small mammals as demonstrated indirectly by a study on the diet of the barn owl and the little owl (*Athene noctua*) a Greek wetland, which found that the diet of these owls in that kind of habitat relies heavily on small mammals (Goutner and Alivizatos, 2003). A recent study, which tested live-trapping in reedbeds as a way to monitor harvest mice in England, has also found that wood mice, bank voles and field voles use this habitat as well as harvest mice (Kettel, Perrow and Reader, 2016). Marques *et al.* (2015) (Marques *et al.*, 2015) highlighted the importance of wetlands, and especially reedbeds, by showing that in the area that they surveyed in Portugal, which also included some agricultural land and woodland, wetlands had the highest small mammal richness. Most studies that involved trapping small mammals have been carried out in dry habitats such as fields, hedges and woodland (Kikkawa, 1964; Ouin *et al.*, 2000; Alain, Gilles and Yannick, 2006; Heroldova, 2007; Michel *et al.*, 2007); however the recent studies showed that live-trapping in wetlands is possible and also very informative as they are amongst the habitats in the UK with the highest small

mammal diversity. (Perrow and Jowitt, 2003; Marques *et al.*, 2015; Kettel, Perrow and Reader, 2016). Therefore, more studies of this kind are necessary to discover the exact role of wetlands as a habitat for all the species of mammals that use them.

1.5. Harvest mice

The harvest mouse *Micromys minutus* (Pallas, 1771) is a small rodent of the Muridae family (Horáček *et al.*, 2013). It is a widely distributed species and it can be found across Europe and Asia (IUCN, 2016). In the UK it is found primarily in England and Wales (Harris, 1979b; Harris *et al.*, 1995). The adults weigh approximately 6 grams (Perrow and Jowitt, 1995), which makes it smaller than most of the other members of its family and the smallest rodent in Europe (Perrow and Jowitt, 1995; Horáček *et al.*, 2013). The prehensile tail of harvest mice makes them immediately recognisable and distinct from the other small mammals that live in the same areas, as well as their small size and a distinctive russet brown colour with a white underbelly (Harris, 1979c, Trout, 1976).

Its small body size and prehensile tail allows the harvest mice to exploit the stalk zone of grasslands and reedbeds, and more generally areas of the vegetation that are not easily accessible to other small mammals (Harris, 1979c, Riordan, Lloyd and MacDonald, 2009). Although the name reveals that traditionally this species was associated with cereal fields, their habitat also includes field margins, wetlands, young woodlands and other habitats with tall

and dense vegetation (Harris, 1979b; Dickman, 1986; Bence, Stander and Griffiths, 2003; Haberl and Kryštufek, 2003; Moore, Askew and Bishop, 2003). Now they are rarely found on arable land and instead they are believed to be commonest in reedbeds (Haberl and Kryštufek, 2003; Surmacki, Goldyn and Tryjanowski, 2005; Kettel, Perrow and Reader, 2016).

Harvest mice make spherical nests from the leaves monocotyledon plants such as grasses and reeds, and they build them off the ground (Harris, 1979b; Dickman, 1986; Surmacki, Goldyn and Tryjanowski, 2005; Hata, 2011). The height of the nests is usually between 15 and 65 cm but it can vary depending on the height of the vegetation as the taller it is, the higher the nest will be located (Dickman, 1986; Surmacki, Goldyn and Tryjanowski, 2005; Hata, 2011). Harvest mice are generalist omnivores so their diet consists mainly of seeds, fruit, leaves and insects, but they occasionally consume fungi and can scavenge on the remains of other vertebrates (Dickman, 1986; Okutsu, Takatsuki and Ishiwaka, 2012).

The average lifetime of the harvest mouse is believed to be approximately 18 months in the wild, while in captivity the species has been known to live up to five years (Trout, 1978a). The majority of litters are born between August and September but in favourable environmental conditions the breeding season can last from May to December (Trout, 1978b; Harris, 1979a). Extremely cold weather can increase the mortality of this species because the combination of their small body size and fur that is not well insulating makes it difficult for them to stay warm enough (Trout, 1978b).

The population numbers have been found to decrease considerably from April to August, followed by a large increase in September (Sleptsov, 1947; Trout, 1976; Trout 1978b). These seasonal changes are so severe that Sleptsov (1947), who recorded the number of mice found dead due to a plague control attempt in Russia, only found 3.6% of the total number of females between April and July and recorded an almost 5-fold increase in September and October. The magnitude of these fluctuations has prompted the suggestion that this may be the result of a change in trappability of the species, but this has never been confirmed (Trout, 1976). 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 (Koskela and Viro, 1976). 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 everywhere. Strong yearly fluctuations have also been recorded, but the studies available to date only span a maximum of four years and therefore do not provide evidence of any regular cycles (reviewed in Trout, 1978b).

The conservation status of the harvest mouse is difficult to assess. In Britain this species has undergone a decline in the arable fields, which is the habitat that it was believed to be mostly associated with (Harris *et al.*, 1995). This could be caused by more intensive agricultural practices, the selection of cereal strains with shorter stems, which make them less suitable for nest-building, and the use of insecticides, which reduced the quantity of insects available as food (Harris, 1979b; Harris *et al.*, 1995; Hata, 2011) (Perrow and Jowitt, 1995). Because of this perceived decline in numbers, the harvest mouse has been listed in the Biodiversity Action Plan (BAP) as a priority species (JNCC, 2010). This has prompted a call for conservation measures and even attempts at reintroducing captive bred harvest mice back into suitable habitats (Kean, 2006). However, the information about the distribution and density of the harvest mouse is outdated and most likely biased because of the difficulties in monitoring this species (Poulton and Turner, 2009; Kettel, Perrow and Reader, 2016).

Live-trapping on the ground is the most commonly used method for surveying small mammals but it has proven of very limited success with harvest mice because of their primarily scansorial lifestyle (Harris, 1979c, Riordan, Lloyd and MacDonald, 2009). As a consequence nest searching has been adopted as the main survey method for this species (Harris, 1979b). A recent study compared nest searches to traditional live-trapping and also tested a new technique of live-trapping above ground by securing the traps to bamboo canes in a reedbed (Kettel, Perrow and Reader, 2016). The results showed that in sites where even an experienced naturalist could not find any nests the

elevated traps successfully caught harvest mice. This suggests that it is likely that the presence of harvest mice has been overlooked in some areas or habitats and therefore this species could be more abundant than it is currently believed (Kettel, Perrow and Reader, 2016).

1.6. Rationale

The population dynamics of small mammals have received a lot of attention for several decades. However, these dynamics are complex and change depending on the species and the geographical location, which causes knowledge gaps, especially when it comes to distinguishing between the actual changes in abundance and the seasonal changes in habitat preference. This is true even for the well-studied wood mouse, but even more so for the bank vole and the very understudied harvest mouse. This study aimed to fill those gaps by intensive field surveying of the small mammal community in four different habitats over a period of nine months, from late winter to early autumn, using a method that has been shown to be effective for all mouse, vole and shrew species. Surveys were conducted every month in all four habitats at one focal site, with additional surveys being conducted in selected habitats in one or two months at each of four additional sites.

The area surveyed is a habitat mosaic that includes reedbed, woodland, arable land and pasture. The arable land is the habitat type that harvest mice were believed to prefer and has been the subject of intense anthropogenic change. The reedbed is a habitat that recently has been shown to be

important for this and other small mammal species, but it has been the subject of very few studies. By selecting these habitats and comparing them to the woodland, which is known to be a good habitat for several small mammal species, this study offers a comprehensive view of the habitat preference of small mammals.

2.

Study sites and methodology

2.1. Study sites

The study was carried in five different sites in Nottinghamshire. All of the sites had at least one reedbed dominated by common reed (*Phragmites australis*). Two of the sites, the Thoresby estate and Sherwood Pines, were already known to have had harvest mice at least at one point in time and the other three, Bevercotes Pit Wood, Clumber Park and Bestwood Country Park, had never been surveyed for small mammals but had a reedbed large enough to support a harvest mouse population. To provide a time-series describing seasonal changes in community composition and habitat use, one trapping session was conducted every month at Thoresby estate between February 2018 and October 2018, resulting in a total of 9 trapping sessions. All the other sites were surveyed once or twice, to provide spatial replication of the observations at Thoresby, but all sites could not be visited in all months due to time constraints (Table 1).

Table 1. Dates of each trapping session

Trapping session	Site				
	Thoresby	Bevercotes	Sherwood pines	Clumber	Bestwood
1	09/02/18 – 23/02/18	-	-	-	-
2	09/03/18 – 23/03/18	-	-	-	-
3	06/04/18 – 20/04/18	20/04/18 – 27/04/18	-	-	-
4	04/05/18 – 18/05/18	-	18/05/18 – 25/05/18	-	-
5	08/06/18 – 22/06/18	-	-	22/06/18 – 29/06/18	-

6	06/07/18 – 20/07/18	-	-	-	20/07/18 – 27/07/18
7	03/08/18 – 17/08/18	-	-	-	-
8	07/09/18 – 21/09/18	-	21/09/18 – 28/09/18	-	-
9	05/10/18 – 12/10/18	-	-	-	12/10/18 – 19/10/18

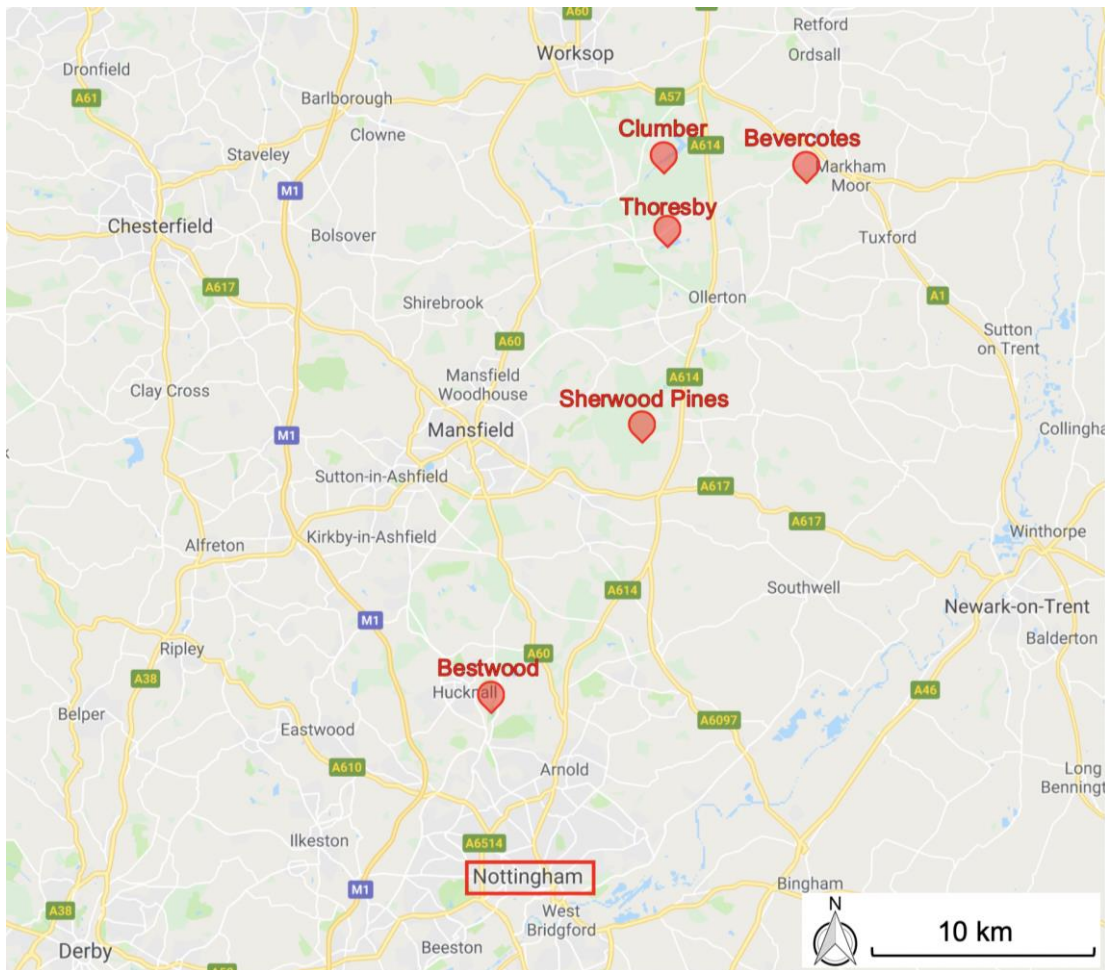


Figure 1: The locations of the field sites in Nottinghamshire (Google, n.d, retrieved from <https://www.google.com/maps>).

Thoresby

The Thoresby estate is a private property situated in the civil parish of Perlethorpe-cum-Budby, about 2 miles north west of Ollerton and 20 miles north of Nottingham. It is a Site of Special Scientific Interest (SSSI) and it

includes the Thoresby lake, which has a reedbed at its western end. The surrounding land is covered by woodland, pasture and arable land, all in close proximity to the reedbed (Figure 2). In 2016 a live-trapping survey was carried out in the reedbed and it showed the presence of harvest mice, wood mice, bank voles, field voles and common shrews. This site was chosen as the focal study site because it has all of the four habitat types of interest for this study, the reedbed was known to be able to sustain a harvest mouse population, and the site was secure, minimising the risk of theft of traps (Tom Reader, personal communication).

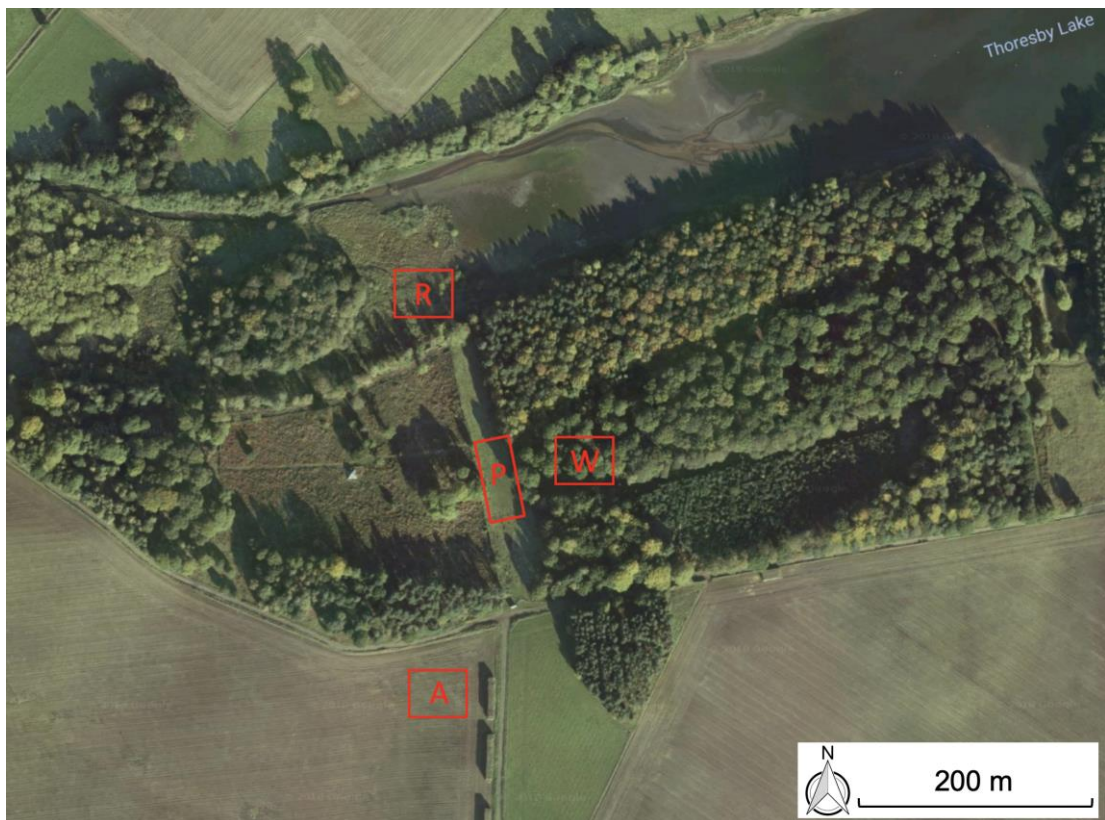


Figure 2: Location of the trapping grids in the Thoresby site. The red shapes represent the grids: reedbed (R), Pasture (P), Woodland (W), Arable (A). (Google, n.d, retrieved from <https://www.google.com/maps>).

Bevercotes

Bevercotes Pit Wood is a site under the management of the Forestry Commission England located between Bothamsall and Gamson, 22 miles north east of Nottingham. It is mostly covered by woodland and it has several streams and ponds. The larger of the ponds has small reedbeds along the edge (Figure 3).



Figure 3: Location of the trapping grids in the Bevercotes site. The red shapes represent the grids: reedbed (R) and Woodland (W) (Google, n.d, retrieved from <https://www.google.com/maps>).

Sherwood Pines

Sherwood pines is a forest park located 5 miles east of Mansfield and 13 miles north of Nottingham. It was originally part of Sherwood Forest and now it is managed by the Forestry Commission England, who have planted pine trees on the majority of it. Rainworth Water flows through the southern part of

it, forming a small reedbed, which has been known to house a population of harvest mice (Andrew Lowe, personal communication) (Figure 4).



Figure 4: Location of the trapping grids in the Sherwood Pines site. The red shapes represent the grids: reedbed (R) and Woodland (W) (Google, n.d, retrieved from <https://www.google.com/maps>).

Clumber

Clumber park is a country park situated 2 miles south east of Worksop and 22 miles north of Nottingham. It is owned by the National Trust and it is designated as a SSSI. It includes woodland, grassland, arable land and wetland. The reedbed, of approximately 3.5 acres is formed where the river Poulter meets Clumber lake (Figure 5).



Figure 5: Location of the trapping grids in the Clumber site. The red shapes represent the grids: reedbed (R) and Woodland (W) (Google, n.d, retrieved from <https://www.google.com/maps>).

Bestwood

Bestwood country park is a country park near Bestwood village, 5 miles north of Nottingham city centre, jointly owned by the Nottinghamshire City Council and the Gedling Borough Council. The village separates the main bulk of the park from the Mill lakes, which is where a one acre reedbed is located, surrounded only by a narrow area of woodland (Figure 6).



Figure 6: Location of the trapping grids in the Bestwood site. The red shapes represent the grids: reedbed (R) and Woodland (W) (Google, n.d, retrieved from <https://www.google.com/maps>).

2.2. Methodology

The four habitat types surveyed were reedbed, woodland, pasture and arable land. Only in Thoresby were all four habitats present, Clumber had reedbed, woodland and arable land and the remaining sites only had reedbed and woodland. Since there were four habitats to survey in Thoresby, two habitats were surveyed in the first week of the session 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. If there was an

additional site to be surveyed then it was done in the following week. Due to time constraints in the last session only the reedbed and the woodland were surveyed in Thoresby. In addition, the trapping in the arable had to be cut short in July and August (session 6 and 7) due to agricultural activities that had to be carried out in the area where the traps were placed. The second time Sherwood pines was surveyed the traps were stolen from the woodland at the beginning of the session and therefore the data were collected only from the reedbed.

The total number of traps available was 60, so since in most sites two habitats were surveyed at once, up to 30 traps were placed in each habitat. It was not always possible to place all 30, due to the size of some of the habitats. In Clumber there were three habitats to survey in one week and so up to 20 traps were placed in each habitat instead (Table 2). When possible, the traps were placed in a 10-meter grid in order to gather information about population size, density and movement. 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 the traps were placed in line transects.

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 by being taped onto a bamboo cane at about 1 m above ground. 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 grown, all

traps were on the ground (Table 2). In the reedbeds, the ground was often covered in water, in which case the traps were taped onto a cane about 10 centimetres above the water level to avoid flooding if the water level was to rise.

Table 2. Number of elevated (E) and ground (G) traps used in each site divided by habitat.

Session	Site	Habitat type											
		Reedbed			Pasture			Woodland			Arable		
		E	G	total	E	G	total	E	G	total	E	G	total
1	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
2	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
3	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
	Bevercotes	15	15	30	-	-	-	15	15	30	-	-	-
4	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
	Sherwood pines	6	6	12	-	-	-	15	15	30	-	-	-
5	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
	Clumber	8	8	16	-	-	-	10	10	20	0	20	20
6	Thoresby	15	15	30	0	30	30	15	15	30	12	18	30
	Bestwood	12	13	25	-	-	-	9	11	20	-	-	-
7	Thoresby	15	15	30	0	30	30	15	15	30	0	0	0
8	Thoresby	15	15	30	0	30	30	15	15	30	0	30	30
	Sherwood pines	9	4	13	-	-	-	-	-	-	-	-	-
9	Thoresby	15	15	30	-	-	-	15	15	30	-	-	-
	Bestwood	15	15	30	-	-	-	3	8	11	-	-	-

Longworth traps were chosen for this study because they are widely used for live-trapping of small mammals and they have been shown to be more effective than other alternatives and nest searching for the monitoring of harvest mice (Kettel, Perrow and Reader, 2016). Parakeet and cockatiel food mixed with sunflower seeds was used as food in the traps and casters were added to ensure the survival of shrews. Cotton wool was used for bedding

because harvest mice are much smaller than all the other small mammals in the community and therefore require extra insulation.

The habitats were surveyed in pairs and trapping sessions lasted one week for each pair of habitats at each site. The following trapping method was repeated every eight days:

- Day 1. The traps were placed and left in the pre-bait position.
- Day 2 and 3. The traps were left undisturbed in order for the animals to explore them and get accustomed to their presence.
- Day 4. Starting from 8am the traps were checked for signs of use such as movement of the bedding, feeding or faeces. If the traps showed these signs they were cleaned and food and bedding was replaced. All the traps were set to catch. At approximately 3pm all the traps were checked again.

If an animal was caught the following was noted:

- Species;
- Sex;
- Fur clippings (if the animal had already been caught);
- Weight (using a Pesola spring balance accurate to 0.1g for individuals weighing less than 10g and one accurate to 0,5 grams for individuals heavier than 10g).

If the individual had never been caught before a fur clipping was taken by cutting a small portion of the brown guard hairs, which revealed the black fur underneath (*Figure 7*). The clippings were taken creating an individual combination of marks that would allow to distinguish

individuals from one another. Each time the traps were checked was considered as a “trapping bout”

- Day 5, 6 and 7. The traps were checked twice a day, the first time starting from 8am and the second time starting from four hours after the last trap was checked in the first round. All the measurements and procedures carried out in day 4 were also carried out whenever an animal was caught.
- Day 8. The traps were checked in the morning and all the measurements and procedures carried out in the previous days were carried out again. The traps were then taken down, cleaned and prepared to be moved to the next habitat or next site.



Figure 7: Harvest mouse with a unique fur clipping on its upper-left side.

Once every session a habitat survey was carried out at each trapping point to determine the dominant vegetation and other habitat characteristics. In the reedbed this involved measuring the reed density by counting the number of reed stems in a 0.5m quadrat placed haphazardly in the vegetation within one meter of the trap. To measure the mean height and stem thickness of the reeds, five reed stems within the area of the quadrat were measured using a tape measure (accurate to 5cm) and callipers (accurate to 0,1mm). The water depth was measured using a tape measure. In the pasture, the arable land and the woodland the height of the vegetation (or the understory in the case of the woodland) was measured using a tape measure and the percentage ground cover and canopy cover were estimated by eye. In the woodland the distance to the closest tree was also measured using a tape measure. Daily environmental data consisting of maximum and minimum temperature, total rainfall, total sunshine and maximum wind gust was taken from the Daily Weather Summary from the Met Office (<https://digital.nmla.metoffice.gov.uk/>).

2.3. Data analysis

The data analysis was carried out only on the harvest mice, because they are the focus species of this study, and on the most common species: wood mice and bank voles. 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 an increase in traps being sprung causes a decrease in trapping efficiency (because once a trap has already sprung it cannot catch

any more animals), half of a trapping bout was subtracted from the trapping effort for each trap used (Nelson and Clark, 1973).

For the analysis of the movement a non-parametric 2-way Analysis of Variance was used to compare the distance travelled between consecutive captures and the distance travelled per bout between wood mice, bank voles and harvest mice and also between the sexes. A Chi-squared was used to test whether the use of the traps by wood mice, bank voles and harvest mice in Thoresby was random or if they showed a preference for certain trap locations.

The effect of several variables on the probability of catching an animal was tested using generalised mixed linear models using R version 3.5.1 (R Core team, 2018). The error structure was assumed to be binomial and it was fitted by Laplace approximation using the glmer function in R. For the main models the fixed effects fitted were session, elevation, habitat and site. Additional models were used to test the effects of the microhabitat and the habitat characteristics were also fitted as fixed effects. The random effects fitted were the trap location within the grid and the bout.

A Principal Component Analyses (PCA) was carried out using R version 3.5.1 (R Core team, 2018) to reduce all the correlated habitat variables into one or two new variables, which were then used as explanatory variables in the models that analysed the effects of the microhabitat on the probability of catching an animal.

3.

Results

3.1. Overall capture rates

The total sampling effort consisted of 9,887 trap bouts and resulted in 1,446 trapping events, which included harvest mice, wood mice, bank voles, field voles, common shrews and pygmy shrews. Wood mice were caught a total of 1,022 times, making this the most frequently caught species; it was also the only one caught in all sites (Table 3). The second most frequently caught species was the bank vole with 252 total captures, followed by the common shrew with 86, the harvest mouse with 70, the field vole with 9 and lastly the pygmy shrew with 7 (Figure 8).

Overall the habitat with the highest catch per unit effort was the reedbed, followed by the woodland, the pasture and lastly the arable (Figure 8). All the species were caught more times in the reedbed, apart for the wood mouse, which was most frequently caught in the woodland (Figure 8). The harvest mouse, the field vole and the pygmy shrew were caught exclusively in the reedbed (Figure 8). Wood mice and bank voles were caught in every session, with wood mice being the most frequently caught out of all species for all the sessions (Figure 9). Shrews were caught mostly from July onwards and the field vole captures only happened in September and October. Harvest mice were also caught exclusively in the last two months of the study (Figure 9). Throughout the study the catch per unit effort was always at least twice as high in Thoresby than in any other site, with the exception of the last month of the study, when Bestwood was approximately equal to Thoresby (Figure 10)

The trapping in this study was carried out both during the night and during the day, and since most small mammals are mostly active just before dawn and after dusk (Greenwood, 1978; Trout, 1978a; Wolton, 1983). This caused the results to show low values for the catch per unit effort and the probability of capture even when there was an extremely high number of captures recorded in the morning bout.

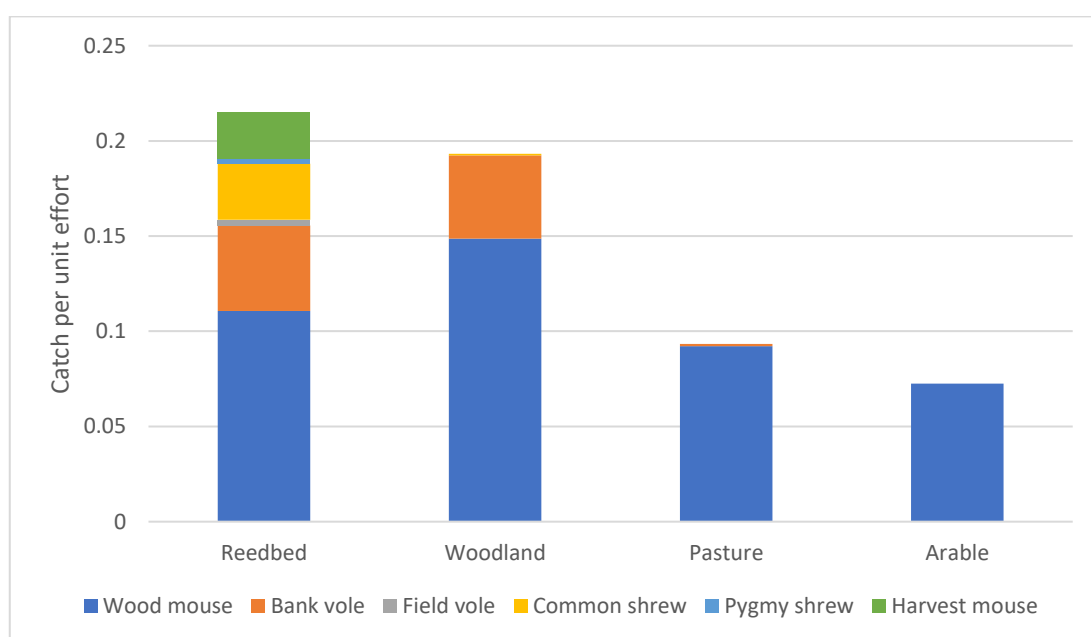


Figure 8: Catch per unit effort of each species caught in the four different habitats.

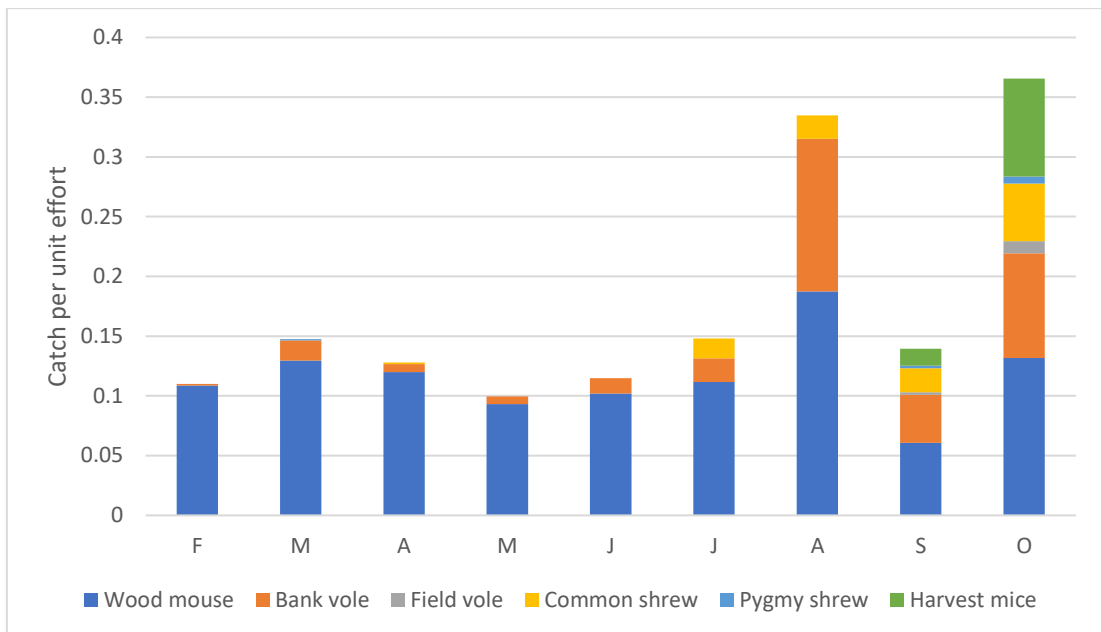


Figure 9: Catch per unit effort of each species caught in each session.

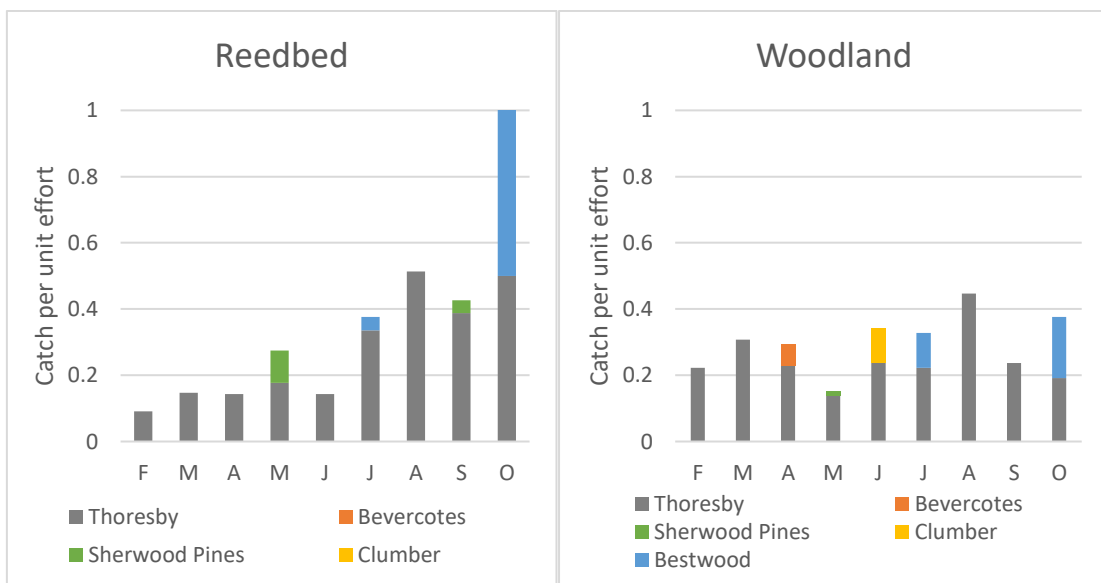


Figure 10: Catch per unit effort of the captures of all the species combined in each month divided by site. Only Thoresby was surveyed in February, March and August. In September the woodland was only surveyed in Thoresby and not in Sherwood.

Table 3: The total number of captures for each species caught in each habitat of the different sites and in brackets is the number of unique individuals caught.

Site	Habitat	Harvest mouse	Wood mouse	Bank vole	Field vole	Common shrew	Pygmy shrew	Total
Thoresby	Arable	0	121 (32)	0	0	0	0	121 (32)
	Pasture	0	170 (20)	2	0	0	0	172 (20)
	Reedbed	38 (13)	284 (55)	95 (22)	7 (2)	65	7	496 (99)
	Woodland	0	369 (71)	103 (27)	0	1	0	473 (98)
	Total	38 (13)	944 (178)	200 (49)	7 (2)	66	7	1262 (249)
Bevercotes	Reedbed	0	0	0	0	0	0	0
	Woodland	0	15 (7)	0	0	0	0	15 (7)
	Total	0	15 (7)	0	0	0	0	15 (7)
Clumber	Arable	0	1 (1)	0	0	0	0	1 (1)
	Reedbed	0	0	0	0	0	0	0
	Woodland	0	4 (1)	12 (4)	0	0	0	16 (5)
	Total	0	5 (2)	12 (4)	0	0	0	17 (6)
Sherwood Pines	Reedbed	0	13 (8)	0	0	0	0	13 (8)
	Woodland	0	3 (1)	0	0	0	0	3 (1)
	Total	0	16 (9)	0	0	0	0	16 (9)
Bestwood	Reedbed	32 (13)	19 (8)	33 (14)	2 (1)	19	0	105 (39)
	Woodland	0	23 (7)	7 (3)	0	1	0	31 (11)
	Total	32 (13)	42 (15)	40 (17)	2 (1)	20	0	136 (50)

3.2. Movement

The movement of individuals was analysed only in Thoresby. The calculation of the total distance travelled between consecutive recaptures and distance per bout only takes into account the movements within any one habitat. The

movements across different habitats were considered separately. Only the harvest mice, wood mice and bank voles were taken into account because they were the other species were either not caught often enough or were impossible to mark.

3.2.1. Distance travelled

Out of the 13 individuals of harvest mice caught in Thoresby, 8 have been caught more than once. The average distance travelled between consecutive recaptures was 10.8 m (± 11.1) and the greatest distance travelled by one individual was 31.6 m.

112 wood mice out of the 178 individuals were caught more than once. This was the species that travelled further. The average distance travelled was 13.7 m (± 12.2) and the maximum distance travelled by one individual was 70 m.

39 out of the 49 individuals of bank voles were caught more than once and they travelled less than both wood mice and harvest mice. The average distance travelled was 9.8 m (± 13.1) and the maximum distance travelled by one individual was 44.7 m.

The average distance travelled between consecutive recaptures by females of harvest mice, wood mice and bank voles combined was 10.3 m (± 10.1) and

the maximum distance travelled by a female was 44.7 m. Males travelled on average 16.4 m (± 14.0) with a maximum of 70.0 m.

The difference between the three species was significant (ANOVA: $F_1 = 10.640$, $P = 0.005$), as was the difference between the sexes (ANOVA: $F_1 = 4.930$, $P = 0.026$). The interaction between the effects of species and of sex was not significant (ANOVA: $F_1 = 4.150$, $P = 0.126$).

3.2.2. Distance per bout

The average distance travelled per bout by harvest mice was 8.0 m (± 9.4) and the maximum distance per bout reached by one individual was 31.6 m.

For wood mice the average distance per bout was 7.3 m (± 7.6) and the maximum distance per bout was 42.4 m.

The average distance per bout travelled by bank voles was 5.7 m (± 8.9) and the maximum distance per bout was 44.7 m.

The average distance per bout travelled by females of harvest mice, wood mice and bank voles combined was 5.5 m (± 6.0) and the maximum was 41.2 m per bout. Males travelled 9.1 m (± 9.4) per bout, with a maximum of 44.7 m per bout.

The difference between the three species was significant (ANOVA: $F_1=7.370$, $P=0.025$). The difference between the sexes was not significant (ANOVA: $F_1=3.780$, $P=0.052$) and neither was the interaction between the effects of species and of sex (ANOVA: $F_1=3.520$, $P=0.172$).

3.2.3. Movement across habitats

30 wood mice were trapped in at least two habitats and all the possible combinations of habitats were represented. Seven individuals were trapped in at least three habitats, out of which only one was caught in all the four habitats.

Nine bank voles were caught in two different habitats and, apart from one that was caught in the pasture and the woodland, for all of them the two habitats were reedbed and woodland. Four out of the eight animals that were trapped in the reedbed and in the woodland, were caught in the woodland first and then in the reedbed, two were caught in the reedbed first and then in the woodland and the remaining two moved back and forth between the habitats.

3.3. Distribution

3.3.1. Harvest mice

In Thoresby Harvest mice showed a significant preference for certain areas of the reedbed (Chi-Squared: $X^2_{(29)} = 80.421$, $P < 0.001$). Plotting the number of captures for each trap on the map of the reedbed in Thoresby shows that they used mostly the area that includes the central portion of the grid and the NE side (Figure 11).

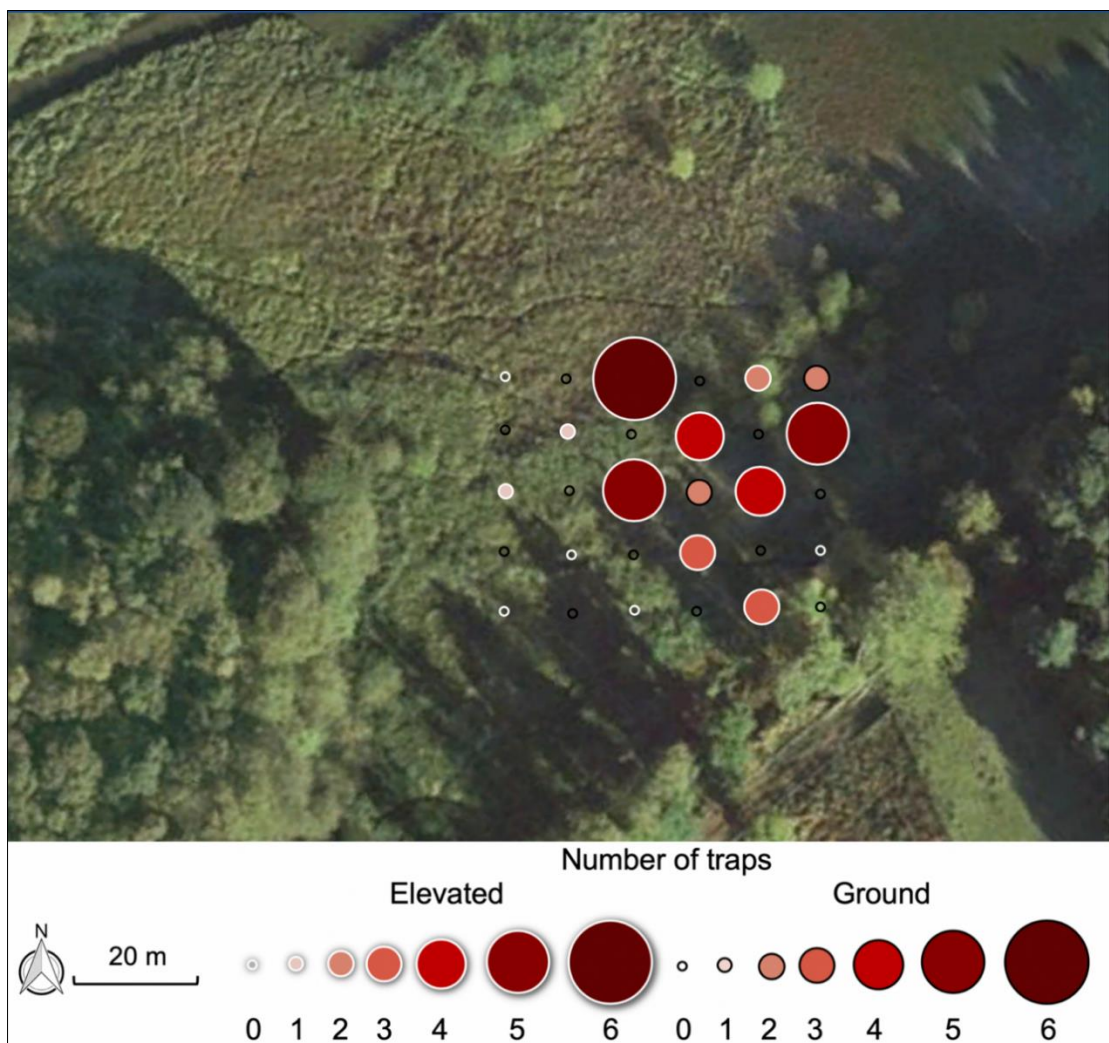


Figure 11: Distribution of harvest mouse captures in the reedbed in Thoresby.

3.3.2. Wood mice

Even though in the reedbed in Thoresby wood mice used all the traps, they showed a significant preference for the ones closer to the edge of the reedbed (Chi-Squared: $X^2_{(29)} = 80.421$, $P < 0.001$) (Figure 12). In the woodland there was a significant preference for the traps in the SW corner of the grid (Chi-Squared: $X^2_{(29)} = 173.683$, $P < 0.001$), which is the side that was closer to the pasture, and only two traps were never used (Figure 13). The captures in the pasture were significantly clustered on the edges of the grid (Chi-Squared: $X^2_{(29)} = 237.647$, $P < 0.001$), 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 (Figure 14). In the arable land there was no significant preference (Chi-Squared: $X^2_{(29)} = 31.479$, $P = 0.343$) (Figure 15).

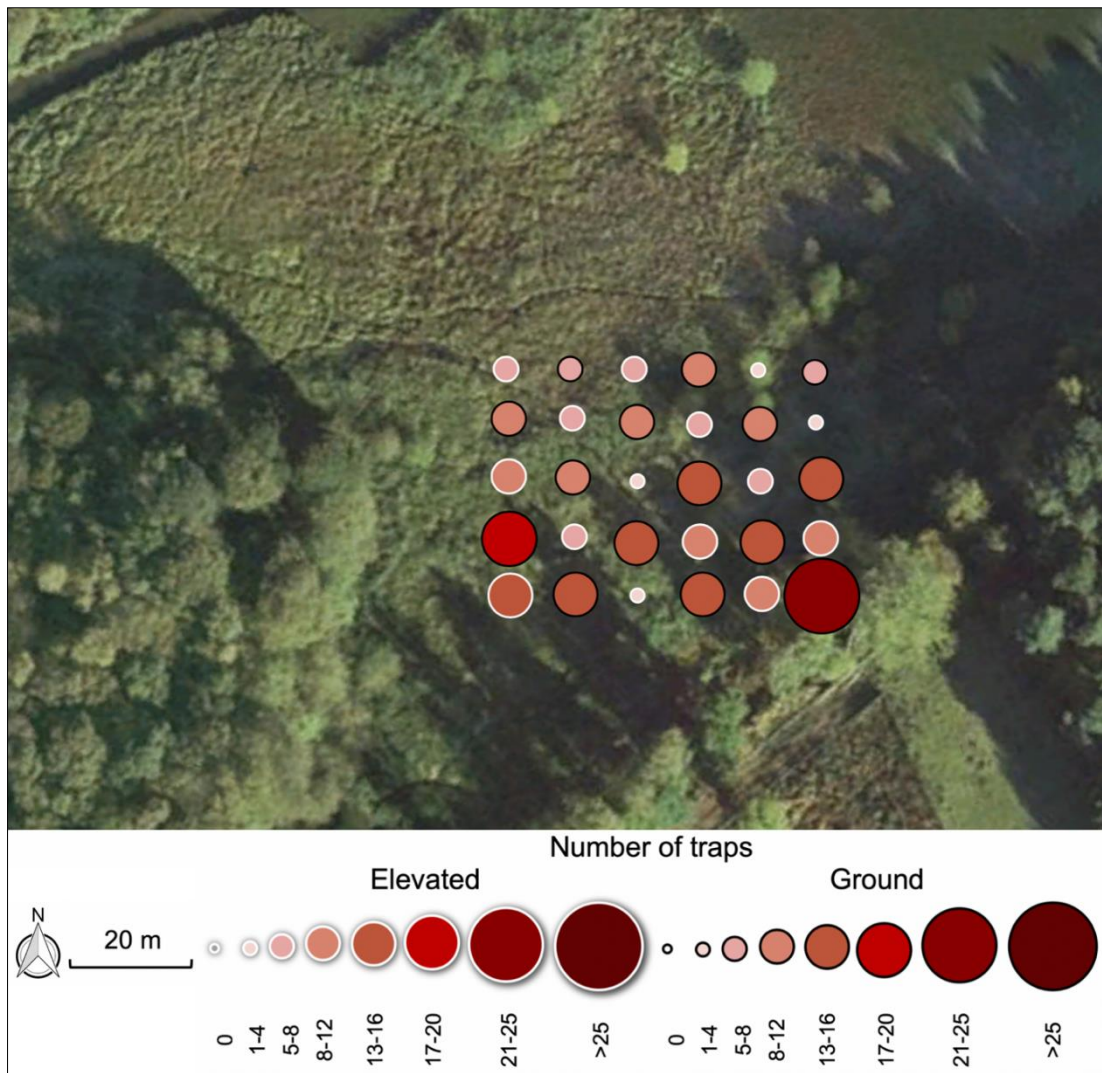


Figure 12: Distribution of wood mouse captures in the reedbed in Thoresby

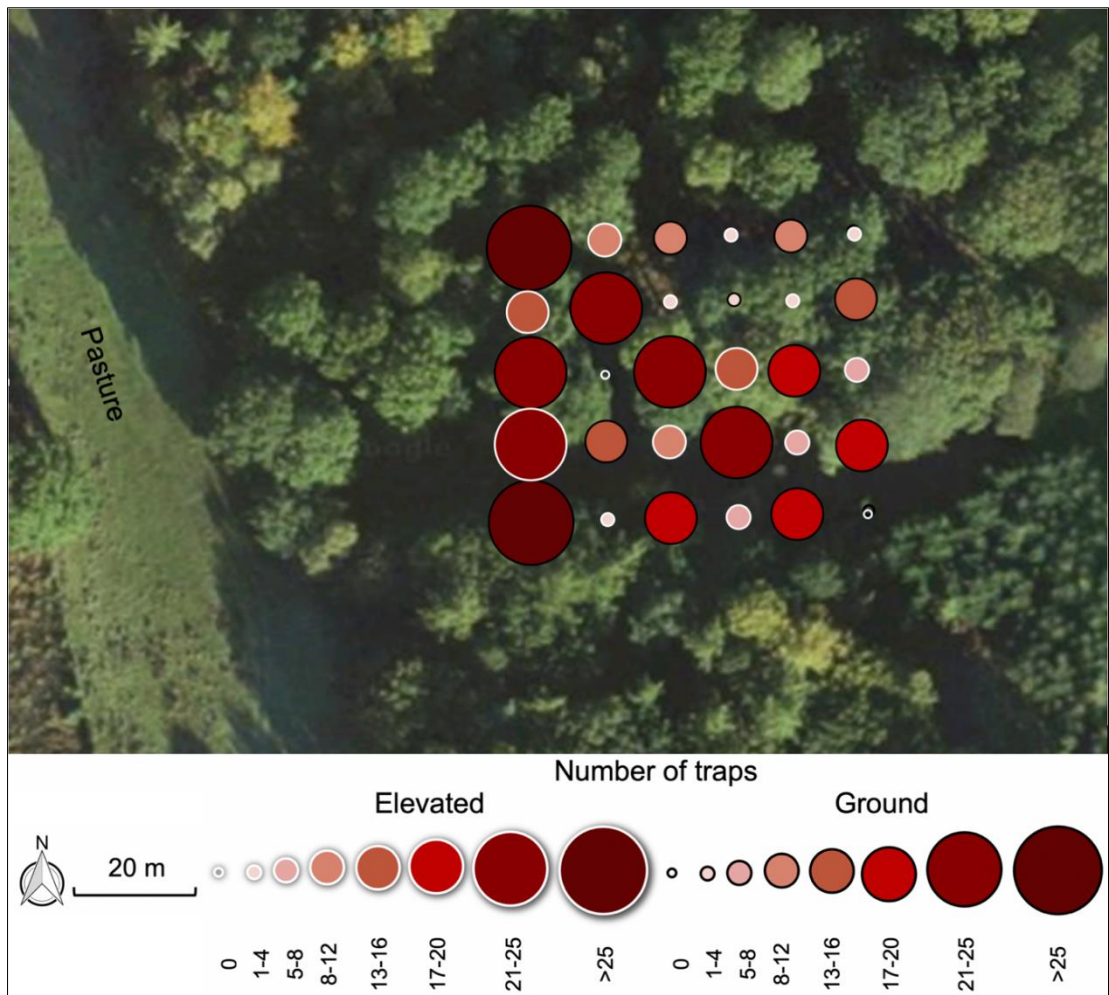


Figure 13: Distribution of wood mouse captures in the woodland in Thoresby

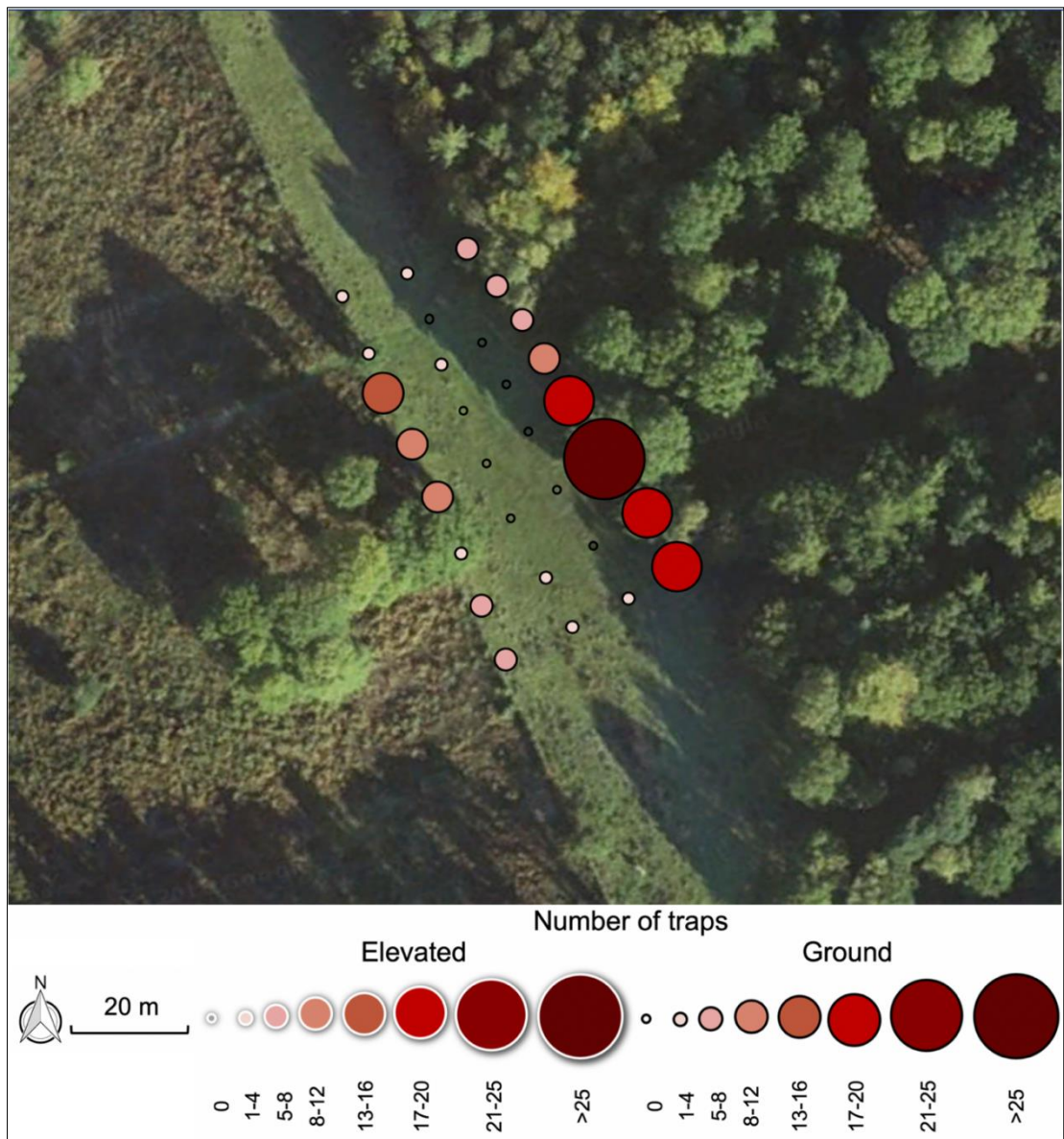


Figure 14: Distribution of wood mouse captures in the pasture in Thoresby

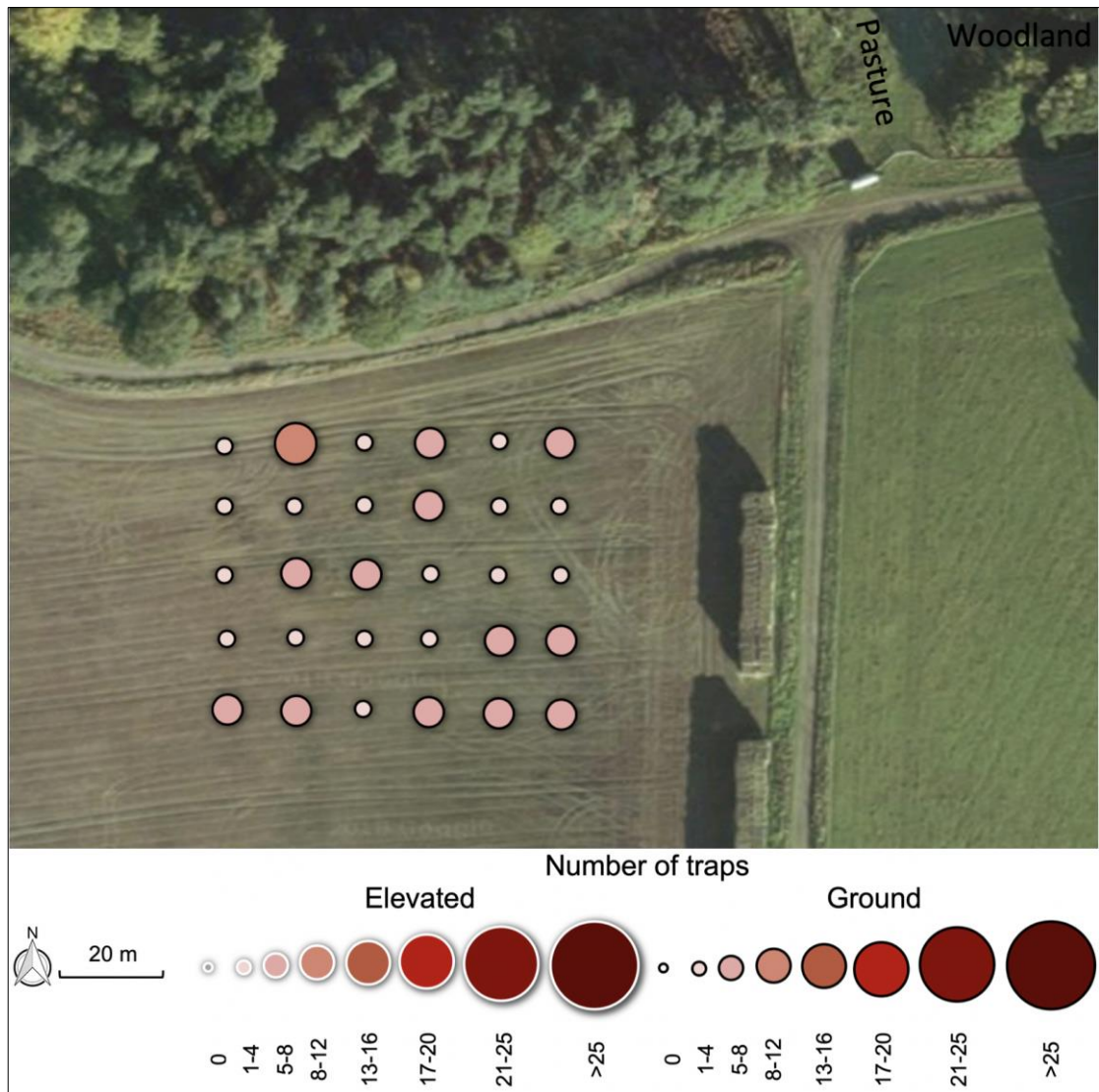


Figure 15: Distribution of wood mouse captures in the arable land in Thoresby

3.3.3. Bank voles

In the reedbed in Thoresby bank voles showed a significant preference for the western half of the grid (Chi-Squared: $X^2_{(29)} = 142.158$, $P < 0.001$) (Figure 16).

In the woodland the captures for this species were significantly clustered in few traps (Chi-Squared: $X^2_{(29)} = 324.864$, $P < 0.001$). The two traps that had

the most captures, located in the northern and central areas of the grid, together amounted to approximately 45% of the total number of captures (Figure 17).

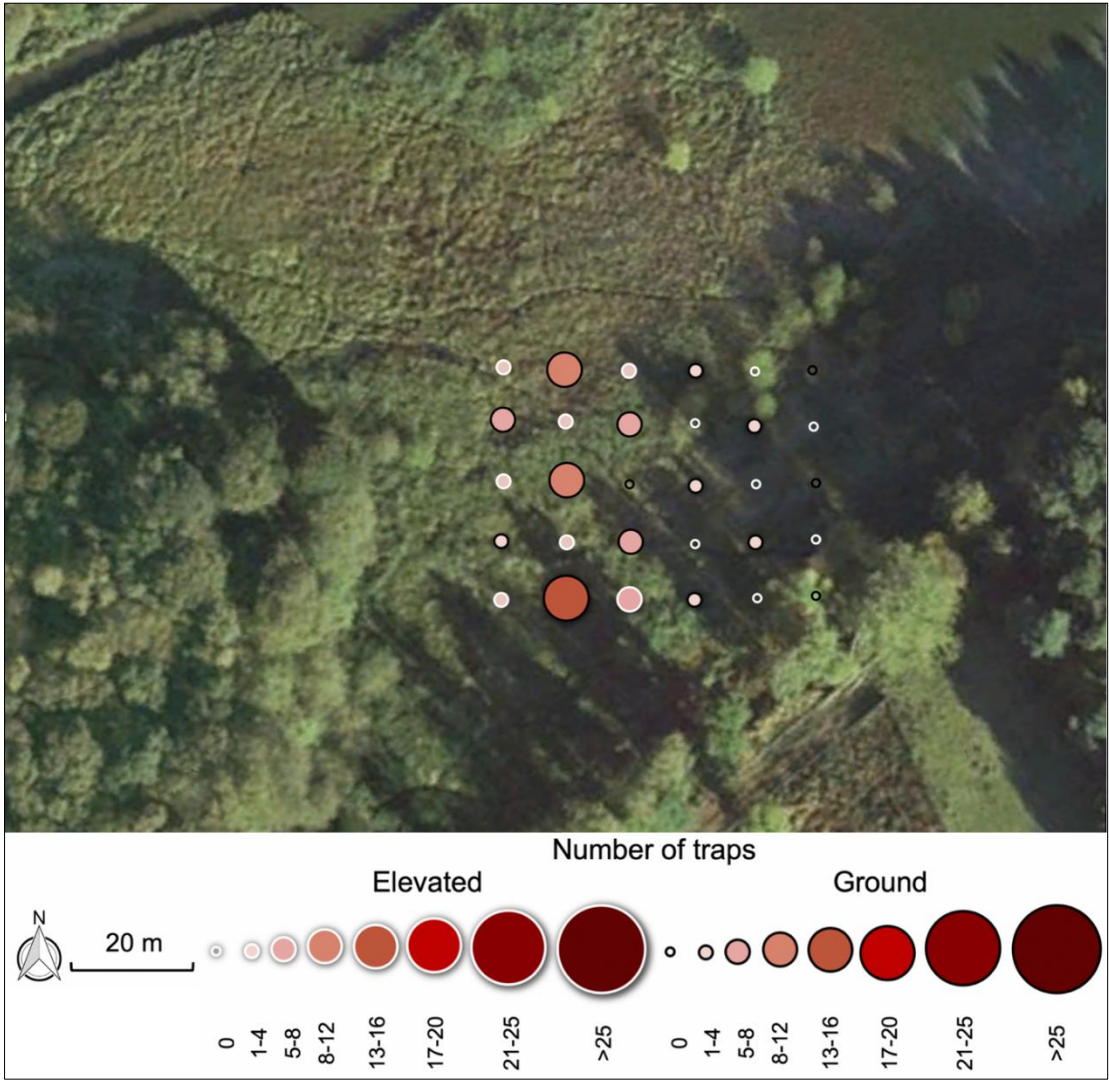


Figure 16: Distribution of bank vole captures in the reedbed in Thoresby

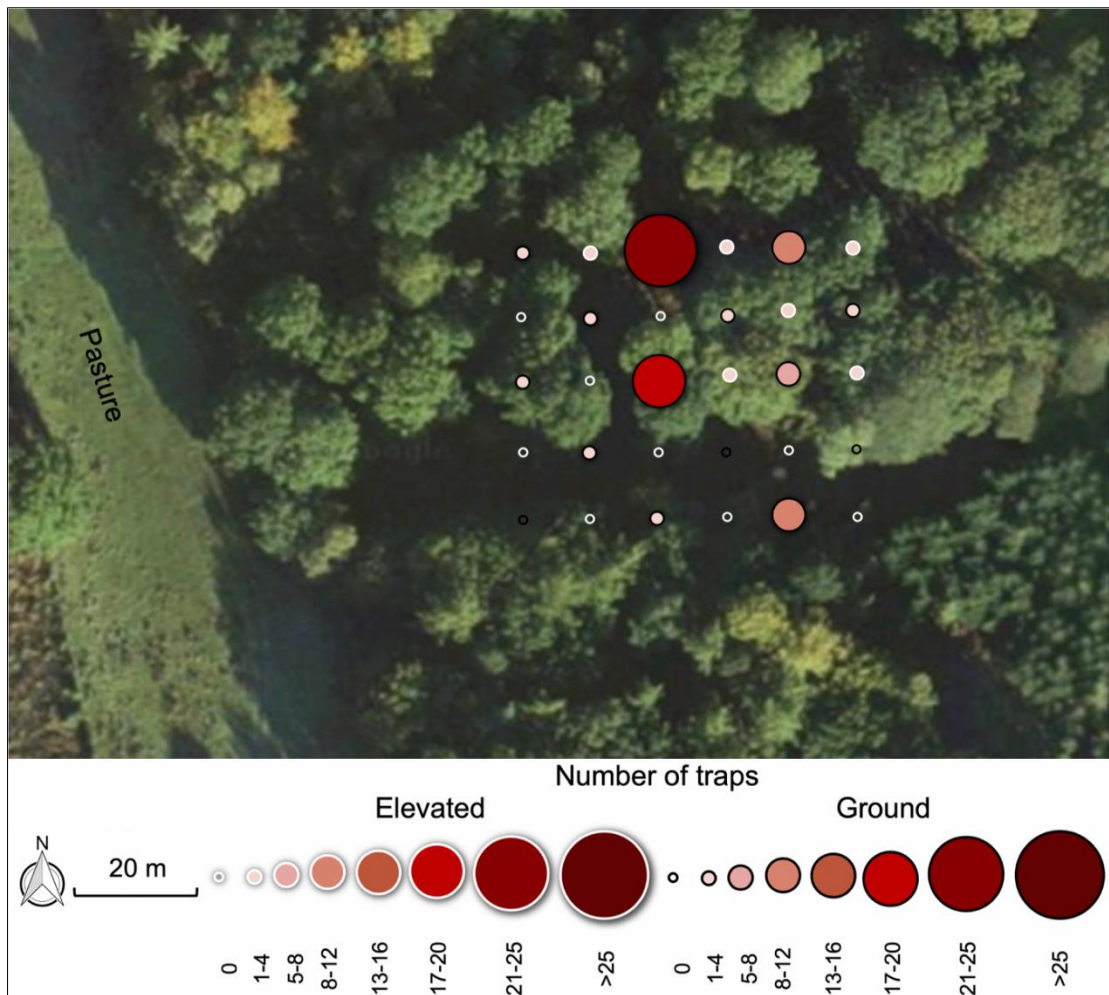


Figure 17: Distribution of bank vole captures in the woodland in Thoresby

3.4. Factors affecting the probability of capture

The factors affecting the probability of capture were calculated twice: first considering only the new individuals caught and then including the recaptures. Since the results of the two analyses were consistent with each other, only the results of the analysis that included the recaptures

3.4.1. Harvest mouse

3.4.1.1. Thoresby

In 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 (Table 3).

When considering all captures (including recaptures) 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 (Table 4). In the elevated traps the probability of catching a harvest mouse is almost ten times higher than in ground traps and in October it was close to double what it was in September (Figure 18).

Table 4: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation and session on the probability of catching a harvest mouse in the reedbed in Thoresby in the September and October sessions.

Term	Df	Change in deviance	P
Elevation	1	11.366	<0.001 ***
Session	1	3.871	0.0491 *
Session x elevation	1	0.690	0.406

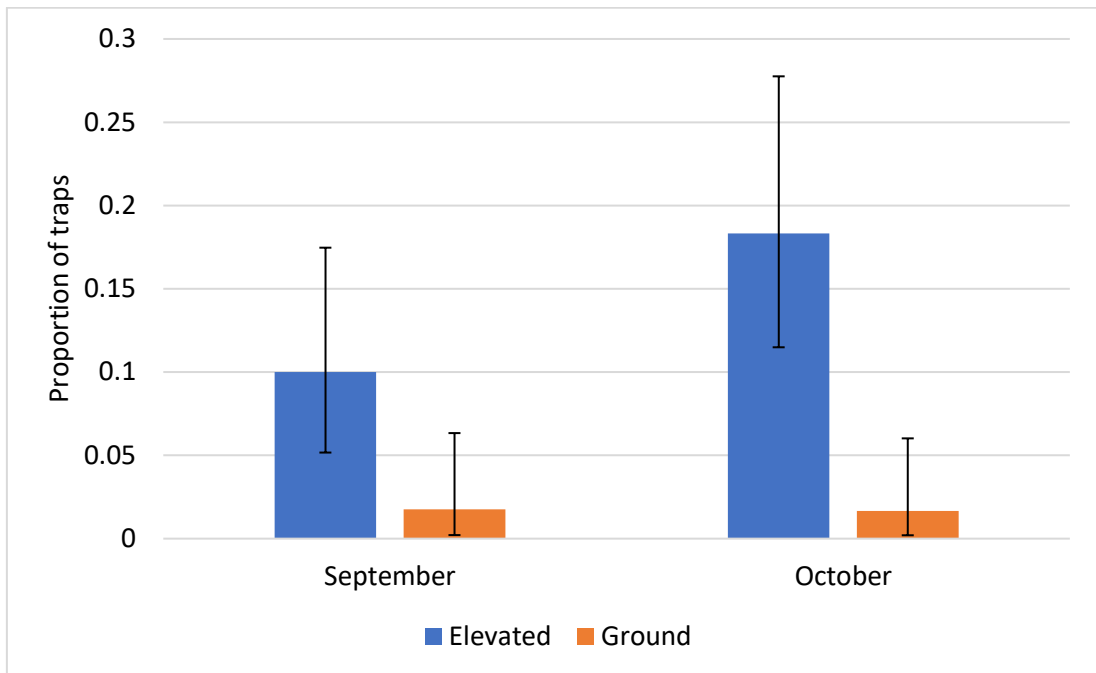


Figure 18: Proportion of elevated and ground traps which caught a harvest mouse during the September and October sessions in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.1.2. Bestwood

The only other site where harvest mice were caught was Bestwood, which was surveyed in July and October. The total number of captures was 32, with 13 unique individuals. Analysing the results for the reedbeds at Bestwood and Thoresby for the two relevant months revealed several significant predictors of harvest mouse captures. The probability of catching a harvest mouse was significantly affected by the session, since no individuals were caught in July, the habitat, since no individuals were caught outside of the reedbed and there was a significant effect of the elevation of the trap, with an almost three-fold

increase in the probability of capture in elevated traps compared to ground traps (Table 5; Figure 19). There was also a significant interaction between the effects of site and elevation since the effect of elevation was much stronger in Thoresby than in Bestwood (Table 5; Figure 19).

Table 5: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session, habitat and site on the probability of catching a harvest mouse in the reedbed and woodland in Bestwood and Thoresby in the October session.

Term	Df	Change in deviance	P
Session	1	89.755	<0.001 ***
Habitat	1	34.693	<0.001 ***
Elevation	1	10.122	0.001 **
Site	1	1.635	0.201
Site x elevation	1	4.909	0.027 *
Session x habitat	1	0	0,999
Site x session	1	0	1
Elevation x session	1	1	0,999
Elevation x habitat	1	0	1
Site x habitat	1	0	0,999

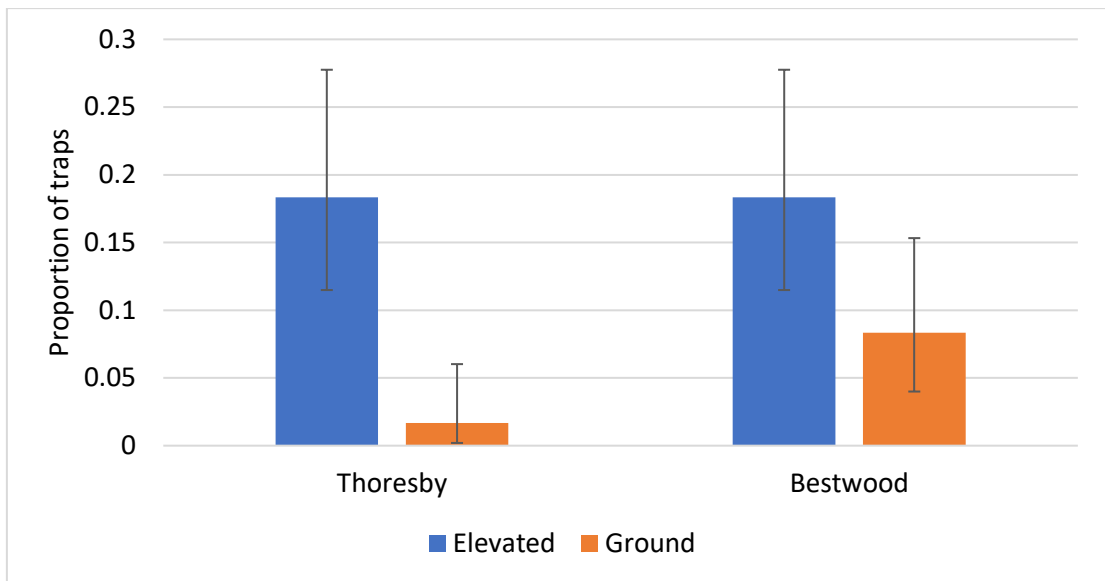


Figure 19: Proportion of elevated and ground traps which caught a harvest mouse during the October session in Thoresby and Bestwood. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.2. Wood mouse

3.4.2.1. Thoresby

In Thoresby the wood mouse was the only species caught in all four habitat types with a total of 944 captures and 178 different individuals. Since the arable and pasture were not surveyed in the last session, it was excluded from the analysis and the probability of catching a wood mouse was significantly affected by the habitat (Table 6). The highest probability was in the woodland, followed by the reedbed, the pasture and lastly the arable (Figure 20). There was a significant effect of elevation, as this species was more likely to be caught on the ground than in elevated traps. 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 and it dropped to less than half of what it was the previous month (Table 6; Figure 20). 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 6). 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 20). The results from analysis of wood mouse captures in only the reedbed and the woodland for all the nine sessions produced very similar results, with the only difference being that habitat did not have a significant effect (Table 7).

Table 6: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session and habitat on the probability of catching a wood mouse in Thoresby. For this model the last session was excluded.

Term	Df	Change in deviance	P
Elevation	1	5.390	0.020 *
Session	7	85.737	<0.001 ***
Habitat	3	46.421	<0.001 ***
Habitat x session	21	179.380	<0.001 ***
Session x elevation	7	63.663	<0.001 ***
Habitat x elevation	2	5.182	0.075 .

Table 7: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session and habitat on the probability of catching a wood mouse in Thoresby. For this model all the sessions were included but only the woodland and the reedbed were considered.

Term	Df	Change in deviance	P
Elevation	1	26.573	<0.001 ***
Session	8	38.094	<0.001 ***
Habitat	1	1.389	0.239
Session x elevation	8	59.569	<0.001 ***
Habitat x session	8	34.499	<0.001 ***
Habitat x elevation	1	2.640	0.104

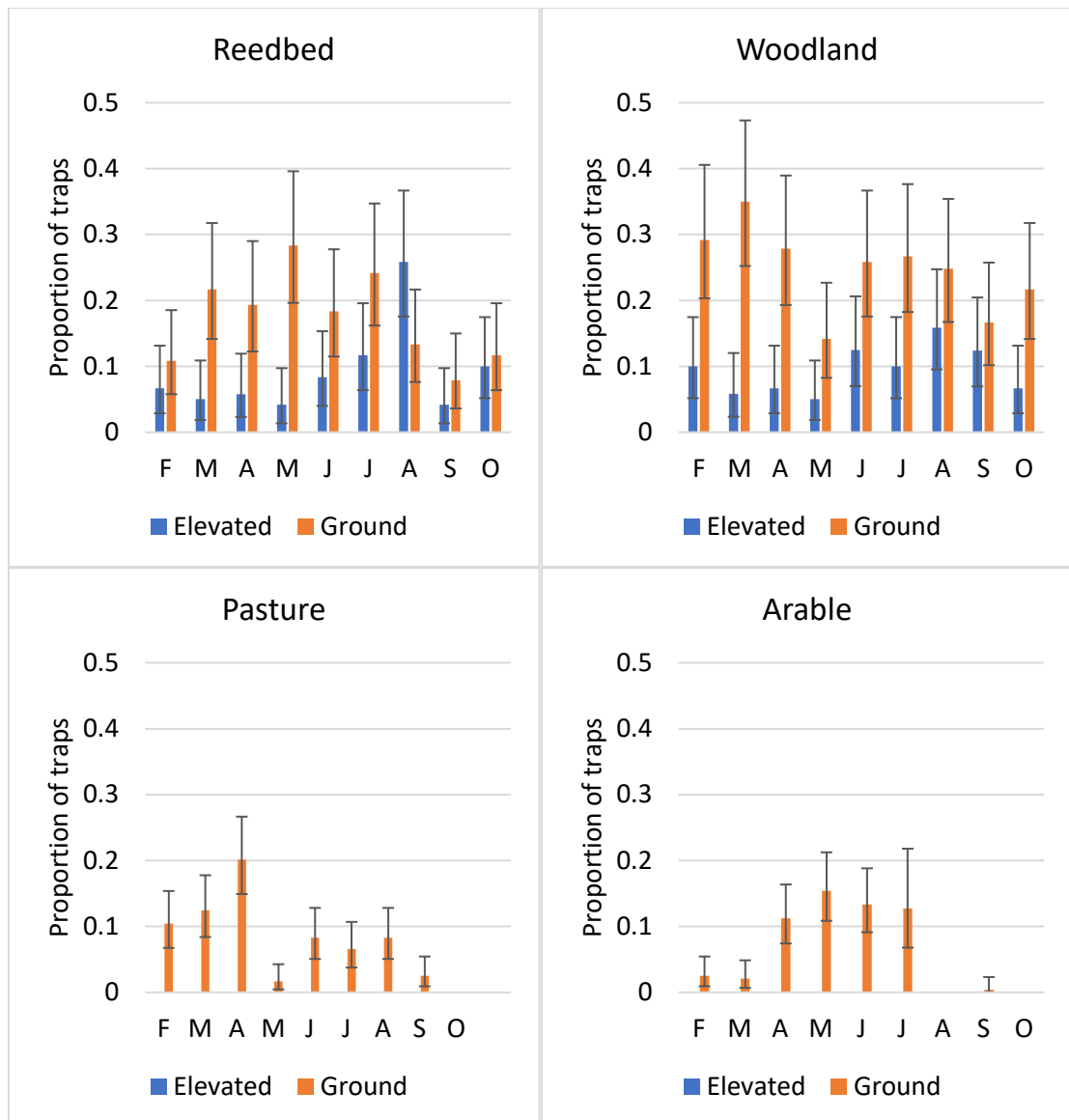


Figure 20: Proportion of elevated and ground traps which caught a wood mouse during each session and in each of the four habitat types in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.2.2. Bevercotes

In April Bevercotes was surveyed as well as Thoresby. The only captures in Bevercotes were in the woodland and they were all wood mice. The

probability of catching a wood mouse was significantly affected by the site, as the probability was much higher in Thoresby than in Bevercotes in the same sessions, and across both sites there was a significant effect of elevation and habitat, with the ground traps and the woodland having a higher probability of capture (Table 8; Figure 21). There was also a significant interaction between the effects of site and habitat (Table 8). Although in both habitats Thoresby had a higher probability of capture than Bevercotes, in the reedbed the difference was more pronounced because in Bevercotes there were no captures at all (Figure 21).

Table 8: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, site and habitat on the probability of catching a wood mouse in Bevercotes and Thoresby in April.

Term	Df	Change in deviance	P
Elevation	1	35.457	<0.001 ***
Site	1	55.187	<0.001 ***
Habitat	1	6.007	0.0142 *
Site x habitat	1	10.233	0.001 **
Site x elevation	1	1.693	0.193
Elevation x habitat	1	1.431	0.232

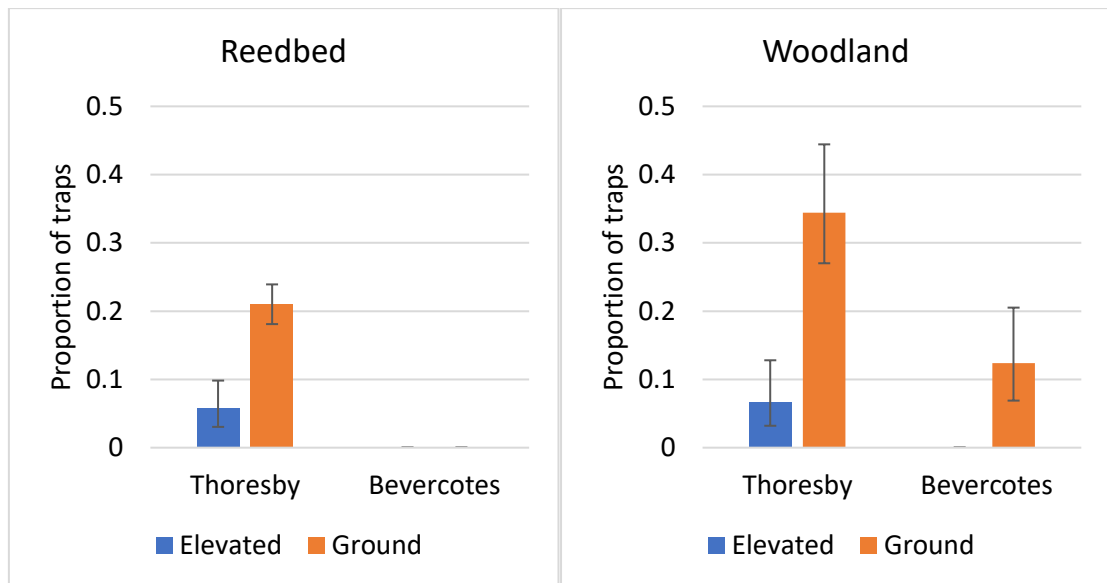


Figure 21: Proportion of elevated and ground traps which caught a wood mouse during the April session in the reedbed and the woodland in Bevercotes and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.2.3. Sherwood Pines

Sherwood Pines was surveyed in May and September. The site had a significant effect on the probability of catching a wood mouse, with Thoresby having double the probability of capture than Sherwood Pines (Table 9; Figure 22). There was a significant effect of habitat, as the probability was higher in the reedbed and of elevation, as the probability was higher in the ground traps. In addition, session had a significant effect, as the probability was higher in September than in May (Table 9;). There was a significant interaction between the effects of site and session because the difference between the probability of capture in Thoresby and in Sherwood pines was

much larger in September than in May (Table 9; Figure 22). The interaction between the effects of elevation and site was also significant due to the fact that, although in Thoresby there were more captures in the ground traps, in Bevercotes there was never a mouse caught in an elevated trap (Table 9; Figure 22). The interaction between elevation and session was also significant.

Table 9: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session, site and habitat on the probability of catching a wood mouse in Sherwood Pines and Thoresby in May and September.

Term	Df	Change in deviance	P
Site	1	89.541	<0.001 ***
Habitat	1	4.810	0.028 *
Elevation	1	35.429	<0.001 ***
Session	1	27.547	<0.001 ***
Site x habitat	1	2.336	0.126
Site x session	1	8.118	0.004 **
Elevation x session	1	6.753	0.009 **
Site x elevation	1	7.364	0.007 **
Session x habitat	1	1.247	0.264
Elevation x habitat	1	0.179	0.672

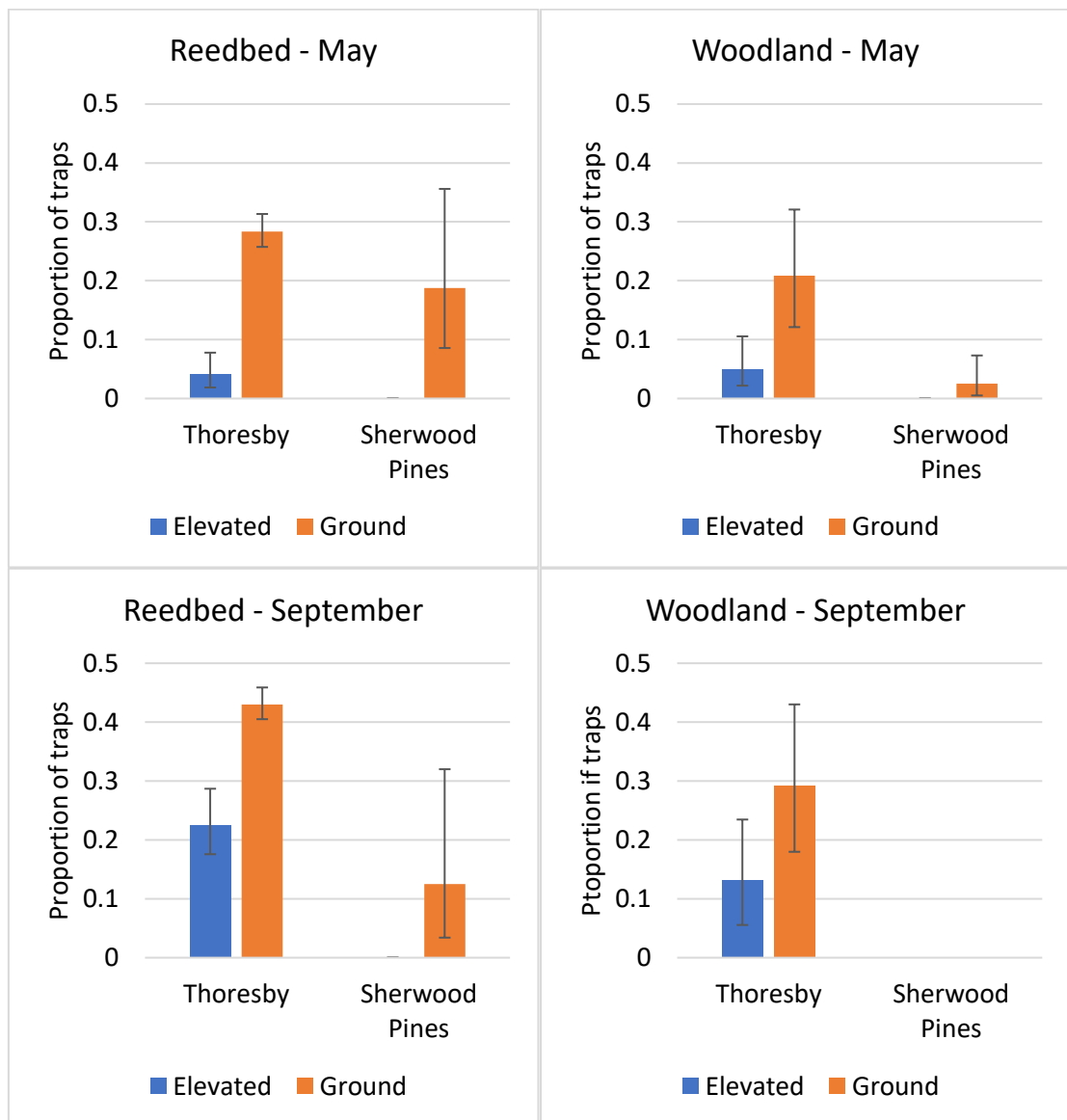


Figure 22: Proportion of elevated and ground traps which caught a wood mouse during the May and September sessions in the reedbed and the woodland in Sherwood Pines and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.2.4. Clumber

Clumber Park was the additional site surveyed in June. The probability of catching a mouse was significantly affected by the elevation of the trap, being approximately twice as high in elevated traps than on the ground ones, and by the habitat, as the reedbed and the arable had a similar probability of capture but it was almost twice as high in the woodland (Table 10; Figure 23). The site also had a significant effect on the probability of capture, which was higher in Thoresby than in Clumber (Table 10; Figure 23). There were no significant interactions between any of the effects (Table 10; Figure 23).

Table 10: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, site and habitat on the probability of catching a wood mouse in Clumber and Thoresby in June.

Term	Df	Change in deviance	P
Site	1	107.190	< 0.001
Elevation	1	6.002	0.014 *
Habitat	2	6.391	0.041 *
Site x habitat	2	1.727	0.422
Site x elevation	1	1.872	0.171
Elevation x habitat	1	0.011	0.915

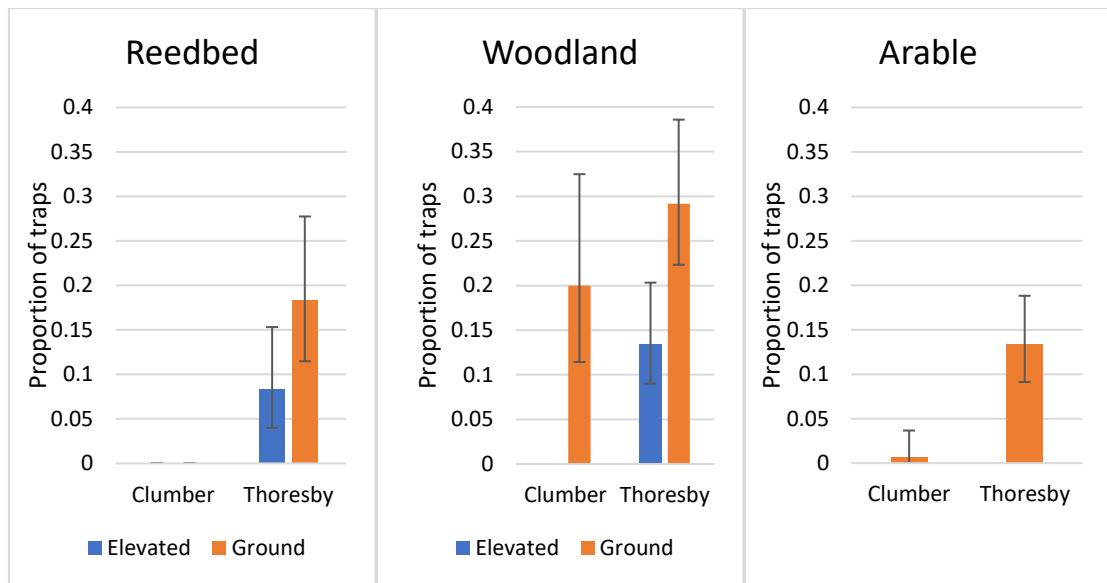


Figure 23: Proportion of elevated and ground traps which caught a wood mouse during the June session in the reedbed, woodland and arable in Clumber and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.2.5. Bestwood

Bestwood was surveyed in July and October. The site had a significant effect on the probability of catching a wood mouse as it was overall higher in Thoresby than in Bestwood. The elevation also had a significant effect, as the probability was higher in the elevated traps (Table 11; Figure 24). Although the effect of the session was not significant, the interaction between the effects of the session and the site was as the increase between July and October was much more pronounced in Bestwood than in Thoresby (Table 11; Figure 24). The effect of habitat was not significant but the interaction between the effects of the habitat and the elevation was, as the difference

between the elevated and the ground traps was much greater in the woodland than in the reedbed (Table 11; Figure 24).

Table 11: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session, site and habitat on the probability of catching a wood mouse in Bestwood and Thoresby in July and October.

Term	Df	Change in deviance	P
Site	1	41.226	<0.001 ***
Elevation	1	27.563	<0.001 ***
Session	1	0.916	0.338
Habitat	1	0.350	0.554
Site x session	1	16.924	<0.001 ***
Elevation x habitat	1	4.871	0.027 *
Site x elevation	1	0.049	0.824
Session x habitat	1	0.674	0.411
Elevation x session	1	1.805	0.179
Site x habitat	1	0.524	0.469

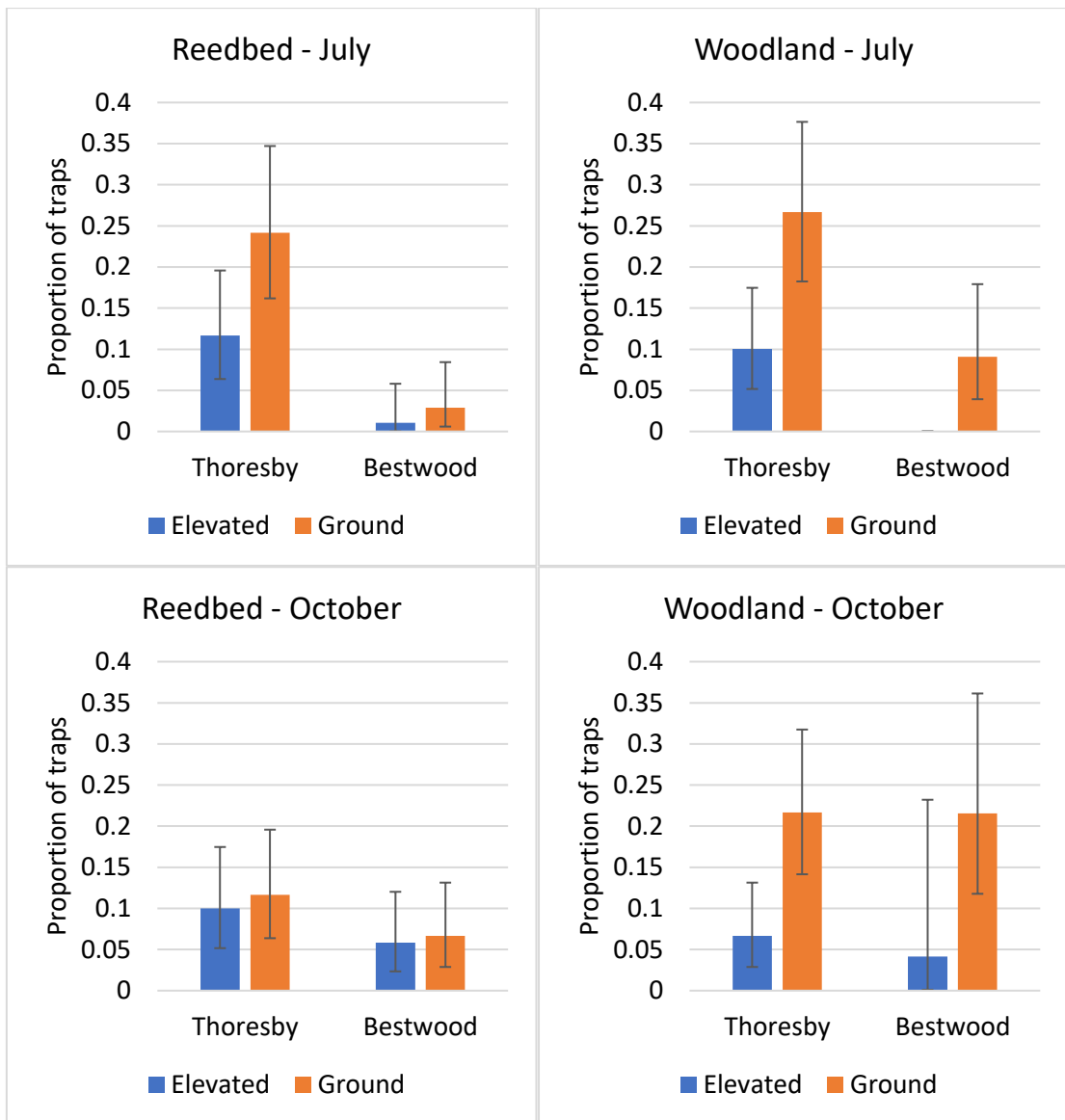


Figure 24: Proportion of elevated and ground traps which caught a wood mouse during the July and October session in the reedbed, woodland and arable in Bestwood and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.3. Bank voles

3.4.3.1. Thoresby

In Thoresby, excluding the last session, there was a significant effect of session, habitat and elevation on the probability of catching a bank vole (Table 12). August had a very high capture probability, almost twice the probability of the second highest session, which was October, then followed by September (Figure 25). 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 25). 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 the one in the woodland, with the exception of August, when the two habitats had an almost identical probability (Figure 25). The analysis of the reedbed and the woodland for all nine sessions confirmed the same results, and showed that the probability of capture is not significantly different between these two habitats.

Table 12: Generalised linear mixed effects model (lmer, link function = binomial) for the effects of elevation, session and habitat on the probability of catching a bank vole in Thoresby. For this model the last session was excluded.

Term	Df	Change in deviance	P
Session	7	233.520	<0.001 ***
Habitat	3	47.201	<0.001 ***
Elevation	1	19.733	<0.001 ***
Habitat x session	21	64.695	<0.001 ***
Session x elevation	7	9.540	0.216
Habitat x elevation	2	0.069	0.966

Table 13: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session and habitat on the probability of catching a bank vole in Thoresby. For this model all the sessions were included but only the reedbed and the woodland were considered.

Term	Df	Change in deviance	P
Session	8	228.450	<0.001 ***
Elevation	1	18.207	<0.001 ***
Habitat	1	0.186	0.667
Habitat x session	8	68.528	<0.001 ***
Session x elevation	8	11.796	0.160
Habitat x elevation	1	0.015	0.901

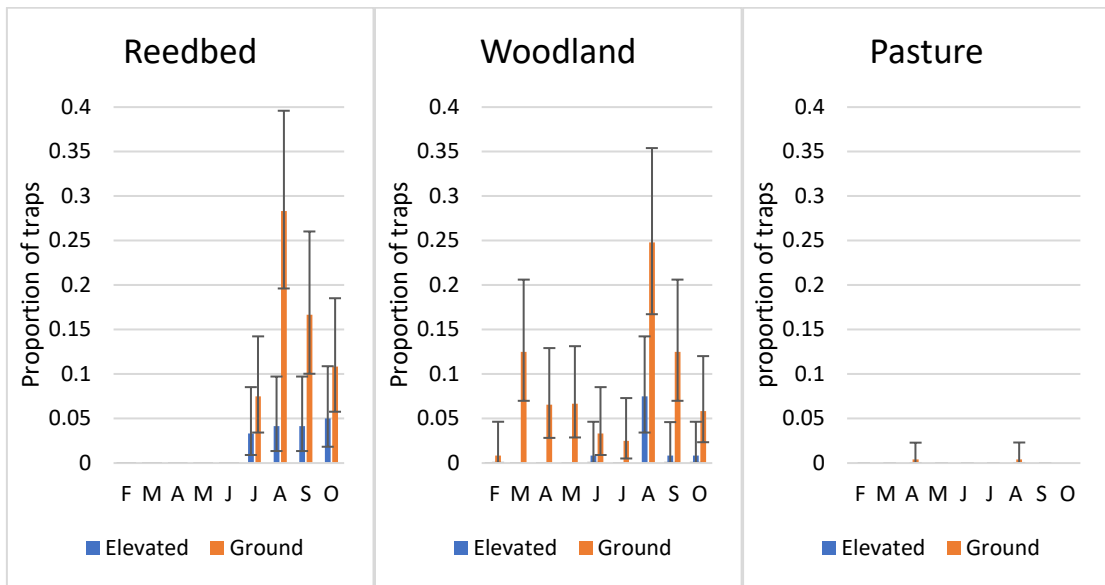


Figure 25: Proportion of elevated and ground traps which caught a bank vole during the different sessions in the reedbed, woodland and pasture in Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.3.2. Clumber

Clumber Park was surveyed in June. The probability of catching a bank vole was significantly affected by the site only (Table 14). There were very few captures in either site but the probability was almost four times higher in Clumber than it was in Thoresby (Figure 26).

Table 14: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, site and habitat on the probability of catching a bank vole in Clumber and Thoresby in April.

Term	Df	Change in deviance	P
Site	1	4.861	0.027 *
Elevation	1	0.104	0.747
Habitat	2	3.714	0.156
Site x elevation	1	3.346	0.067 .
Site x habitat	2	0	1
Elevation x habitat	1	0	1

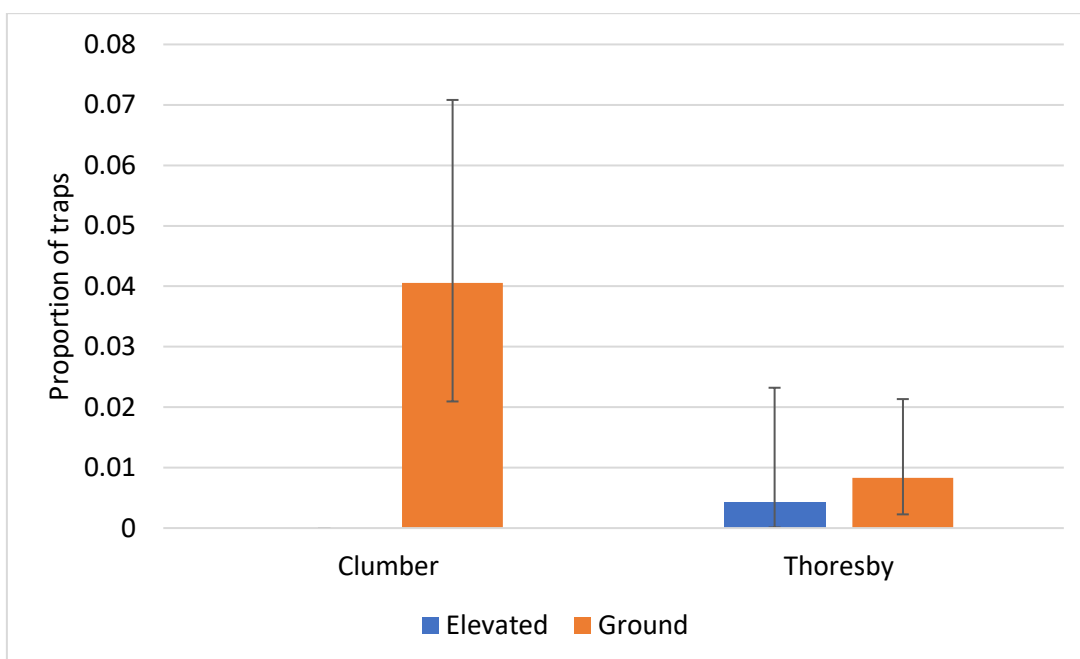


Figure 26: Proportion of elevated and ground traps which caught a bank vole during the June session in the woodland in Clumber and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.4.3.3. Bestwood

Bestwood was surveyed in July and October. The probability of catching a bank vole was significantly affected by the month as there were over twice as many captures in October than in July (Table 15, Figure 27). Elevation had a significant effect on the probability of capture, with the ground traps being much more successful than the elevated ones (Table 15, Figure 27). In the reedbed the probability was over twice as high as in the woodland and this was a significant difference (Table 15, Figure 27). There was also a significant interaction between the effects of site and elevation: although in both sites the ground traps had a higher probability of capture, in Thoresby there were some captures in the elevated traps, while in Bestwood the probability in the elevated traps was zero (Table 15, Figure 27). The interaction between the effects of site and month was also significant as in July the probability of capture was slightly higher in Thoresby, while in October the probability was almost twice as high in Bestwood as it was in Thoresby (Table 15, Figure 27).

Table 15: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing the effects of elevation, session, site and habitat on the probability of catching a bank vole in Bestwood and Thoresby in July and October.

Term	Df	Change in deviance	P
Session	1	19.918	8.084e-06 ***

Elevation	1	28.986	7.291e-08 ***
Habitat	1	9.0385	0.002644 **
Site	1	0.4524	0.5012
Site x elevation	1	18.824	1.433e-05 ***
Site x session	1	7.5562	0.005981 **
Session x habitat	1	2.8938	0.08892 .
Elevation x session	1	0.0312	0.8598
Elevation x habitat	1	1.2853	0.2569
Site x habitat	1	0.518	0.4717

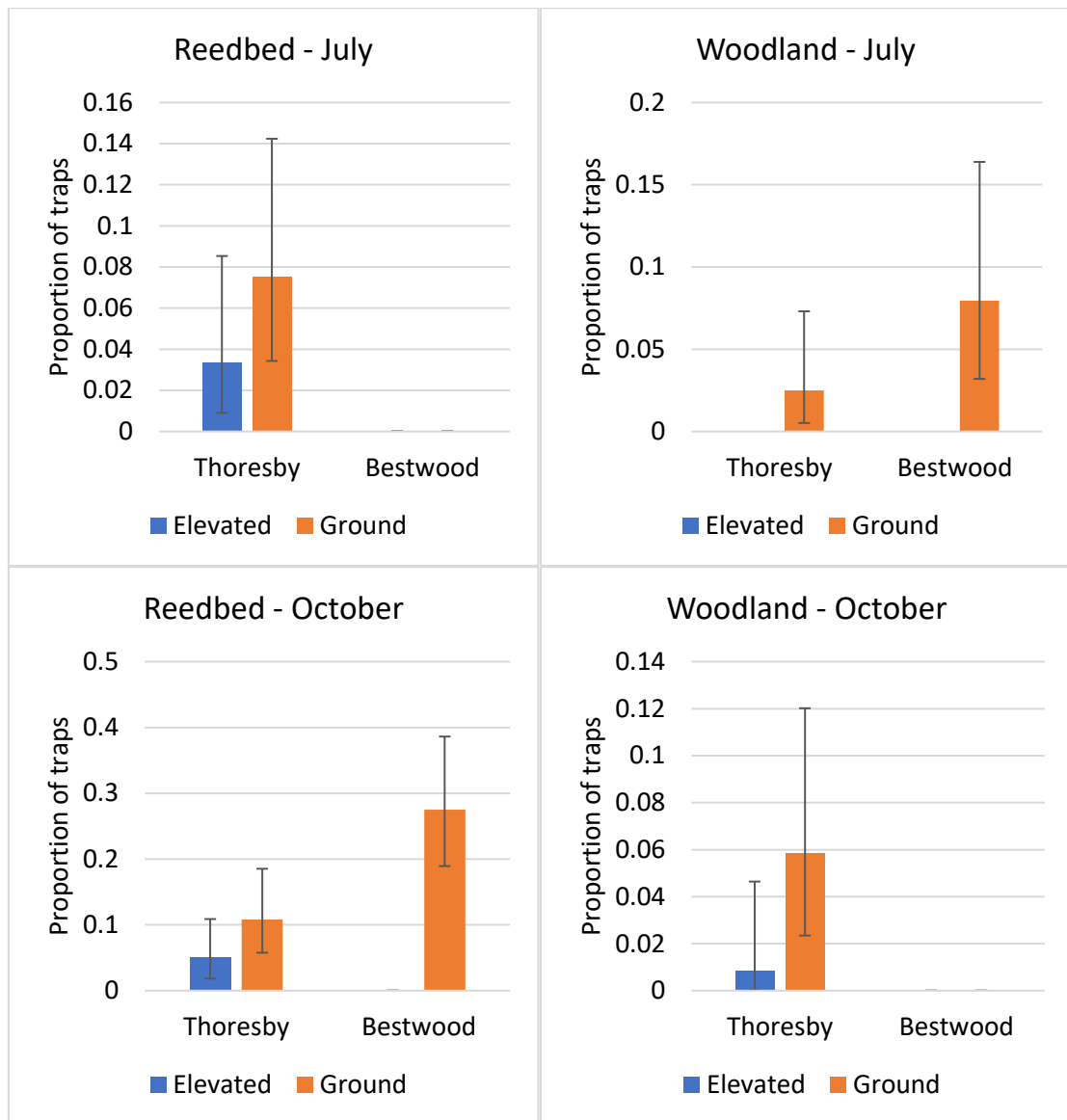


Figure 27: Proportion of elevated and ground traps which caught a bank vole during the July and October sessions in the reedbed and woodland in Bestwood and Thoresby. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5. Habitat factors affecting the probability of capture

This section looks at the effect of microhabitat characteristics on the probability of capture and since these are not comparable between habitats, a separate analysis is carried out for each habitat. A principal component analysis (PCA) was done in order to collapse the variables into two components, or one when possible. The effect of the habitat factors on the probability of capture of harvest mice was analysed in both the sites where this species was trapped, while for the other species only the data from Thoresby were analysed. In Thoresby the initial analysis reflected the seasonality of the habitat because the PCA assigned a score for the characteristics of each trap location in a specific session. In order to have a representation of the microhabitat of each trap location compared to the rest of the grid, the PCA was repeated for this habitat, and this time the average characteristics of the trap locations across the sessions were used instead. The following models include the factors analysed in the previous sections but, since the results for those factors are consistent with what the previous models showed, they will not be repeated in this section.

3.5.1. Reedbed

3.5.1.1. Harvest mice

3.5.1.1.1. Thoresby

In the reedbed in Thoresby the PCA yielded two components worth analysing: component 1 correlated positively with the height of the vegetation, the reed stem diameter and the water level; component 2 had a strong positive correlation to the density of reed stems, a weaker one to the height of the vegetation and a negative correlation to the reed stem diameter and water level.

The analysis of the data from the reedbed in Thoresby showed that there is a significant effect of component 1 on the probability of catching a harvest mouse, as harvest mice being caught more frequently in the traps with a higher score for reed height, stem diameter and water level (Table 16; Figure 28).

Table 16: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a harvest mouse in the reedbed in Thoresby.

Term	Df	Change in deviance	P value
Elevation	1	11.482	<0.001 ***
Session	8	130.190	<0.001 ***

Component 1	1	7.545	0.006018 **
Component 2	1	3.453	0.06313 .
Session x elevation	8	0.469	0.9999
Session x Component 2	8	2.734	0.9499
Session x Component 1	8	1.482	0.993
Elevation x Component 1	1	0.641	0.4235
Component 1 x Component 2	1	1.703	0.1919
Elevation x Component 2	1	0.026	0.8723

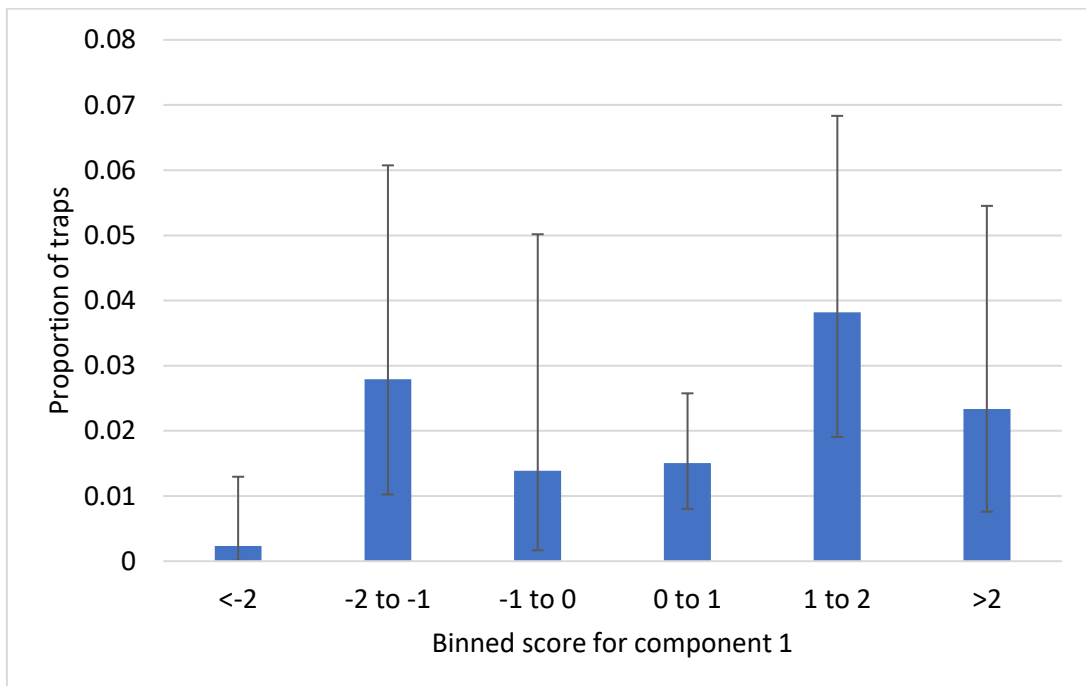


Figure 28: Proportion of traps which caught a harvest mouse during all the sessions in the reedbed in Thoresby. The captures are plotted against their score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.1.1.2. Bestwood

In the reedbed in Bestwood and Thoresby component 1 correlated positively with the height of the vegetation, the diameter of the reed stems and the water level and negatively with the density of reed stems. Component 2 correlated positively with the height of the vegetation and negatively with the water level.

The analysis of the data for Bestwood and Thoresby in July and October showed that the probability of catching a harvest mouse in the reedbed was significantly affected by component 2, as this species was only caught in traps that scored above -1 but mostly between -1 and 0 (Table 17, Figure 29).

There was also a significant interaction between the effects of site and of component 2 as the probability of capture in Thoresby was higher in the traps that scored above 0 than in those that scored between -1 and 0 (Table 17, Figure 29).

Table 17: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a harvest mouse in the reedbed in Bestwood and Thoresby in July and October.

Term	Df	Change in deviance	P value
Session	1	86.211	<0.001 ***
Elevation	1	10.122	0.001 **
Component 2	1	0.816	0.036 *

Site	1	2.077	0.150
Component 1	1	0.454	0.500
Site x component 2	1	6.215	0.013 *
Site x session	1	0	0.999
Site x elevation	1	2.563	0.109
Session x elevation	1	0	0.999
Session x Component 2	1	0	0.999
Elevation x Component 1	1	0.013	0.909
Elevation x Component 2	1	0.173	0.678
Session x Component 1	1	0	0.999
Component 1 x Component 2	1	0.201	0.654
Site x Component 1	1	0.896	0.344

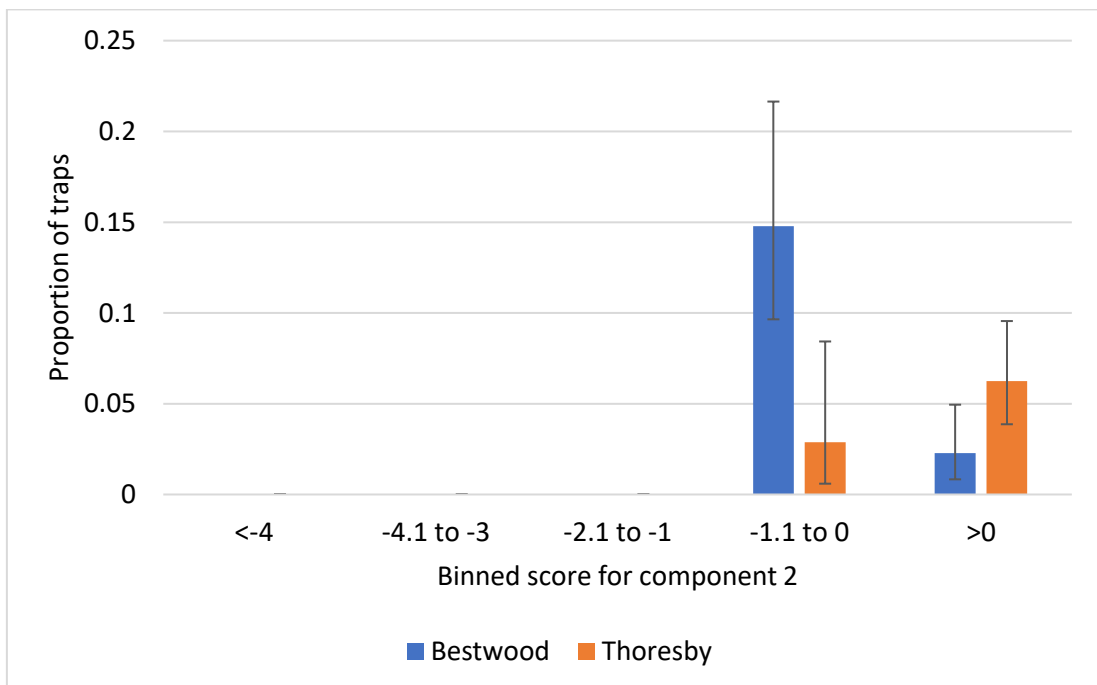


Figure 29: Proportion of traps which caught a harvest mouse during the September and October sessions in the reedbed in Bestwood and Thoresby.

The captures are plotted against their score for component 2, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.1.2. Wood mice

The probability of catching wood mice in the reedbed in Thoresby was significantly affected by component 1 (Table 18). There were more captures in the traps with a low score for reed height, stem diameter and water level (Figure 30). In addition, there was a significant interaction between the effect of component 2 and both the effects of session and elevation (Table 18). Most ground traps had a higher probability of capture than the elevated ones, especially the ones with the lowest score for reed density and height, with the exception of the traps with the highest score, where the captures only happened in the elevated traps (Figure 31). The effect of component 2 changed in every session but the most apparent result is that in June, July and August there was an increase in the captures in the traps with the highest score for reed density and height (Figure 32).

Table 18: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a wood mouse in the reedbed in Thoresby.

Term	Df	Change in deviance	P value
------	----	--------------------	---------

Elevation	1	12.670	<0.001 ***
Session	8	41.993	<0.001 ***
Component 1	1	4.208	0.040 *
Component 2	1	0.386	0.534
Session x Component 2	8	19.389	0.013 *
Session x elevation	8	71.491	<0.001 ***
Elevation x Component 2	1	4.442	0.036 *
Session x Component 1	8	4.113	0.847
Elevation x Component 1	1	2.067	0.150
Component 1 x Component 2	1	3.101	0.078 .

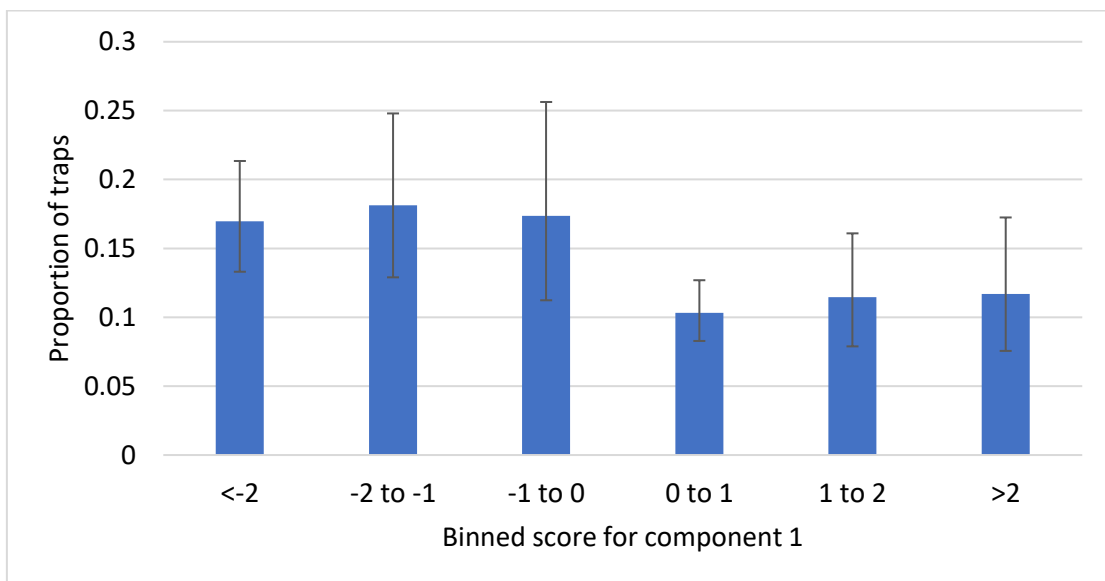


Figure 30: Proportion of traps which caught a wood mouse in the reedbed in Thoresby. The captures are plotted against their score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

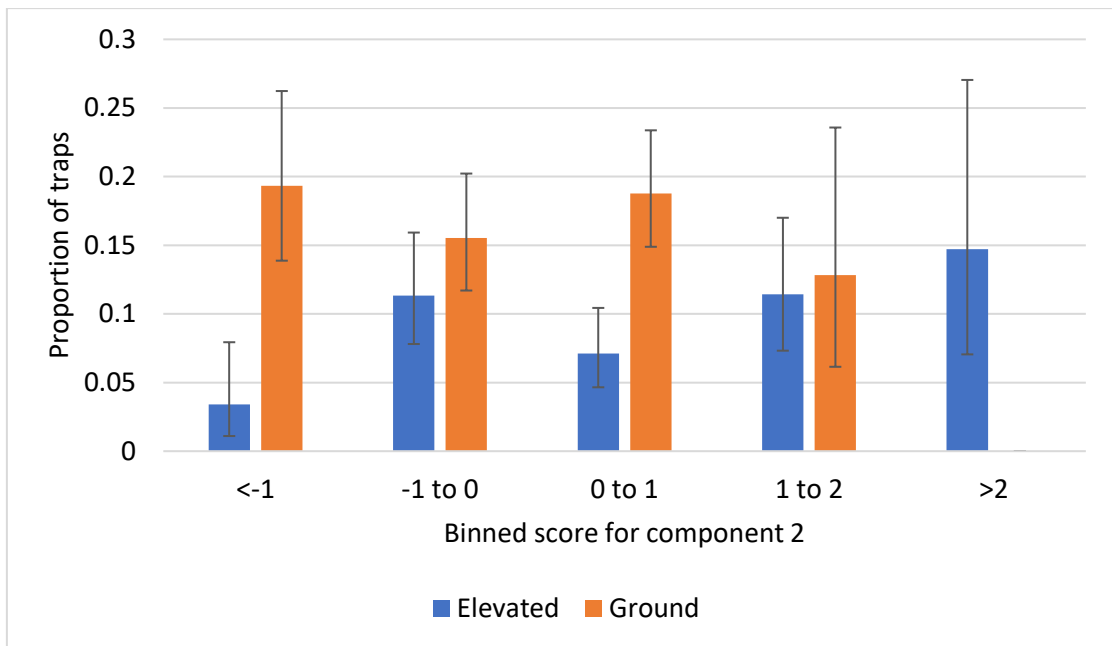


Figure 31: Proportion of elevated and ground traps which caught a wood mouse in the reedbed in Thoresby. The captures are plotted against their score for component 2, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

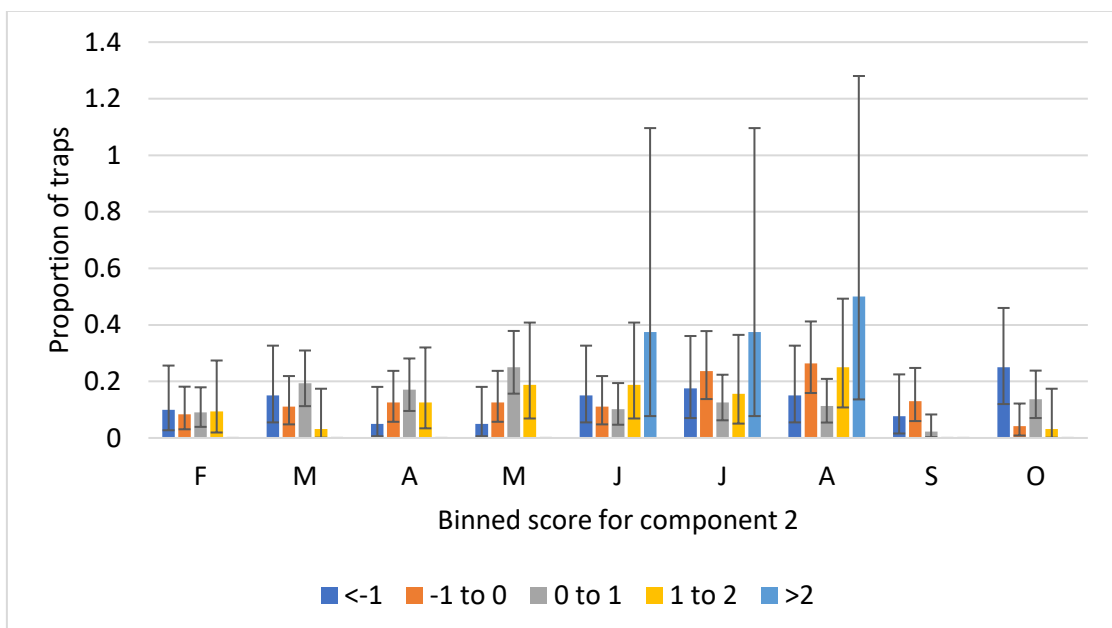


Figure 32: Proportion of traps which caught a wood mouse during each

session in the reedbed in Thoresby. The different coloured bars show the score for component 2, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.1.3. Bank vole

In the reedbed in Thoresby the probability of catching a bank vole was not significantly affected by component 1 or component 2 and there were no significant interactions between any of the effects (Table 19).

Table 19: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a bank vole in the reedbed in Thoresby.

Term	Df	Change in deviance	P value
Elevation	1	8.583	<0.001 ***
Session	8	202.180	<0.001 ***
Component 1	1	1.765	0.184
Component 2	1	0.057	0.812
Session x Component 2	8	0.412	0.999
Session x elevation	8	10.090	0.259
Elevation x Component 2	1	0.025	0.873
Session x Component 1	8	2.436	0.966

Elevation x Component 1	1	3.348	0.067 .
Component 1 x Component 2	1	1.020	0.313

3.5.2. Woodland

In the woodland in Thoresby component 1 correlated positively with the height of the understory and the distance to the nearest tree and negatively with the canopy cover. Component 2 correlated positively with the height of the understory and the canopy cover and negatively with the ground cover and the distance to the nearest tree.

3.5.2.1. Wood mice

In Thoresby the probability of catching a wood mouse in the woodland was not significantly affected by component 1 or 2 but there was a significant interaction between the effect of component 1 and both the session and the elevation of the traps (Table 20). The effect of component 1 was different for each session (Figure 33). The effect of elevation was very strong for the traps with a low score as the elevated traps that scored below one had a probability of capture that was less than half that of the ground traps. The effect was weaker for the traps that scored between one and four and was reversed for the ones that scored above four (there were no captures in ground traps with that score) (Table 20; Figure 34).

Table 20: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a wood mouse in the woodland in Thoresby.

Term	Df	Change in deviance	P value
Session	7	25.483	<0.001 ***
Elevation	1	14.871	<0.001 ***
Component 1	1	1.697	0.193
Component 2	1	0.877	0.3489
Session x component 1	7	30.106	<0.001 ***
Session x elevation	7	23.086	0.002 **
Elevation x component 1	1	4.852	0.028 *
Comp1 x component 2	1	0.412	0.521
Session x component 2	7	9.548	0.216
Elevation x component 2	1	1.567	0.211

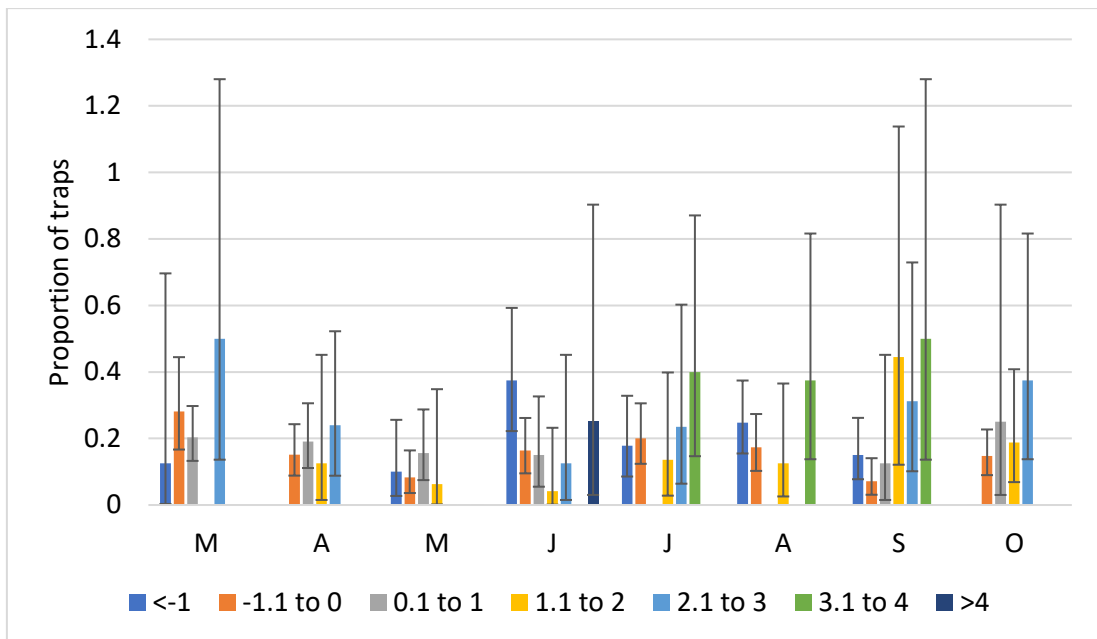


Figure 33: Proportion of traps which caught a wood mouse during each session in the woodland in Thoresby. The different coloured bars show the score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

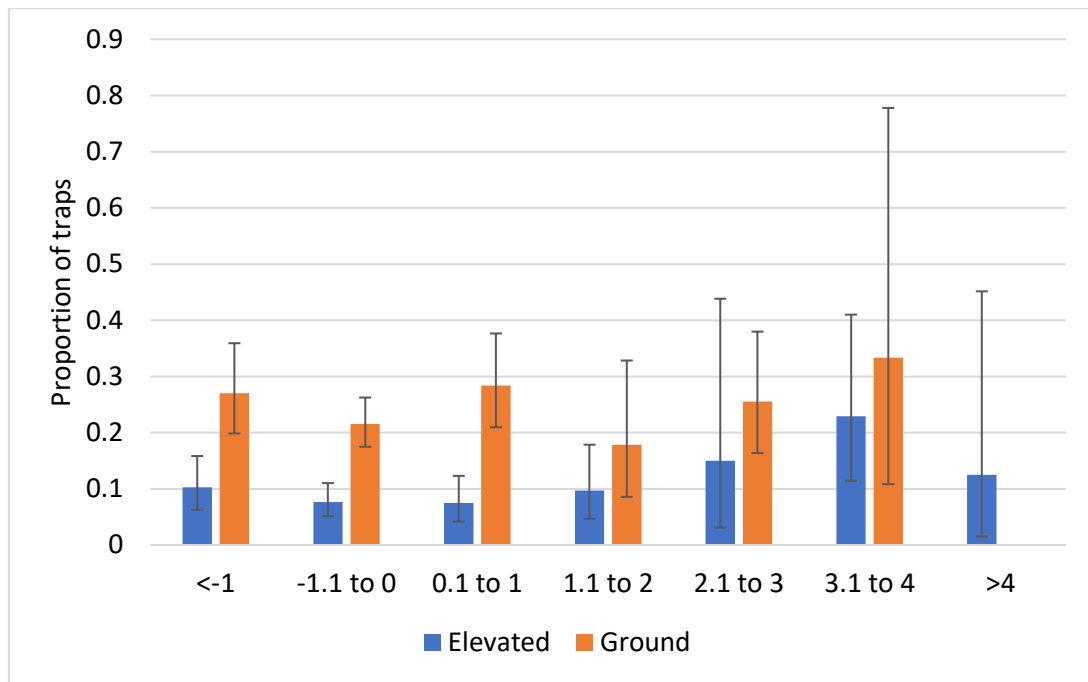


Figure 34: Proportion of elevated and ground traps which caught a wood mouse during each session in the woodland in Thoresby. The captures are plotted against their score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.2.2. Bank voles

In Thoresby the probability of catching a bank vole in the woodland across all the sessions was not significantly affected by the two components but there was a significant correlation between the effects of session and of component 1 (Table 21). The traps that scored between -1 and 1 had a probability of captures that was below 0.2, the traps that scored between 1 and 2 had a very low probability in June but a much higher one in August and the traps that had a score between 2 and 3 had a high score in September and an even

higher one in August. There were no captures in the traps that scored above 3 (Figure 35).

Table 21: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a bank vole in the woodland in Thoresby.

Term	Df	Change in deviance	P value
Session	7	80.366	<0.001 ***
Elevation	1	8.480	0.004 **
Component 1	1	0.632	0.426
Component 2	1	0.189	0.663
Session x component 1	7	26.769	<0.001 ***
Session x elevation	7	13.599	0.059 .
Elevation x component 1	1	1.736	0.188
Comp1 x component 2	1	1.015	0.313
Session x component 2	7	12.102	0.097 .
Elevation x component 2	1	1.567	0.211

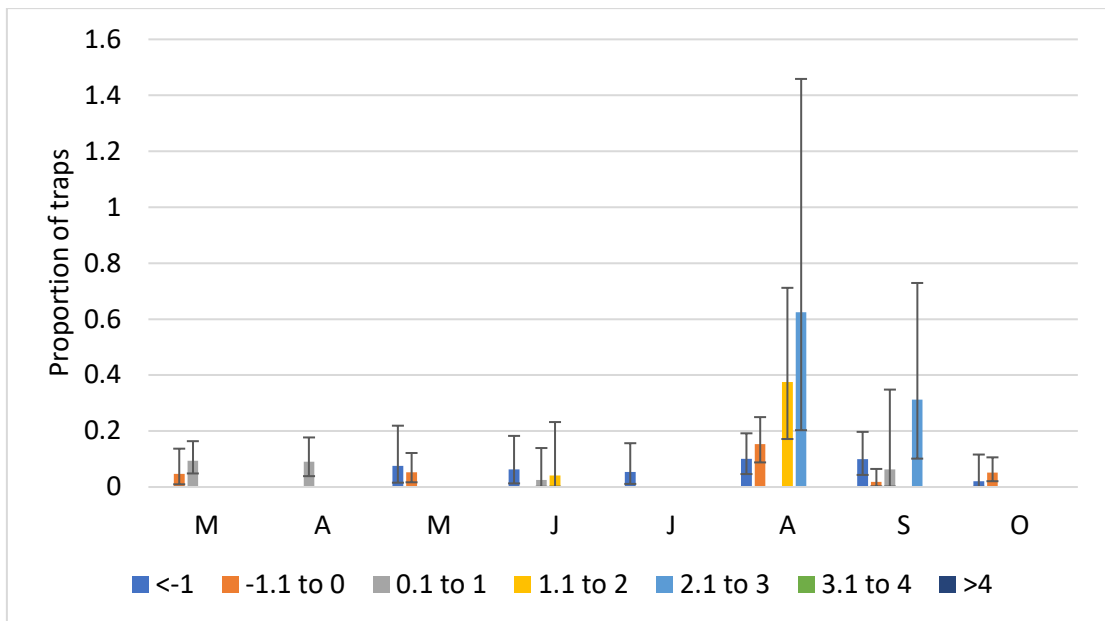


Figure 35: Proportion of traps which caught a bank vole during each session in the woodland in Thoresby. The different coloured bars show the score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.3. Pasture

The pasture was only surveyed in Thoresby and the habitat variables were combined into one principal component. Component 1 correlated positively with the height of the vegetation and the canopy cover and negatively with the ground cover.

Only wood mice were caught in the pasture with the exception of two bank voles. The probability of capture was significantly affected by component 1 as there was a decline in captures as the score of the trap decreased, with the

exception of the traps that scored between 0 and 1, which had the highest probability of capture (Table 22; Figure 36). There was also a significant interaction between the effects of the session and component 1 with some complex season-specific effects (Figure 36).

Table 22: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a wood mouse in the pasture in Thoresby.

Term	Df	Change in deviance	P value
Session	6	106.330	<0.001 ***
Component 1	1	5.688	0.017 *
Session x component 1	6	18.578	0.005 **

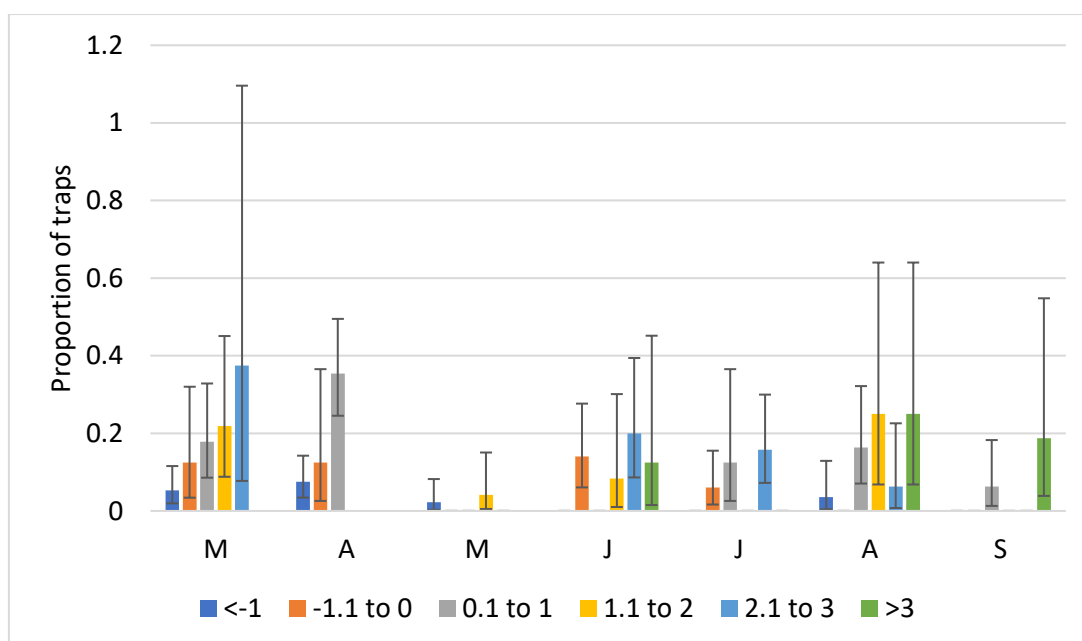


Figure 36: Proportion of traps which caught a wood mouse during each session in the reedbed in Thoresby. The different coloured bars show the

score for component 1, which is a measure of the microhabitat characteristics of each trap. The error bars show 95% confidence intervals calculated from the binomial distribution.

3.5.4. Arable

Although the arable land was surveyed in Clumber as well as in Thoresby, in Clumber there was only one capture and so it was not analysed. In Thoresby all there were only two variables measured: height of the vegetation and the ground cover. Therefore there was no need to create a new variable with a PCA and both the original variables were included in the model.

The only species caught in this habitat type was the wood mouse. There was no significant effect of height of the vegetation or of ground cover on the probability of catching a wood mouse but there was a significant interaction between their effects, as well as a significant interaction between the effects of the session and the ground cover (Table 23; Figure 37; Figure 38).

Table 23: Results from a generalised linear mixed effects model (lmer, link function = binomial) testing for the effects of elevation, session, component 1 and component 2 on the probability of catching a wood mouse in the arable in Thoresby.

Term	Df	Change in deviance	P value
Session	6	77.867	<0.001 ***

Height	1	0.256	0.613
Ground cover	1	0.057	0.811
Height x ground cover	1	4.918	0.027 *
Session x ground cover	5	15.226	0.009 **
Session x height	5	6.918	0.140

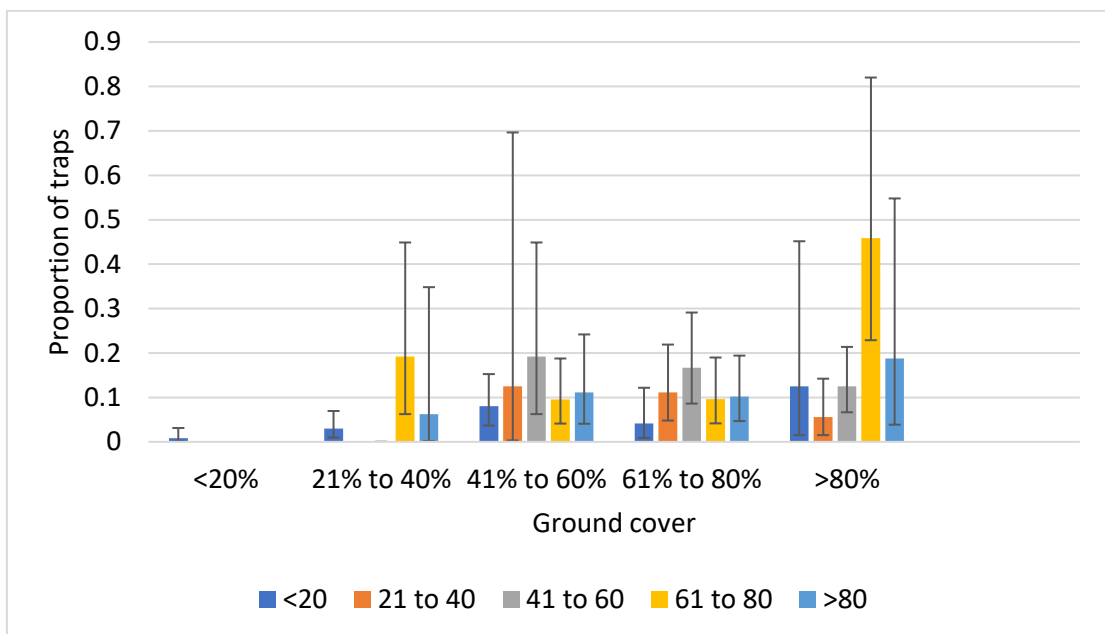


Figure 37: Proportion of traps which caught a wood mouse during each session in the arable in Thoresby. The captures are plotted against the ground cover and the different coloured bars show the height of the vegetation. The error bars show 95% confidence intervals calculated from the binomial distribution.

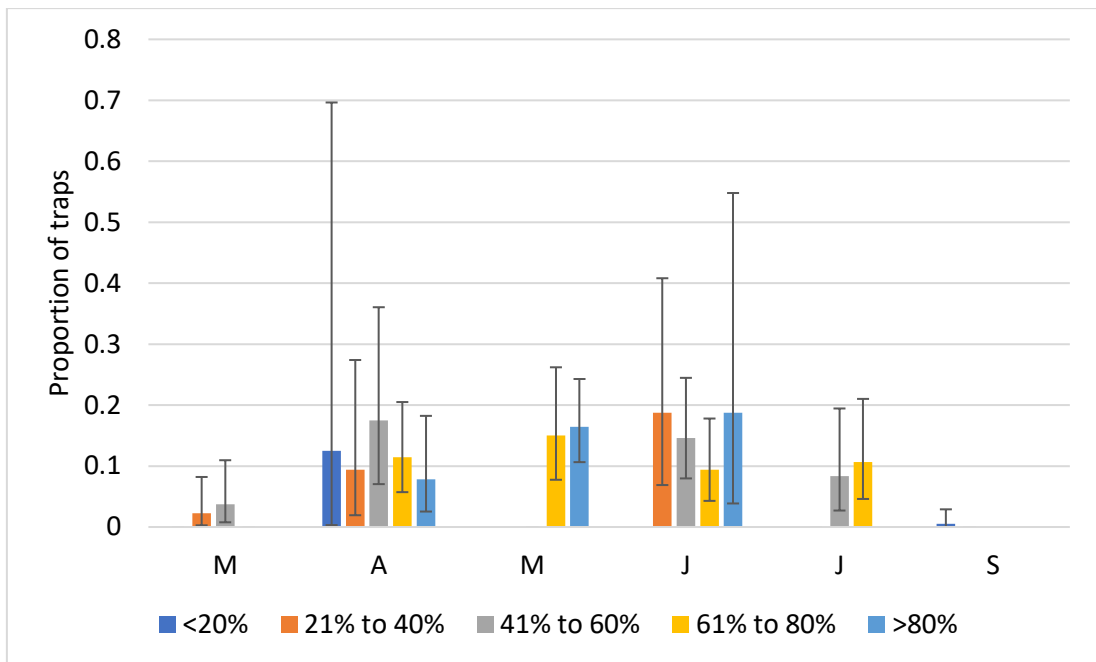


Figure 38: Proportion of traps which caught a wood mouse during each session in the arable in Thoresby. The different coloured bars show the ground cover. The error bars show 95% confidence intervals calculated from the binomial distribution.

4.

Discussion

Reedbeds represent a refuge for small mammals and are a hotspot of biodiversity (Perrow and Jowitt, 2003; Marques *et al.*, 2015). All of the habitats surveyed in this study had at least one species of small mammal present. At the focal study site the reedbed was the habitat with the highest number of species and it had species that were not found anywhere else, such as the harvest mouse, the pygmy shrew and the field vole. This supports previous findings on the role of wetlands for small mammals, showing that reedbeds can be extremely important habitats for these species (Marques *et al.*, 2015; Kettel, Perrow and Reader, 2016). Reedbeds have a complex habitat structure and an abundance of food sources such as easily accessible seeds and insects, and therefore are ideal to support a varied small mammal community (Canova and Fasola, 1991; Marques *et al.*, 2015).

My focal study site, Thoresby, was the site with the highest capture rate per unit effort. Since it was the only site surveyed consistently every month it is possible that this is partly a result of an increase in trappability, as the animals become habituated to the traps. However, the increase in catches observed after the first session is not large enough to account for the difference between Thoresby and the other sites, and therefore it is likely that Thoresby genuinely supported a large population of small mammals during the study period. In Thoresby the reedbed is very large and has both wet and dry areas at all times of the year, meaning that there is greater habitat diversity available all year round. The study area is surrounded by several large patches of woodland connected to each other and by arable fields with varied crops. The woodland in Thoresby is predominantly composed by oak trees (*Quercus*

spp.), which are known to be a valuable food source for wood mice (Watts, 1969; Flowerdew and Gardner, 1978), and by a very dense and tall understory that provides the structural complexity, which is particularly suitable for small mammals (Canova and Fasola, 1991; Marques *et al.*, 2015). Also, the proximity of several different arable crops could have a positive impact on the food available at various times of the year. All these factors are likely to have contributed to the higher captures per unit effort in Thoresby compared to the other sites.

In Bevercotes there were no captures in the reedbed, probably because it is very small, arranged in a thin strip around the edge of a pond, and it is isolated from the woodland by open grassland. The woodland at this site also had very few captures, and this could be caused by the type of vegetation, as it is composed mainly of young trees and does not have much understory. In Sherwood Pines there were some captures in the reedbed, which is small but connected to the woodland. Similarly to Bevercotes, the low number of captures in the woodland can be ascribed to the lack of understory. The woodland at Clumber, which has a dense understory, had a catch per unit effort that was comparable to Thoresby, but there were no captures in the reedbed. The reedbed in Clumber is larger than the one in Thoresby but it does not have any dry areas and wood mice and bank voles, which were the species caught in Thoresby in July, seem to prefer the dry areas of the reedbed. Bestwood was the site that was most similar to Thoresby, despite being the most distant geographically. The reedbed in Bestwood is smaller than the one Thoresby but it was almost completely dry when surveyed, which

could be the reason why wood mice and bank voles were captured in it. Although these two species are known to utilise wetland habitats, they are mostly associated with woodlands and other dry habitats (Kikkawa, 1964; Crawley, 1970; Ouin *et al.*, 2000; Rosalino *et al.*, 2011), and even this study has found them to prefer the dry parts of the reedbed. The woodland has oak trees and a dense and tall understory, similar to Thoresby. These are factors that could have caused the differences between the sites but it is impossible to rule out any other causes related to the individual characteristics of each site.

4.1. Harvest mice

The main aim of this study was to shed light on the habitat preferences in harvest mice, and whether there are seasonal changes in preferences which might explain the apparent absence of this species from reedbeds in the summer. The results contribute to the limited knowledge on the habitat use by this species by confirming their presence in the reedbeds in autumn and their preference for the wet areas, with tall and thick reeds.

4.1.1. Seasonal fluctuations in abundance

In Thoresby harvest mice were only caught in September and October and only in the reedbed. Although previous studies have shown that harvest mice become extremely scarce during the summer, their complete absence in the

late winter and spring was unexpected. In the literature there is evidence that extremely cold temperatures cause an increase in mortality (Sleptsov, 1947; Trout, 1978b; Perrow and Jowitt, 1995). Since the winter before the start of the study was extremely prolonged, with unusually cold temperatures especially in December and March (Parker, Legg and Folland, 1992), this could have had a negative effect on the population numbers and caused them to be so low that they were not detectable. The absence of harvest mice in Bestwood in July and their appearance in October seems to confirm that what happened in Thoresby was indicative of a general trend of the harvest mouse populations in the area, rather than a peculiarity of one particular site. In Sherwood Pines, which was the additional site surveyed in May and September, there were never any harvest mouse captures, even though it was a site where harvest mice have been recorded in the reedbed in previous years (Andrew Lowe, personal communication). The reedbed in this site is much smaller than the ones in Thoresby and Bevercotes and therefore it is possible that the population took longer to recover from the winter, and was still undetectably low in September. 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 quickly recover 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 but not enough is known about the behaviour of this species in the wild to support this conclusion.

4.1.2. Effect of elevation

Harvest mice were much more likely to be trapped in the elevated traps than in the ground traps in both sites. This reflects what is already known about their scansorial habits from the fact that they nest at an elevation and from the few successful live trapping studies for this species (Harris, 1979c; Surmacki, Goldyn and Tryjanowski, 2005; Hata, 2011; Riordan, Lloyd and MacDonald, 2009; Hata, 2011). 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, Perrow and Reader, 2016). In Bestwood the difference between the elevated traps and ground traps was not as great as it was in Thoresby. This might be caused by the fact that the reedbed in Bestwood had fewer captures of wood mice than Thoresby did, which may decrease the competition for the lower parts of the vegetation and result in more available ground traps, or it could be caused by different habitat characteristics of the two sites.

4.1.3. Effect of habitat

In both sites where they were found, harvest mice were only ever trapped in the reedbed. This confirms the findings of several recent studies on this species that have found a preference for reedbeds (Harris, 1979b; Haberl and Kryštufek, 2003; Surmacki, Goldyn and Tryjanowski, 2005; Kettel, Perrow and Reader, 2016). However no other study that included several habitat types has found harvest mice exclusively reedbeds (Harris, 1979b; Haberl and

Kryštufek, 2003). A possible explanation for this result is that this study was able to capture only the initial phases of the population expansion for this species. If the trapping had been carried out for a longer period and the population had continued growing, harvest mice might have started to occupy the surrounding habitats too.

The complete lack of harvest mice in the other habitats, including the arable fields during the months of maximum growth of the crop is a surprising finding, as for a very long time this species was thought to inhabit mostly cereal fields (Trout, 1978b; Harris, 1979b). The intensification of agricultural practices, which include the extensive use of pesticides and the selection of short-stemmed cereal strains, are believed to have affected small mammal communities by negatively impacting rare and specialist species and favouring generalists (Harris *et al.*, 1995; Perrow and Jowitt, 1995; de la Peña *et al.*, 2003; Michel, Burel and Butet, 2006). Although harvest mice are generalists, they are probably more affected by the reduction in vegetation height than wood mice because of their scansorial lifestyle (Dickman, 1986; Surmacki, Goldyn and Tryjanowski, 2005). If the optimal height at which harvest mice move and nest coincides with the top of the plants, this would not provide them with enough structural stability and cover from predators, making the habitat unsuitable. However, the fact that harvest mice were not present in any other habitat in the months of maximum growth of the crop means that their absence was not necessarily connected to the characteristics of the field. It is plausible that this result was caused by extremely low numbers of harvest mice present in the area due to the harsh winter, and it is

impossible to exclude the possibility that if there had been higher numbers of mice in the reedbed before the start of the summer, some would have moved into the arable area once the crop started to grow. Another explanation could be that in spring and summer harvest mice use habitats that were not surveyed in this study or become less trappable when using habitats other than the reedbed. There is a possibility that they might use the woodland canopy or other parts of the surveyed habitats where they could not be trapped.

The results showed that in Thoresby harvest mice were most likely to be caught in the areas of the reedbed with tall and thick reed stems and a higher water level. In Bestwood harvest mice were more likely to be caught in the areas of the reedbed with an intermediate to high score for reed height and low for water level. The apparent preference of this species for dry areas in Bestwood is confounded by the fact that in this site the reedbed was always completely dry. The preference for the trap locations associated with a higher water level is in contrast with a previous finding, which suggested that harvest mice only use the dry parts of the reedbed and not the wet areas (Surmacki, Goldyn and Tryjanowski, 2005). However previous studies had found that this species frequently nests on wetland plants (Harris, 1979a). The most recent study that analysed the habitat preference of harvest mice in the reedbed found that they were most strongly associated with the wetter parts (Kettel, Perrow and Reader, 2016). Overall the result of this study support the preference of this species for the wet areas of the reedbed. From the analysis of the distribution of harvest mice captures it is clear that they preferred the

central and NE area of the trapping grid at Thoresby, which in the winter and spring months was the wettest part. Avoiding the edges of the reedbed could be a strategy to reduce competition with wood mice and bank voles, as these species used mostly those areas. In addition, the edges of the reedbed are known to have a higher risk of predation for birds, so it is possible that this is true for harvest mice too and therefore they use the interior of the reedbed to avoid this risk (Báldi and Batáry, 2005).

4.2. Wood mice

4.2.1. Seasonal fluctuations in abundance

Wood mice were the most frequently caught species in every session. They were the only species caught in all habitats in Thoresby, which confirms what is known about this species, as they are known to be generalists and able to exploit most habitat types (Canova and Fasola, 1991; Michel *et al.*, 2007; Mortelliti *et al.*, 2009; Marques *et al.*, 2015). They were caught at least in the woodland in every site and they were only absent from the reedbed in Bevercotes and Clumber, but no other species was captured there either. The fact that wood mice were so widespread in this study is not surprising as they are known to be particularly good at exploiting most habitats and they are not sensitive to anthropogenic disturbance, which often causes them to be the dominant species in small mammal assemblages in human-influenced habitats like those studied here (Canova and Fasola, 1991; Michel *et al.*, 2007; Mortelliti *et al.*, 2009; Marques *et al.*, 2015).

Wood mice are known to undergo seasonal fluctuations in abundance and most studies that looked at their population dynamics agree that their number decrease in spring and increase in autumn (Watts, 1969; Crawley, 1970; Montgomery, 1989; Fernandez, Dunstone and Evans, 1996). This study did not register a dramatic decrease in the numbers of wood mice in the 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 moved into arable fields in the late spring and summer. The results of this study therefore support the more recent idea that the apparent fluctuations in numbers are at least partially caused by a change in habitat preference (Kikkawa, 1964; Ylönen, Altner and Stubbe, 1991; Ouin *et al.*, 2000; Todd, Tew and Macdonald, 2000).

The data from this study also show an large decline in wood mouse population numbers in September, which according to the literature should be a time of population expansion, as it is a time when the new young born in the summer enter the population (Montgomery, 1989; Fernandez, Dunstone and Evans, 1996). The reason for this unusual drop could be the change in temperature from a summer that was warmer than average to a suddenly colder period in September (Parker, Legg and Folland, 1992). This might have caused a sudden surge in mortality, especially since the population had a high

proportion of young individuals at that point and they are more susceptible to changes in external conditions (Watts, 1969).

4.2.2. Effect of elevation

The probability of catching wood mice was much higher in the ground traps; however, in the habitats where elevated traps were placed, they were also used. A previous study found that even though wood mice spend most of their times close to the ground, they occasionally exploit the upper parts of the vegetation, especially if the population density in the area is high (Buesching *et al.*, 2008). Since the population density in this study was sometimes high, it is likely that this is what encouraged wood mice to use the elevated traps. Interestingly, in the reedbed in Thoresby in August wood mice were found more often in elevated traps than in the ground ones. 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 and that is probably why they were the species that was displaced (Buesching *et al.*, 2008).

4.2.3. Effect of habitat

The plot of the spatial distribution of the captures in Thoresby shows that although wood mice were caught more in the SE corner of the grid, which is closest to the edge of the reedbed, they were present in the whole grid,

including the internal areas of the reedbed. This, coupled with the fact that the difference between the probability of capture between this habitat and the woodland was not significant, confirms that reedbeds are important habitat for wood mice too. Even though wood mice had been found to occupy wetlands before, they had not been found to use reedbeds to this extent (Perrow and Jowitt, 2003; Marques *et al.*, 2015; Kettel, Perrow and Reader, 2016). The analysis of the effects of the microhabitat characteristics of the probability of catching a wood mouse showed that they had a slight preference for the dry areas of the reedbed. These results reflect the fact that this species lives mostly on the ground when possible but is able to use the wet areas due to its agility (Buesching *et al.*, 2008). There was an increase in the use of the trap locations associated with denser and taller reeds in the summer months, which could represent an increase the density of predators resulting in the need to seek cover.

In the woodland there were also no overall effects of habitat characteristics on the probability of capturing wood mice, but there were some complex season-specific effects of these variables on the presence of this species. The effect of the elevation also differed depending on the microhabitat of the habitats in which traps were located: there was a stronger effect in the traps with a low score for height of the understory and high for distance to the nearest tree. This probably reflects the fact that wood mice found it easier to climb onto the elevated traps that were surrounded by tall vegetation and also felt safer to do so because a taller understory provides more protection from predators (Buesching *et al.*, 2008).

The use of the pasture by wood mice seems to be a consequence of the proximity to the woodland rather than their preference for this kind of habitat. This is especially clear when looking at the distribution of the captures, which are focused on the edges of the pasture, and mostly on the side that bordered the woodland. The central areas of the pasture were hardly used, probably because there was not enough cover from predators, which has been shown to be an important factor in the habitat use of small mammals (Kikkawa, 1964). The analysis of the effect of the microhabitat on the probability of capture confirmed that traps with a higher score for the height of the vegetation and for the canopy cover had a higher probability of capture. In addition, there was a slightly stronger effect of the microhabitat on the probability of captures as the study progressed. This could reflect the fact that the vegetation grew taller and denser with the change of the season and therefore the captures inevitably happened in traps surrounded by taller vegetation later in the study. However, the change in vegetation happened mostly in the spring and early summer months, while the increase in captures in the traps associated with taller vegetation and higher canopy cover continued after that. Therefore it is possible that there is an alternative explanation for this change; for example, an increase of grazers or predators in those months could have caused the mice to only visit the traps that provided better cover (Kikkawa, 1964; Buesching *et al.*, 2008).

Wood mice were the only species trapped in the arable land. Their use of this habitat is consistent with previous studies on this species, which found that

wood mice become more abundant in the fields as the crop grows, encouraged by the availability of food and cover from predators (Kikkawa, 1964; Ouin *et al.*, 2000). The steep decrease of number of captures in the woodland and pasture in May, coupled with the increase in captures in the arable, also seem to suggest a movement of individuals between these habitats, as previously reported by Ouin *et al.* (2000). This is supported by the fact that the same individuals were sometimes caught in different habitats, meaning that they did travel between them. The microhabitat characteristics measured for this habitat were the height of the vegetation and the ground cover. Neither of these significantly affected the probability of capture but there was a significant interaction between their effects, caused by the fact that as the crop grew taller, it also increased the amount of vegetation covering the ground. There was also a significant interaction between the effects of session and ground cover. In the months in which the crop was fully grown the probability of capture in the traps that scored higher for ground cover was higher. The effect of ground cover was more important than the effect of the height of the vegetation, probably because the crop was fairly uniform in height. A higher ground cover in this kind of habitat is associated with a higher density of plants, which provide more cover from potential predators and therefore is advantageous for small mammals (Kikkawa, 1964).

4.3. Bank voles

In Thoresby bank voles were caught in every session, mostly in the woodland and reedbed, but there were two captures in the pasture too. In addition, they

were caught in the woodland in Clumber and in the woodland and reedbed in Bestwood. The reason why bank voles were caught in the woodland in these three sites only is probably that the dense understory that distinguishes them from the other sites, which is known to be an important habitat characteristic for this species (Mazurkiewicz, 1994; Olsson *et al.*, 2005). The reedbeds where they were caught are both large and dry compared to the others, which suggests that these are important properties for their ability to use this habitat.

4.3.1. Seasonal fluctuations in abundance

The change in abundance throughout the seasons clearly supports the previous evidence for seasonal fluctuations in the population numbers of the bank vole (Lambin, Petty and Mackinnon, 2000). The data show very low numbers of voles from February to July and an large increase in August. The scarcity of captures in February is in contrast with the literature, from which it appears that the decline in numbers should happen in spring, so a plausible explanation is the initial shyness of bank voles towards the traps. This species is known to be less agile and active than the wood mouse and therefore it is possible that it took longer for them to start exploring the traps (Bergstedt, 1966; Buesching *et al.*, 2008). Another explanation could be that the prolonged winter that seems to have affected the harvest mice could have increased the mortality in bank voles too. Similarly to the wood mice, bank voles showed a drop in numbers in September followed by another increase in October and the reason for this can again be found in a decrease in temperature in September.

4.3.2. Effect of habitat

The high number of bank vole captures in the reedbed, which equalled the ones in the woodland in Thoresby, once again confirms its importance as a habitat for small mammals (Perrow and Jowitt, 2003; Marques *et al.*, 2015). The plot of the distribution of the captures of bank voles in the reedbed show that this species used mostly the dryer SW end of this habitat. This is probably caused by the fact that they are not very agile compared to harvest mice and wood mice and therefore would have struggled to navigate the areas where the ground was inaccessible because it was covered by water (Buesching *et al.*, 2008). In the woodland, bank voles were caught repeatedly in some traps and never in others. This can be an indication of their more sedentary and less explorative behaviour compared to wood mice (Buesching *et al.*, 2008). The two captures in the pasture most likely represent an overspill from the woodland and indicate that this species does not use open habitats.

Although overall there was a high probability of capture in the reedbed, looking at the changes over the sessions shows that bank voles only started appearing in this habitat in July. A plausible explanation to this phenomenon is that the increase in population density in the woodland caused the population to expand into the reedbed in search of space. However, from July onwards there were more captures in the reedbed than in the woodland, which suggests a change in habitat preference. This is supported by the fact that among the individuals of this species that moved across different habitats the

most frequent movement was from the woodland to the reedbed. This change in preference could be caused either by a decrease in the water level in the reedbed or by the increase in interspecific competition with wood mice in the woodland. The number of wood mice in September and October decreased in the reedbed but not in the woodland, which suggests that there could be a mechanism of avoidance between the two species when their density starts rising. The presence of competition between these two species is supported by the results of an experiment by Fasola and Canova (Fasola and Canova, 2000), which reported that the removal of wood mice affected the density of bank voles.

4.3.3. Effect of elevation

Bank voles were much more likely to be captured in the ground traps than in the elevated ones. Although arboreality can have some benefits for small mammals, especially when the interspecific or intraspecific competition is high, it is not surprising that bank voles did not use the elevated traps often. 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 predators and more on hiding from them (Buesching *et al.*, 2008).

4.4. Movement

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 between the species, as 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, Miller and Buskirk, 1986). 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). The results for the distance travelled per bout were not in agreement with the ones for the total distance travelled between recaptures. On average harvest mice were the species that travelled the greatest distance per bout, followed by the wood mice and lastly by the bank voles. This could be caused by the fact that harvest mice, being very small and with a poorly insulating fur (Trout, 1978b), move more within their limited home range in order to gather enough food to satisfy their high metabolic requirements. 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.

4.5. Suggestions for further research

The findings of this study shed some light on the community composition and the seasonal habitat preference of small mammals. The use of elevated and ground traps allowed me to monitor a wide range of species, including the harvest mouse, which is a species frequently overlooked by other methods. This method can be used to extend the currently limited knowledge about the status of this species and inform conservation practices as well as their interactions with other species. The harvest mouse is a BAP priority species in the UK, but most of the current knowledge on their numbers and distribution is based on nest searching, which has proven to be less effective than live trapping at an elevation. For this reason more sites throughout the country need to be surveyed using this new method in order to acquire a better understanding of this understudied species.

Trapping in several habitat types throughout the best part of a year has provided insights into small mammal population dynamics and also determine changes in habitat preference at different times of the year. Future studies on the population dynamics of small mammals should be carried out in habitat mosaics in order to avoid confusing movements with changes in numbers. Wetlands appear to have particularly high diversity and abundance, and future research should focus on this habitat type more. However, changes in the environmental conditions can have a strong effect on small mammal species and therefore further studies should span more than one year. Applying this method to a longer study could uncover whether the complete lack of harvest

mice and the low numbers of bank voles at the beginning of the study are recurring trends or only the result of a harsh winter.

In this study the microhabitat characteristics were assessed using a PCA for each trap location in each session and in some cases this caused the results to reflect the changes in the habitat with the seasons rather than the actual habitat preference of the animals. Due to time constraints it was possible to repeat the analysis combining the microhabitat characteristics of each trap location over the sessions only the reedbed but not in the other habitats. A future study could correct this mistake in order to collect more data on the microhabitat preference of small mammals.

Marking the individuals by clipping the fur has proven to be an inexpensive method to monitor the recaptures of small mammals and allowed some information about their movements. However, this method may be unsuitable for long term studies because the fur can grow back and make the mark invisible. Alternatives such as radio-tracking could be used to monitor the movements of small mammals in the future, allowing to gather information about home ranges and short-term movements. In addition, this would be a useful method to detect any changes in habitat preference in different seasons and could help to differentiate between changes in abundance due to mortality and apparent fluctuations caused by movement to different habitats.

5.

Conclusion

The study of small mammals has for a long time focused mainly on explaining their effect as pests in agricultural landscapes and the multiannual cycles of lemmings and vole in arctic regions. However, the importance of this group as a component of biodiversity creates the need to know more about their ecology. They are important sources of food for protected species and often are themselves the focus of conservation practices, in addition to affecting the recruitment of plants. The population dynamics of small mammals in the wild show interesting seasonal fluctuations but for most species but there is little evidence on whether these are changes in numbers or changes in habitat preference.

The harvest mouse is believed to be in decline in the UK and therefore is a BAP priority species (Harris *et al.*, 1995; JNCC, 2010). Despite that, it is still very understudied compared to other small mammals and therefore more information is necessary to inform conservation practices for this species. There is some evidence of an extreme decline in population numbers during the summer but there is very little information on the habitat preference and seasonal changes in this species.

Wetlands are an important habitat for many animals, including small mammals. Reedbed are known to have an extremely high small mammal diversity and are home to some very rare species like the harvest mouse, the water vole and the water shrew. However, most studies that involve live-trapping small mammals are still being conducted in dry habitats and reedbeds are only surveyed when targeting wetland specialists. The

importance of reedbeds for small mammals was confirmed in this study as it was the only habitat where harvest mice, field voles and pigmy shrews were captured. Furthermore, this habitat it was used extensively by the other generalist species found on the sites: wood mice, bank voles and common shrews.

This study has provided some evidence of seasonal changes in habitat preference by the wood mouse and the bank vole. The evidence suggests that wood mice do not have dramatic changes in abundance as some studies have found in the past, but rather move from the woodland and pasture to the arable when the crop starts maturing. For bank voles this study showed a dramatic increase in abundance in the late summer months but no obvious switch in habitat preference, which reflects what was previously known about this species. Unfortunately, this study was not successful at determining whether harvest mice really experience a strong decline in the summer or change habitat preference, because they were captured only in the reedbed at the end of the study. The current evidence suggests that this species can recover quickly and go from undetectable to fairly common in few weeks. However, by the disadvantageous environmental conditions could have caused this result. Therefore, it is still possible that harvest mice change habitat preference throughout the year and that they might use a habitat type or part of a habitat not surveyed in this study, such as tree canopies.

This study has provided information about seasonal changes in habitat preference and population dynamics in small mammals. It also contributed to

the few records for harvest mice in the UK and supported previous evidence on their microhabitat preference. However, more research is still needed to have a better understanding of the status and ecology of the harvest mouse at all times of the year.

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