

THE HARVEST MOUSE (*Micromys minutus*) NEST DENSITY AND DIMENSIONS IN SLOVAKIA

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Received: 9 May 2025 / **Accepted:** 27 September 2025

Abstract

Tej B., Csanády A.: The harvest mouse (*Micromys minutus*) nest density and dimensions in Slovakia. Ekológia (Bratislava), Vol. 44, No. 2, p. 138–146, 2025.

Our research in Slovakia identified key plant species that support nesting by the Eurasian harvest mouse (*Micromys minutus*) in field-edge and marginal habitats. Nests were most often found in couch grass (*Elymus repens*), reed canary grass (*Phalaris arundinacea*), blackthorn (*Prunus spinosa*) and bramble (*Rubus plicatus*). They were typically circle and oval and located in the middle part of the plant, with nest height depending on the height of the vegetation. Nest density varied greatly between sites and years, ranging from 1 to 3 nests/ha to over 270 nests/ha. The highest values were recorded in the Košická kotlina basin, such as 279.4 nests/ha in Košice part Šebastovce (Line 1) in 2021. These findings suggest that well-structured edge habitats can support high harvest mouse densities and play a key role in species conservation.

Key words: agricultural landscape, Slovakia, mammals, nests, dimensions.

Introduction

Field margins, hedgerows and shelterbelts are important landscape features that play a crucial role in ecosystems adjacent to agricultural fields. Their significance lies in providing protection for crops and livestock, delineating field boundaries and supplying resources, such as fuel, timber and food (Marshall, Arnold, 1995; Marshall, 2002, 2005; Marshall, Moonen, 2002; Montgomery et al., 2020).

Agricultural landscapes – also referred to as cultural landscapes – are described as mosaics composed of fields, linear features, woodlands and other natural habitats (Marshall, Moonen, 2002). According to Montgomery et al. (2020), older hedgerows often stand out due to their higher species richness and functional diversity, as they offer a greater variety of ecological niches.

Although fields typically occupy the largest portion of cultural landscapes, significant changes in agricultural practices and land use have occurred over the past several decades, particularly in the last 50 years (Stoate et al., 2001, 2009). This shift is also evident across Western Europe, where land-use intensification has contributed to a severe biodiversity crisis (Stoate et al., 2001, 2009; Robinson, Sutherland, 2002; Gregory et al., 2004; Smart et al., 2006). For instance, Sklenicka et al. (2009) reported that 71% of hedgerows were lost in the Plzeň region of the Czech Republic between 1959 and 2005. The resulting decline in ecological heterogeneity has led to the loss of suitable habitats and, consequently, a decrease in both faunal and floral diversity (Donald et al., 2001; Benton et al., 2003).

These habitats typically offer ideal conditions for various invertebrates, such as mollusks, arthropods and insects, which serve as an essential food source for a wide range of vertebrates, including birds, rodents, insectivores and other species (Dover, 2019; Feber et al., 2019; Montgomery et al., 2020).

Several studies on rodents and insectivores in Slovakia have shown that small mammals – such as mice, voles and shrews – form an important component of the fauna inhabiting field margins, hedgerows and shelterbelts. Their populations tend to be higher near these edges than within the fields themselves (e.g., Štollmann, Dudich, 1984, 1985; Májsky, 1985; Pelikán, 1986, 1989; Stanko, 1994a,b; Stanko, Miklisová, 1995; Stanko et al., 1999). However, their relationship with these habitats is complex, as they may use the edges for nesting while foraging in adjacent fields.

This study focuses on the occurrence of the harvest mouse (*Micromys minutus* Pallas, 1771) in these types of habitats. Suitable environments for *M. minutus* include both natural and anthropogenic areas containing grasses, reeds and other tall vegetation that provide cover, nesting sites and shelter (Kminiak, 1968a,b; Harris, 1979; Surmacki et al., 2005; Hata et al., 2010; Hata, 2011; Darinot et al., 2021; Balčiauskas, Balčiauskienė, 2023). It has been confirmed that such habitats support the persistence of *M. minutus* in ecologically neutral associations, as indicated by direct observations, live trapping and the discovery of nests (Dickman, 1986; Balčiauskas, Balčiauskienė, 2023; own unpublished data), as well as indirect evidence such as owl pellets, remains left by raptors and other predator-related findings (see review by Darinot, 2016).

While reed beds are considered preferred habitats by several authors (Harris, 1979; Surmacki et al., 2005; Darinot et al., 2021; Balčiauskas, Balčiauskienė, 2023), other vegetation types have also been found to be important. For instance, patches of nettles (*Urtica dioica*) and American goldenrod (*Solidago gigantea*) are especially valuable in autumn, while unmown areas play a critical role during winter (Vecsernyés, 2020).

In intensively managed agricultural landscapes, the harvest mouse (*Micromys minutus*) shows a preference for various types of shrubs, small trees and grasses along the edges of arable fields. These include bramble (*Rubus plicatus*), common hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), couch grass (*Elymus repens*) and reed canary grass (*Phalaris arundinacea*), among others (Bence et al., 2003; Lloyd, Kirk, 2021; Čanádý, 2012, 2013; Csanádý, 2022). In these habitats, it constructs its characteristic spherical nests above ground level within the vegetation.

During nest construction, the species not only adapts to the surrounding vegetation structure (Hata, 2011) but also selects plant species based on stem density and leaf coverage (Kuroe et al., 2007), which likely offer greater concealment and stability.

Due to a lack of confirmed records and limited data on the presence of the harvest mouse along field edges – despite previous studies on small mammal captures in Slovakia – we investigated the role of these habitat margins in the occurrence of this species, using summer nests as indicators.

The primary objective of this study was to evaluate the size of harvest mouse nests, density and their spatial distribution within arable field margins under Slovakian conditions.

Material and methods

This study presents data on the occurrence of summer nests of *Micromys minutus* collected between 2010 and 2024 from 71 locations across seven geomorphological units in eastern Slovakia: the Košická kotlina Basin, Čierna hora Mts., Šarišská vrchovina Mts., Slanské vrchy Mts., Ondavská vrchovina Mts., Laborecká vrchovina Mts. and the Východoslovenská rovina Plain.

Nests were systematically searched for by hand during detailed linear inspections of habitat edges – 1–1.5 metres wide – located along the boundaries of arable fields and adjacent to various forest types (e.g., oak–beech, beech–hornbeam, hornbeam–elm) and shrub-dominated stands. The surveys also included structurally diverse hedgerows and shelterbelts of varying widths and vegetation composition. All nests were located by a single researcher (A.Cs.), and nest densities were recorded per hectare. The surveyed edges typically represented transitional ecotones between open agricultural land and semi-natural or natural vegetation. Field inspections were conducted during late autumn and winter, outside the breeding season, after the nests had been abandoned. This period was chosen specifically to ensure greater visibility of vegetation and improve nest detectability. Nests of harvest mice were identified and reliably distinguished from those of similar species, particularly the hazel dormouse (*Muscardinus avellanarius*), based on structural characteristics described by Wachtendorf (1951).

These edge habitats were primarily dominated by a diverse mix of grasses and herbs, including stinging nettle (*Urtica dioica* L.), giant goldenrod (*Solidago gigantea* Ait.), reed canary grass

(*Phalaris arundinacea* L.), tansy (*Tanacetum vulgare* L.), couch grass (*Elymus repens* (L.) Gould) and sedges (*Carex* spp.), along with other species from the Poaceae, Brassicaceae and Asteraceae families. The shrub layer was mainly composed of species such as blackthorn (*Prunus spinosa* L.), blackberry (*Rubus plicatus* Weihe & Nees), raspberry (*R. idaeus* L.), elder (*Sambucus nigra* L.), common dogwood (*Cornus sanguinea* L.), common hawthorn (*Crataegus monogyna* Jacq.) and dog rose (*Rosa canina* L.) (cf. Čanádý, 2012, 2013; Csanádý, 2022).

Following the methodology of several previous studies (e.g., Szunyoghy, 1952; Kminiak, 1968a,b; Hata et al., 2010; Hata, 2011; Čanádý, 2013, 2015; Csanádý, 2022), we recorded the same key parameters: the plant species supporting each nest, the height of the nest above the ground, its linear dimensions (length, width and height) and calculated volume.

All nest dimensions were measured using a standard ruler. The vertical position of each nest was determined using a 5-metre measuring tape, measured from the ground surface to the highest point of the nest structure (i.e., the upper edge of the enclosing leaves). Nest volume was calculated using the standard geometric formulas for a sphere or an ellipsoid depending on the nest shape.

The collected metrics were evaluated using standard statistical measures: minimum and maximum values (min, max), mean (M), standard deviation (SD) and coefficient of variation (CV). Normality of the data distribution was assessed with the D'Agostino–Pearson omnibus test and the Shapiro–Wilk test. A 95% confidence level was considered significant. To compare nest positions and their dimensions (length, height and width) among the four main plant species – *Elymus repens*, *Phalaris arundinacea*, *Prunus spinosa* and *Rubus plicatus* – we applied the Kruskal–Wallis H test followed by Dunn's multiple comparison post hoc test, along with Spearman's rank correlation (r_s). These species were chosen because they constitute the dominant vegetation hosting the majority of nests; less frequently used species were excluded to focus the analysis and ensure meaningful comparisons. It should be noted, however, that excluding some species limits the scope for drawing comprehensive conclusions about nest dimensions across all vegetation types. All analyses were carried out using MS Excel 2010 on Windows XP and GraphPad Prism version 5.01 (GraphPad Software, Inc., San Diego, CA, USA).

Results

Over a 15-year survey period (2010–2024), a total of 924 summer nests of *Micromys minutus* were recorded across the monitored sites ($519 + 405 = 924$; see Table 1 and Appendix 1), distributed among various plant species (Table 2). Table 1 summarises the density of Eurasian harvest mouse (*M. minutus*) nests recorded at various sites across Slovakia between 2010 and 2024. Nest density varied widely depending on locality, habitat type and year. The highest densities were generally found in hedgerows and field margins, which provide dense, structurally complex vegetation favourable for nesting. For example, in 2011, a hedgerow at Košice–Šebastovce (Line 1) reached 279.4 nests/ha, while a field margin at Haniska (Line 5) in 2021 recorded 217.5 nests/ha. Similarly, high values were observed at Kendice (253.3 nests/ha) and Haniska (Line 4), with 271.8 nests/ha in a shelterbelt habitat.

In contrast, woodland edge habitats tended to support lower nest densities, often below 50 nests/ha. Several sites recorded very low densities, such as Budimír in 2023 (2.9 nests/ha) and Petrovany in 2024 (2.1 nests/ha), highlighting the

variability across both space and time. Survey transects were uniform in width (c. 1.5 m), but lengths ranged from 660 m to over 5 km; therefore, nest densities were standardised per hectare.

Table 1. List of *Micromys minutus* nests found in various localities across Slovakia during a multi-year inspection, covering the period 2010–2024.

Locality	GPS*	Year	Habitat type	Dimensions**	Σ nests	Σ nests/ha.
Košická kotlina basin						
Budimír	48°47'56"N, 21°17'09"E	2021	hedgerow	2300x1.5	7	20.3
Budimír	48°47'56"N, 21°17'09"E	2023	hedgerow	2300x1.5	1	2.9
Haniska pri Košiciach (Line 2)	48°36'50"N, 21°16'45"E	2021	hedgerow	660x1.5	2	20.2
Haniska pri Košiciach (Line 2)	48°35'55"N, 21°16'52"E	2023	field margin	1900x1.5	21	73.7
Haniska pri Košiciach (Line 2)	48°35'55"N, 21°16'52"E	2024	field margin	1900x1.5	2	7.2
Haniska pri Košiciach (Line 4)	48°35'45"N, 21°15'54"E	2021	windbreak	1300x1.5	53	271.8
Haniska pri Košiciach (Line 4)	48°35'45"N, 21°15'54"E	2023	windbreak	1300x1.5	3	15.4
Haniska pri Košiciach (Line 5)	48°35'55"N, 21°16'52"E	2021	field margin	1900x1.5	62	217.5
Haniska pri Košiciach (Line 5)	48°35'55"N, 21°16'52"E	2024	field margin	1900x1.5	4	14.0
Kendice (Line 1)	48°56'19"N, 21°14'23"E	2021	hedgerow	1000x1.5	38	253.3
Kendice (Line 1)	48°56'19"N, 21°14'23"E	2024	hedgerow	1000x1.5	2	13.3
Košice part Šebastovce (Line 1)	48°39'29"N, 21°15'47"E	2011	hedgerow	2100x1.5	88	279.4
Košice part Šebastovce (Line 1)	48°39'29"N, 21°15'47"E	2012	hedgerow	2100x1.5	10	31.7
Košice part Šebastovce (Line 1)	48°39'29"N, 21°15'47"E	2013	hedgerow	2100x1.5	4	12.7
Košice part Šebastovce (Line 1)	48°39'29"N, 21°15'47"E	2021	hedgerow	2100x1.5	38	120.6
Petrovany (Line 2)	48°56'12"N, 21°15'37"E	2021	woodland edge	3150x1.5	3	6.3
Petrovany (Line 2)	48°56'12"N, 21°15'37"E	2024	woodland edge	3150x1.5	1	2.1
Trstené pri Hornáde (Line 3)	48°34'23"N, 21°19'37"E	2021	field margin	1700x1.5	44	172.5
Trstené pri Hornáde (Line 3)	48°34'23"N, 21°19'37"E	2022	field margin	1700x1.5	5	19.6
Šemša	48°40'51"N, 21°07'17"E	2011	woodland edge	2400x1.5	15	41.7
Šemša	48°40'51"N, 21°07'17"E	2012	woodland edge	2400x1.5	2	5.6
Šemša	48°40'51"N, 21°07'17"E	2013	woodland edge	2400x1.5	3	8.3
Šemša	48°40'51"N, 21°07'17"E	2014	woodland edge	2400x1.5	1	2.8
Šarišská vrchovina Mts.						
Drienovská Nová Ves (Line 1)	48°53'23"N, 21°14'37"E	2021	woodland edge	1500x1.5	4	17.8
Drienovská Nová Ves (Line 2)	48°53'20"N, 21°14'41"E	2021	field margin	2000x1.5	1	3.3
Lemešany – Chabžany	48°50'04"N, 21°15'38"E	2019	hedgerow	2700x1.5	3	7.4
Lemešany – Chabžany	48°50'04"N, 21°15'38"E	2021	hedgerow	2700x1.5	3	7.4
Lemešany – Chabžany	48°50'04"N, 21°15'38"E	2022	hedgerow	2700x1.5	1	2.5
Ondavská vrchovina Mts.						
Duplín (Line 1)	49°14'19"N, 21°38'03"E	2010	woodland edge	5100x1.5	11	14.6
Duplín (Line 1)	49°14'19"N, 21°38'03"E	2011	woodland edge	5100x1.5	31	41.0
Duplín (Line 1)	49°14'19"N, 21°38'03"E	2012	woodland edge	5100x1.5	7	15.9
Duplín (Line 1)	49°14'19"N, 21°38'03"E	2013	woodland edge	5100x1.5	1	1.3
Stropkov	49°11'32"N, 21°13'53"E	2010	hedgerow	2100x1.5	13	41.3
Stropkov	49°11'32"N, 21°13'53"E	2011	hedgerow	2100x1.5	4	12.7
Stropkov	49°11'32"N, 21°13'53"E	2012	hedgerow	2100x1.5	22	69.8
Krušinec	49°14'25"N, 21°39'03"E	2011	woodland edge	2100x1.5	5	15.9
Krušinec	49°14'25"N, 21°39'03"E	2012	woodland edge	2100x1.5	2	6.3
Potoky	49°15'26"N, 21°37'52"E	2012	woodland edge	2200x1.5	1	3.0
Potoky	49°15'26"N, 21°37'52"E	2013	woodland edge	2200x1.5	1	3.0
Total					519	

Note: The GPS coordinates listed here show the location of the line being checked, usually in the middle of the line, **length x width of line.

Marked temporal fluctuations were observed even at the same sites. For instance, Košice–Šebastovce (Line 1) declined from 279.4 nests/ha in 2011 to just 12.7 nests/ha in 2013 and then rose again to 120.6 in 2021. Similar year-to-year variation occurred at Haniska and Duplín.

The measurements of nests found in Slovakia are listed in Table 3, which includes 884 of the total 924 recorded nests. The remaining 40 nests were excluded from measurement due to various forms of damage that affected their shape. Similarly, it was not possible to measure the height of the plant or the position of the nest in all cases. This accounts for the varying total numbers shown in the table. The results showed a wide range of nest sizes, with most nests being circular ($n = 752$, 85.1%), followed by oval-shaped nests ($n = 132$, 14.9%). Despite minor differences in the dimensions of nests from the four selected plant species (see Table 3), the Kruskal–Wallis H test results indicated no significant differences in width, height and volume ($p > 0.05$). Only nest length showed a slight but significant difference among the four nest-bearing plant species ($H = 15.84$, $p = 0.0012$, $p < 0.01$), specifically between *Elymus repens* and *Prunus spinosa* ($p < 0.05$) and *Elymus repens* and *Rubus plicatus* ($p < 0.01$).

Correlation analysis revealed a significant positive relationship between certain nest dimensions ($p < 0.0001$, Table 4). Moreover, the analyses confirmed a positive correlation between the distance of the nest from the ground and plant height, regardless of the plant species used for nesting: *Elymus repens* ($n = 266$, $r_s = 0.314$, $p < 0.001$), *Phalaris arundinacea* ($n = 257$, $r_s = 0.200$, $p < 0.001$), *Prunus spinosa* ($n = 131$, $r_s = 0.275$, $p < 0.001$) and *Rubus plicatus* ($n = 116$, $r_s = 0.624$, $p < 0.0001$).

Discussion

Data from Lloyd and Kirk (2021) showed that harvest mouse nest density was very high in some years. Both study sites peaked in 2014 and then dropped in 2015. These changes were likely caused by outside factors, not natural population cycles like in voles or lemmings (Selås, 2006). One factor was duck farming introduced at Sheerland Farm in 2006, which likely increased rat numbers near the reservoir. Rats eat small mammals (Shepherd, Ditgen, 2012), which may have reduced the harvest mouse population. When ducks were removed and rats were controlled in 2007, nest numbers rose but dropped again in 2008.

Willow growth around the reservoir reduced suitable plants like grasses and sedges. Nest numbers also changed along field edges, but a few were still found in high-density years (1.85 nests/ha in 2004 and 2007). Fences and grazing may have damaged habitats, but nest numbers increased again after the plants recovered. Flooding also reduced nest numbers, but mice were still present the following year.

Our results are consistent with those reported by Lloyd and Kirk (2021) in their multi-year observations of year-to-year density changes. Although our observations were not uniform across all sites (see Tables 1 and 2), it is evident from Table 1 that nest density varied from year to year. These patterns likely reflect changes in vegetation structure, climate, agricultural activity, or population dynamics, emphasising the importance of long-term monitoring to understand harvest mouse ecology across different habitats. The results of our study support the findings of Lloyd and Kirk (2021), who observed strong year-to-year fluctuations

Tab. 2. List of plant species in which harvest mouse nests were found for the period 2010–2024 in Slovakia.

Species	n	%
Couch grass (<i>Elymus repens</i> (L.) Gould)	297	32.1
Reed canary grass (<i>Phalaris arundinacea</i> L.)	262	28.4
Blackthorn (<i>Prunus spinosa</i> L.)	131	14.2
Blackberry (<i>Rubus plicatus</i> Weihe & Nees)	118	12.8
Sedges (<i>Carex</i> spp.)	20	2.1
Meadow fescue (<i>Festuca pratensis</i> (Huds.))	13	1.4
Giant goldenrod (<i>Solidago gigantea</i> Aiton)	13	1.4
on ground	13	1.4
Bristlegrass (<i>Setaria</i> spp.)	11	1.2
Common dogwood (<i>Cornus sanguinea</i> L.)	9	1.0
Cock's-foot (<i>Dactylis glomerata</i> L.)	6	0.6
Common nettle (<i>Urtica dioica</i> L.)	5	0.5
Common reed (<i>Phragmites australis</i> (Cav.) Trin. ex Steud.)	4	0.4
Lady's bedstraw (<i>Galium verum</i> L.)	4	0.4
Dog rose (<i>Rosa canina</i> L.)	2	0.2
European spindle (<i>Euonymus europaeus</i> L.)	2	0.2
Tansy (<i>Tanacetum vulgare</i> L.)	2	0.2
Field maple (<i>Acer campestre</i> L.)	1	0.1
European hornbeam (<i>Carpinus betulus</i> L.)	1	0.1
Creeping thistle (<i>Cirsium arvense</i> (L.) Scop.)	1	0.1
unknown	9	1.0
Total	924	

in harvest mouse nest densities, likely driven by external environmental factors. For example, at Košice–Šebastovce (Line 1), nest density was exceptionally high in 2011 (279.4 nests/ha), dropped sharply in 2012 (31.7 nests/ha) and 2013 (12.7 nests/ha), and rose again in 2021 (120.6 nests/ha). A similar trend is seen at Haniska pri Košiciach (Line 4), where nest density reached 271.8 nests/ha in 2021 but fell to only 15.4 nests/ha in 2023. These fluctuations are unlikely to result from natural population cycles alone and instead may reflect habitat changes, predation pressure, or weather-related impacts – just as Lloyd and Kirk suggest. Furthermore, sites such as Trstené pri Hornáde (Line 3) also show a steep decline from 172.5 nests/ha in 2021 to 19.6 nests/ha in 2022, again matching the pattern of instability noted in their work. These examples reinforce the conclusion that harvest mouse populations can respond rapidly to external pressures, resulting in notable variability in nest densities over short time spans.

Therefore, long-term monitoring of a smaller number of selected sites (habitats) will be necessary in the future to draw more specific conclusions about population density.

Monitoring harvest mouse nests over multiple years is important, yet few studies have addressed this. Most research has focused on the nest size, placement within habitats, or nests recorded incidentally during live-trapping studies (Bence et al., 2003; Surmacki et al., 2005; Riordan et al., 2009; Čanádý, 2012, 2013; Darinot, 2019; Csanádý, 2022). Lloyd and Kirk (2021) highlighted these challenges and conducted a multi-year nest survey, but their data were limited to a specific region and a

Table 3. Measurements (cm) and volume (cm³) of harvest mouse nests from arable landscape of Slovakia (N – number; Range – interval of margins; M – mean, SD – standard deviation; CV – coefficient of variance). Notes: nest position: distance of nest from the ground.

	N	M±SD	Range	CV
Total material				
plant height [cm]	857	107.9±55.22	15.00–1103.00	51.2
nest position [cm]	868	43.03±17.45	8.00–115.00	40.6
length [cm]	884	6.31±1.02	4.00–14.00	16.2
width [cm]	884	6.07±6.19	4.00–10.00	14.4
height [cm]	884	6.12±0.88	4.00–10.00	14.5
volume [cm ³]	884	129.2±58.43	33.50–523.6	45.2
Circle				
plant height [cm]	722	106.9±56.7	15.00–1103.00	53.1
nest position [cm]	732	42.03±17.09	10.00–115.00	40.7
length [cm]	752	6.14±0.03	4.00–10.00	14.4
width [cm]	752	6.14±0.03	4.00–10.00	14.4
height [cm]	752	6.14±0.03	4.00–10.00	14.4
volume [cm ³]	752	128.50±58.46	33.50–523.60	45.5
Oval				
plant height [cm]	132	112.60±45.63	30.00–280.00	40.5
nest position [cm]	132	48.92±18.43	8.00–90.00	37.7
length [cm]	132	7.27±1.21	5.50–14.00	16.7
width [cm]	132	6.06±0.88	4.00–8.00	14.5
height [cm]	132	5.97±0.87	4.00–9.00	14.6
volume [cm ³]	132	133.30±58.36	46.10–376.90	43.8
<i>Elymus repens</i>				
plant height [cm]	266	96.35±26.73	30.00–180.00	27.7
nest position [cm]	269	34.35±12.49	10.00–75.00	36.4
length [cm]	269	6.09±0.84	4.00–9.00	13.8
width [cm]	269	6.07±0.82	4.00–8.00	13.6
height [cm]	269	6.05±0.81	4.00–8.00	13.4
volume [cm ³]	269	121.4±49.59	33.50–268.1	40.8
<i>Phalaris arundinacea</i>				
plant height [cm]	257	119.7±67.98	30.00–1103.00	56.8
nest position [cm]	258	44.51±15.99	8.00–110.00	35.9
length [cm]	260	6.32±0.97	4.00–10.00	15.3
width [cm]	260	6.13±0.88	4.00–10.00	14.3
height [cm]	260	6.11±0.89	4.00–10.00	14.6
volume [cm ³]	260	128.60±56.96	33.50–523.6	44.3
<i>Prunus spinosa</i>				
plant height [cm]	131	135.80±53.95	55.00–300.00	38.9
nest position [cm]	131	57.45±20.35	25.00–115.00	35.4
length [cm]	131	6.48±1.19	4.50–10.00	18.3
width [cm]	131	6.02±0.97	4.00–10.00	16.1
height [cm]	131	6.03±0.98	4.00–10.00	16.3
volume [cm ³]	131	129.7±67.37	47.70–523.60	52.0
<i>Rubus plicatus</i>				
plant height [cm]	116	68.41±57.40	15.00–623.00	83.9
nest position [cm]	116	41.61±16.89	15.00–90.00	40.6
length [cm]	116	6.60±1.24	5.00–14.00	18.7
width [cm]	116	6.26±0.85	4.00–8.00	13.6
height [cm]	116	6.25±0.83	4.00–8.00	13.3
volume [cm ³]	116	139.4±57.87	46.10–359.2	41.5

shorter time frame. Here, we build on their work by presenting 15 years of nest survey data from a different country, providing a broader temporal and geographical perspective. For example, Hata (2011) conducted a 5-year study (1999–2005) at three sites but only reported total nest numbers per site without yearly breakdowns.

Earlier estimates of aerial nest densities have been provided by several authors (Sleptsov, 1947; Kminiak, 1968a, b; Trout, 1976 in Trout, 1978a, b), offering valuable historical context. For instance, Sleptsov (1947, cited in Trout, 1978) recorded nest counts in eight habitat types over four consecutive years (1941–1944). He found significant variation in nest density between habitats and years, ranging from 71 nests/ha in *Calamagrostis* reed in 1944 to 398 nests/ha in a rice field in 1941. The highest densities were observed in all habitats in 1941, with the lowest in 1942, suggesting synchrony in harvest mouse populations across habitats. These historical data complement modern long-term studies and help to better understand population fluctuations and habitat preferences over time.

Our multi-year nest study in Slovakia showed varying nest densities depending on habitat type and year, ranging from 2.1 to 271.8 nests/ha depending on locality and habitat. These values are consistent with or even exceed ranges reported in previous studies (e.g., Trout, 1976; Sleptsov, 1947). According to Trout's (1976) approach – where each nest potentially represents one breeding female and average brood sizes range from 3 to 5 offspring – our highest observed density of about 270 nests/ha could correspond to a local production of approximately 800–1,350 young/ha. However, it is important to note that not all nests serve as breeding nests; some may be used solely for resting, and a single individual can have multiple nests, which can significantly affect population estimates. This introduces uncertainty when directly linking nest density to population size. Nevertheless, our data provide valuable insights into spatial and temporal variations in nest density and offer a foundation for estimating the local population size in Slovakia.

According to Lloyd and Kirk (2021), geographical location, changes in habitats and land management since the 1940s may have contributed to the decline of harvest mouse populations in Britain (Matthews, Harrower, 2020).

Long-term studies conducted in Slovakia (Čanádý, 2012, 2013; Čsanádý, 2022; results of this work) revealed the characteristics of plant species that support nesting along field edges and in marginal habitats. The results confirmed that the main supporting plant species in these areas were *Elymus repens*, *Phalaris arundinacea*, *Prunus spinosa* and *Rubus plicatus*. The dimensions of the nests did not differ significantly from those reported in previous studies from various habitat types – such as peat bogs and cornfields – in the Czech Republic (Farský, 1963), western Slovakia (Kminiak, 1968a,b) and neighbouring Hungary (Szunyoghy, 1952). Kminiak (1968a,b), based on many nests ($n = 1450$) from wet habitats near drainage channels dominated by thick-stemmed plants such as *Phragmites* spp., *Typha* spp. and *Carex* spp., reported average nest width $\times$ height (5 $\times$ 6.5 cm). A comparison of our data (see also Čanádý, 2013) with Kminiak's findings confirmed that the nest sizes did not differ, despite originating from two distinct habitat types.

Although slight differences in nest dimensions were observed between the plant species (*Prunus spinosa*, *Rubus plicatus*, *Elymus repens* and *Phalaris arundinacea*), the analysis showed

Table 4. Spearman's correlation coefficients (r_s) for harvest mouse nest measurements across all plants ($n = 884$). All comparisons were highly significant with p -values < 0.0001 .

	length	width	height
width	0.84		
height	0.83	0.98	
volume	0.90	0.96	0.96

that these differences were not statistically significant. Only minor variations in nest length were noted depending on the plant used for anchoring. We believe that these variations resulted from structural limitations of the plants – either dense branching or stem instability – particularly in the case of *Elymus repens* and *Phalaris arundinacea*. This was especially evident in the nest sizes supported by shrub branches (*Prunus spinosa*, *Rubus plicatus*), which were generally larger than those supported by grasses (*Elymus repens*, *Phalaris arundinacea*). These findings regarding nest placement were consistent with those reported by Szunyoghy (1952).

Our long-term observations confirmed that the nests were typically circular to oval, although precise categorisation proved difficult. The overall structure likely reflects a combination of nesting behaviour, the type of vegetation used for support and environmental factors, particularly weather conditions, as the nests were primarily surveyed during the autumn–winter period.

The nest heights recorded in this study confirmed previous findings (Bence et al., 2003; Surmacki et al., 2005; Hata et al., 2010; Hata, 2011; Čanádý, 2013) that variation in nest height is mainly driven by differences in the plant height. Hata et al. (2010) and Hata (2011) demonstrated that elevated nests can reduce the risk of ground predation. Surmacki et al. (2005) investigated the occurrence of *Micromys minutus* nests in relation to peatland structure in Poland. Based on their results, the authors concluded that harvest mice preferred peatlands with low, thin and sparse stems and a high proportion of *Carex*/grass species while avoiding areas with dense herbaceous vegetation.

In western Slovakia, Kminiak (1968a, b) reported an average nest height of 37.6 cm above ground level in peat bogs. In contrast, harvest mice in Hungarian peatlands built their nests at heights of 70–80 cm (Szunyoghy, 1952). In our study, the position of nests on the four main plant species (*Prunus spinosa*, *Rubus fruticosus*, *Elymus repens* and *Phalaris arundinacea*) in eastern Slovakia was predominantly in the middle parts of the plants. This likely provided increased nest stability and better protection within the denser growth of grasses and shrub branches (Čanádý, 2013).

In conclusion, long-term research in Slovakia identified key plant species supporting the nesting of the Eurasian harvest mouse (*Micromys minutus*) in edge habitats, notably *Elymus repens*, *Phalaris arundinacea*, *Prunus spinosa* and *Rubus plicatus*. The nest sizes were consistent across plant species, with minor variations linked to the plant structure. Nests were generally circular to oval and located in the mid-sections of plants, providing stability and protection. Nest height corresponded with plant height, reducing predation risk. Harvest mice favoured habitats with dense vegetation and abundant grasses and shrubs, which

serve as important refuges in intensively managed agricultural landscapes. Nest densities varied widely between sites and years, ranging from 2.1 to 271.8 nests/ha. However, as nests may be used for resting as well as breeding, and individuals can occupy multiple nests, nest density alone does not directly reflect the population size but remains a valuable indicator for habitat use and monitoring.

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Appendix 1. List of *Micromys minutus* nests found (only once) in various localities across Slovakia covering the period 2010–2024.

Locality	GPS [*]	Year	Habitat type	Dimensions ^{**}	Σ nests	Σ nests/ha.
Košická kotlina basin						
Belža (Line 1)	48°35'43"N, 21°16'12"E	2021	field margin	1500x1.5	7	31.1
Bočiar (Line 1)	48°35'13"N, 21°14'11"E	2021	field margin	1000x1.5	4	26.7
Bočiar (Line 2)	48°35'03"N, 21°14'17"E	2021	field margin	1400x1.5	7	33.3
Bretejovce (Line 1)	48°50'03"N, 21°17'30"E	2021	field margin	380x1.5	2	35.1
Čaña (Line 1)	48°36'26"N, 21°18'03"E	2021	field margin	2000x1.5	5	16.7
Čaña (Line 2)	48°36'27"N, 21°18'04"E	2021	hedgerow	900x1.5	10	74.1
Drienov	48°36'27"N, 21°18'04"E	2021	woodland edge	7400x1.5	11	9.9
Gyňov (Line 1)	48°35'06"N, 21°19'47"E	2021	hedgerow	2095x1.5	21	66.8
Gyňov (Line 2)	48°35'18"N, 21°19'01"E	2021	field margin	890x1.5	4	30.0
Haniska pri Košiciach (Line 1)	48°37'00"N, 21°15'53"E	2021	hedgerow	1000x1.5	8	53.3
Haniska pri Košiciach (Line 3)	48°36'58"N, 21°16'28"E	2021	hedgerow	1000x1.5	6	40.0
Haniska pri Prešove	48°56'45"N, 21°14'39"E	2021	hedgerow	1500x1.5	23	102.2
Janovík	48°50'09"N, 21°17'34"E	2021	field margin	200x1.5	5	166.7
Kendice (Line 2)	48°56'19"N, 21°14'23"E	2021	hedgerow	1200x1.5	26	144.4
Kendice (Line 3)	48°56'12"N, 21°14'21"E	2021	hedgerow	400x1.5	6	83.3
Ličartovce (Line 3)	48°52'11"N, 21°15'07"E	2021	field margin	240x1.5	6	166.7
Milhost' (Line 1)	48°31'55"N, 21°16'19"E	2021	field margin	580x1.5	2	22.9
Milhost' (Line 2)	48°31'43"N, 21°16'24"E	2021	field margin	1200x1.5	26	144.4
Milhost' (Line 3)	48°32'00"N, 21°16'50"E	2021	hedgerow	1400x1.5	8	38.1
Obišovce (Line 1)	48°51'48"N, 21°15'21"E	2021	field margin	2300x1.5	5	14.5
Petrovany (Line 4)	48°56'12"N, 21°15'37"E	2021	hedgerows	500x1.5	4	53.3
Prešov	48°56'17"N, 21°14'48"E	2023	field margin	660x1.5	8	80.8
Ploské	48°49'20"N, 21°20'21"E	2021	hedgerow	2700x1.5	22	54.3
Seniakovce (Line 1)	48°49'23"N, 21°17'57"E	2021	field margin	2900x1.5	52	119.5
Seniakovce (Line 2)	48°49'19"N, 21°17'46"E	2021	hedgerow	1100x1.5	34	206.1
Sokolany	48°35'52"N, 21°13'49"E	2021	field margin	850x1.5	8	62.7
Trstené pri Hornáde (Line 1)	48°34'29"N, 21°21'18"E	2021	hedgerow	490x1.5	5	68.0
Seňa	48°34'50"N, 21°14'15"E	2021	hedgerow	1250x1.5	4	21.3
Valaliky	48°38'46"N, 21°16'44"E	2021	wetland	1500x1.5	3	13.3
Ždaňa/Čaña	48°36'30"N, 21°20'53"E	2021	field margin	3000x1.5	18	40.0
Veľká Ida	48°36'47"N, 21°08'23"E	2024	field margin	300x1.5	1	22.2
Kechnec	48°33'22"N, 21°14'13"E	2012	drainage canal	766x1.5	19	165.4
Šarišská vrchovina Mts.						
Drienovská Nová Ves (Line 1)	48°53'23"N, 21°14'37"E	2021	woodland edge	1500x1.5	4	17.8
Drienovská Nová Ves (Line 2)	48°53'20"N, 21°14'41"E	2021	field margin	2000x1.5	1	3.3
Ličartovce (Line 1)	48°53'11"N, 21°14'40"E	2021	woodland edge	400x1.5	9	150.0
Ličartovce (Line 2)	48°53'14"N, 21°14'45"E	2021	field margin	330x1.5	3	60.6
Obišovce (Line 2)	48°52'02"N, 21°14'00"E	2021	woodland edge	1400x1.5	1	4.8
Ondavská vrchovina Mts.						
Jurkova Voľa	49°19'25"N, 21°31'37"E	2011	woodland edge	500x1.5	1	13.3
Korunková	49°12'36"N, 21°45'02"E	2015	woodland edge	1500x1.5	2	8.9
Mrázovce	49°06'23"N, 21°40'39"E	2013	woodland edge	1500x1.5	1	4.4
Solník	49°12'59"N, 21°44'47"E	2017	woodland edge	1600x1.5	1	4.2
Lomné	49°06'39"N, 21°37'07"E	2012	woodland edge	1200x1.5	5	27.8
Miňovce	49°07'22"N, 21°39'20"E	2012	woodland edge	1400x1.5	3	14.3
Tokajík	49°06'51"N, 21°42'18"E	2013	woodland edge	1500x1.5	1	4.4
Duplín	49°14'21"N, 21°38'02"E	2013	woodland edge	5100x1.5	1	1.3
Vyšná Olšava	49°10'08"N, 21°35'52"E	2015	woodland edge	600x1.5	1	1.1
Mirola	49°20'04"N, 21°43'53"E	2014	woodland edge	850x1.5	1	7.8
Total					405	

Note: The GPS coordinates listed here show the location of the line being checked, usually in the middle of the line, ^{**}length x width of line.