

Article

Isotopic Space of the House Mouse in the Gradient of Anthropogenic Habitats

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Abstract: The house mouse (*Mus musculus*) is a most extensively distributed omnivorous rodent species, usually living in close association with humans. Its diet includes various vegetable matter, insects and any available human food. For the first time, we assessed the dietary niche of this species by the isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) compositions of animal hair samples in the gradient of habitats, ranging from natural to fully commensal. The main factors explaining the differences in the isotopic niche of the mice, being the proxy of their diet, were the season and the source of available food. Influence of the habitat was weak, while gender, age, body mass and body condition had no influence on the diet differences. We found that *M. musculus* dietary niches overlap between different habitats if mice have access to human food. Niches diverge when mice forage outdoors on natural food compared to farms where livestock feed is available. Compared to omnivorous bank vole (*Clethrionomys glareolus*) living synoptically, *M. musculus* has much wider dietary niche and consumes more foods of animal origin. Variability of the diet increases the ecological plasticity of this strongly commensal species and, together with behavioural and reproductive adaptability, allows irresistibly occupy various environments.

Keywords: *Mus musculus*; isotopic niche; species proportion; habitat gradient



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1. Introduction

The house mouse (*Mus musculus*) is a Palaearctic species, currently the most widespread invasive mammal due to its commensal nature, synanthropy and agrophilia [1–5]. *M. musculus* inhabits all continents except Antarctica [2,6]. Wild populations of this species live in agropastoral areas, grasslands and shrublands [7,8]. However, the main habitats of *M. musculus* are man-made, mainly buildings and farms [1,8,9], where it becomes commensal and storage pest [10].

In Lithuania, *M. musculus* is a widespread and very common species that is exterminated as an indoor pest [11,12]. In the wild, the species seems not abundant, but agricultural areas have not been intensively surveyed [13,14]. Eventually, *M. musculus* accounted for 0.97% of all small mammals captured and 0.90% of Tawny owl (*Strix aluco*) and Long-eared owl (*Asio otus*) prey between 1975 and 2021 [14]. In synanthropy, the species proportions ranged from zero [15] to 32.4% [16] and 95.5% [17] of the total number of small mammals trapped. Two of the former null sites began to be colonized by mice between 2021 and 2022 (see below).

Feral populations of *M. musculus* are not stable in temporal, spatial, and social aspects in contrast with commensal populations [18]. This species has exceptional ecological adaptability, allowing it to live in a wide range of environments [19]. The differences in ecology of a species are well reflected in the diversity of its diets [20,21]. As a highly omnivorous species [19], *M. musculus* can have impact on plant, invertebrate and vertebrate populations [5,22,23]. The most considerable damages might be inflicted in the isolated

islands [22,24,25]. On the other hand, variability in diet and resource partitioning allows habitat sharing with the other sympatric or syntopic small mammals [26]. The diet of *M. musculus* can vary depending on food availability, food quality and competition with other coexisting species [22,27], intraspecific competition and structure of the habitat [28].

The diet composition in small mammals can be investigated with several methods, including faecal analysis [29] and stomach content analysis [30], currently enhanced by using metabarcoding [31]. Field observation of feeding and analysis of food remains [22] is hardly acceptable due to shy behaviour of mice [3,19].

Therefore, the analysis of stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) ratios is now used to determine small mammal trophic levels and diet [22], resource partitioning [26,32] and trophic interactions [33]. As there may be uncertainties in identifying specific taxa consumed by rodents [34] and discrimination values may vary [35], it is preferable to estimate diet by multiple methods, but this is rarely done. Dietary niche reflects the consumed food, meanwhile isotopic niche reflects the consumed food via animal tissues, as they were formed from the routed dietary nutrients [36]. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been determined in various tissues, faeces and hair of rodents [37–39]. Thus, isotopic niche as a proxy of a diet may reflect dietary niche spaces as they both are related to animal's diet [33,40].

The studies using mammalian hair as a source for measuring $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, has a long history, but is still widely used [39,41,42]. Depending on the pattern of moulting, hair may reflect seasonal, annual or lifelong diets [43,44]. We studied hair samples from small mammals, so most individuals had the same body mass of 15–20 g. Therefore, our samples were not enriched in isotopes due to body mass [45], were not affected by lipid content, which can alter the isotopic ratio in some tissues [46], and were independent of sample fixation [47]. It is known that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values might differ according to the resources present [48], and so was the case of herbivores, granivores and omnivorous bank vole (*Clethrionomys glareolus*) in our studies of Lithuanian small mammals in natural [26,49], agricultural [50–52] and anthropogenic habitats [15]. However, *M. musculus* was not analysed.

The aim of the study was to analyse the proportions of *M. musculus* in small mammal communities, to investigate the variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (as an indicator of the species diet) along a gradient of natural, agricultural and common habitats and to assess the influence of season, food source, sex and age of the individual on the variation of the isotopic values in the hair of the individuals.

2. Materials and Methods

2.1. Study Sites and Sampling

Investigation of *M. musculus* were conducted at 10 sampling sites between 2018 and 2022 (Figure 1). Represented habitats, in order of increasing degree of anthropisation, were: a meadow; two apple orchards, two currant and one raspberry plantation; kitchen garden (limited number of buildings, additional food available only in warm period); two homesteads (various buildings, human food available in the most of the year, no livestock, poultry or rabbit feed) and two farms (various buildings, unlimited access to human food and livestock poultry or rabbit feed).

In all habitats, small mammals were snap-trapped. Small mammals were trapped in summer and autumn in gardens and plantations, but all year round in shared habitats; therefore, four seasons were used for analysis. Traps were set in rows of 25 traps at 5 m spacing in meadows (as control habitats for the orchards), orchards and berry plantations, as described in [13,26,50–52]. In kitchen gardens, homesteads and farms, particularly inside structures, small mammals were trapped opportunistically using 5 to 20 traps in and around all accessible buildings [15]. Therefore, relative abundance, expressed as the number of individuals per 100 trap days, was not always available.

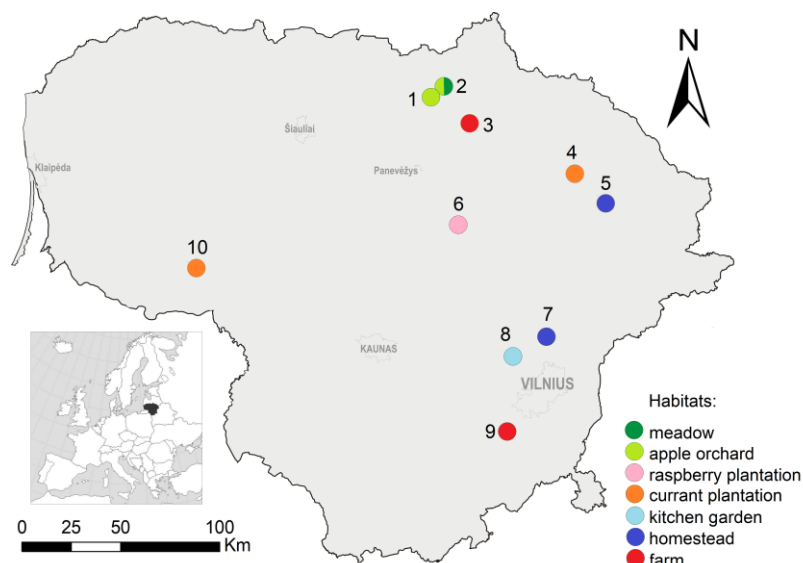


Figure 1. Study sites in Lithuania, 2018–2022. Habitats, in order from natural to most commensal, indicated by colour.

Habitats present in homesteads and farms were gardens (including vegetable gardens and orchards), buildings with available human food (such as houses, porches, cellars, box-rooms, barns and greenhouses) and outbuildings without human food available (such as the bathhouse, garage and tool shed). In the investigated farms there were also buildings with livestock feed available for mice all year round, such as sheds and storage rooms. Food availability in commercial orchards depended on agricultural measures, such as grass mowing or soil scarification and, therefore, its seasonality was not pronounced.

M. musculus were identified according to the notch in the upper incisive and the characteristic smell, while other trapped small mammal species were identified by external features and teeth according to the identification key [11]. The gender and age group (adult, sub-adult or juvenile) were assessed at dissection, more detailed information is given in [15,17,26]. We calculated body condition index C based on the body length and body mass, with the weight of the uterus with embryos excluded in pregnant females, according to Moors [53].

Hair samples from trapped *M. musculus* were collected by cutting small hair tufts from the back. The samples were stored in a refrigerator in separate bags. We collected 105 *M. musculus* hair samples between 2018 and 2022. Very dirty *M. musculus* individuals or those damaged by insects were not sampled. Sample breakdown by site and habitat, age and gender of animals is shown in Table 1.

Table 1. *M. musculus* sample size for stable isotope analysis.

Site No	Year	Habitat	N	Males	Females	Adults	Subadults	Juveniles
1	2022	Apple orchard	1	1	0	0	0	1
2	2022	Apple orchard	2	2	0	0	2	0
2	2018, 2021	Meadow	4	2	2	2	0	2
3	2021–2022	Farm	65	43	22	38	12	15
4	2018	Currant plantation	1	1	0	0	0	1
5	2022	Homestead	1	1	0	0	1	0
6	2018–2019	Raspberry plantation	2	1	1	1	1	0
7	2022	Homestead	4	2	2	1	0	3
8	2022	Kitchen garden	3	1	2	2	1	0
9	2018	Farm	21	11	10	10	3	8
10	2019	Currant plantation	1	1	0	1	0	0
In total			105	66	39	55	20	30

2.2. Stable Isotope Analysis of Hair

Dirty hair samples were washed in deionized water and methanol, then desiccated. Dry samples were weighted (0.5–1 mg) into tin capsules and stored in the sample plate before analyses. The prepared samples were analysed for carbon and nitrogen isotopic ratios using an elemental analyser (Flash EA1112) coupled to an isotope ratio mass spectrometer (Thermo Delta V Advantage) via a ConFlo III interface in Centre for Physical Sciences and Technology, Lithuania. The stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) are expressed relative to the international standards Vienna Pee Dee Belemnite and atmospheric air, respectively. A total of 5 out of 105 samples were analysed in duplicate and the results obtained for these samples were averaged [52].

Caffeine IAEA-600 ($\delta^{13}\text{C} = -27.771 \pm 0.043\text{‰}$, $\delta^{15}\text{N} = 1 \pm 0.2\text{‰}$), ammonium sulphate IAEA-N-1 ($\delta^{15}\text{N} = 0.4 \pm 0.2\text{‰}$) and graphite USGS24 ($\delta^{13}\text{C} = -16.049 \pm 0.035\text{‰}$), provided by the International Atomic Energy Agency, were used as the reference materials. The standards were resampled every 12 samples, yielding $\text{SD} = 0.06\text{‰}$ for carbon and $\text{SD} = 0.10\text{‰}$ for nitrogen.

2.3. Data Analyses

The proportion of *M. musculus* among all trapped small mammals (Table 2) was presented as average and the 95% CI for each locality, differences in the proportions were evaluated using the G test. We also present species richness (S) and diversity (Shannon's H) as a measure of the diversity of the sampled communities calculated from the pooled data. Differences of Shannon's indices were calculated using bootstrap with $n = 9999$. In PAST, the given number of random samples was produced, each with the same total number of individuals as in the original sample.

Table 2. Characteristics of small mammal communities in relation to gradient of habitats, from natural to farms. N—number of trapped small mammal individuals; S—number of trapped species; H—diversity (Shannon's index); P%—proportion of *M. musculus* (95% CI); RA—relative abundance of *M. musculus* (individuals per 100 trap days). Superscript letters denote differences of the values in columns, significant at $p < 0.05$.

Habitat	Year	N	S	H	P%	RA
Meadow	2018–2022	152	10	1.48 ^a	3.3 ^a (CI = 1.1–7.5)	0.05
Apple orchard	2018–2022	134	8	1.35 ^a	2.2 ^a (CI = 0.5–6.4)	0.03
Currant plantation	2018–2019	92	6	0.96 ^b	2.2 ^a (CI = 0.3–7.6)	0.02
Raspberry plantation	2018–2019	7	3	0.96 ^b	28.6 ^b (CI = 3.8–71.0)	0.19
Kitchen garden	2019–2022	361	9	1.24 ^c	0.8 ^a (CI = 0.2–2.4)	n/a
Homestead	2019–2022	645	11	1.36 ^a	0.9 ^a (CI = 0.3–2.0)	n/a
Farm	2018, 2021–2022	289	6	1.26 ^c	59.2 ^b (CI = 53.3–64.9)	6.67

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the hair samples were expressed as the arithmetic mean ± 1 SE and the range (min–max), wider range corresponding to more variable diet. The isotopic values of species and intraspecific groups, including those with sample size $n < 5$, were visualized in isotopic biplots. The isotopic niches were analysed using the parameters of TA (total area) and SEA (standard ellipse area), unbiased for the sample size [36].

We used GLM to find the influence of the habitat, season, food origin – available food source, gender and age of mice as categorical factors on the dependent parameters: the hair $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of *M. musculus*. Habitats were orchard, homestead, kitchen garden and farm; seasons—spring, summer, autumn and winter; and food sources were natural food, human food and livestock feed. Body mass of an individual and body condition coefficient were set as continuous predictors to control data variability. We

also tested if body mass and body condition index were correlated with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Hotteling's two sample T^2 test for significance was used to test the significance of the model and eta-squared for the species and habitat influence. Outliers were not excluded. Differences between groups were evaluated with the post hoc Tukey's test, pairwise comparisons with Student's t . As we did not find differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sites (post hoc, nonsignificant), data were pooled on the habitat basis.

The normality of the distributions of the hair $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values *M. musculus* were evaluated using Kolmogorov–Smirnov's D test online [54].

The minimum confidence level was set as $p < 0.05$. Calculations were done in Statistica for Windows, version 6.0 (StatSoft, Inc., Tulsa, OK, USA), biplots were drawn in SigmaPlot ver. 12.5 (Systat Software Inc., San Jose, CA, USA), diversity estimates were calculated in PAST ver. 2.17c (Ø. Hammer, D.A.T. Harper, Oslo, Norway). The isotopic niches were calculated with SIBER [36] under R version 3.5.0 (<https://cran.r-project.org/bin/windows/base/rdevel.html>, accessed on 12 September 2020).

3. Results

3.1. House Mouse in Small Mammal Communities

The surveyed small mammal communities in natural and indoor habitats differed in terms of diversity (Table 2) and in the representation of *M. musculus*. This species was best represented in the less species-rich communities, with between three and six species. The most species-rich habitats were farmsteads, meadows and kitchen gardens and community diversity was also high in apple orchards.

In the kitchen garden and one of the two homesteads, *M. musculus* were trapped only in 2022; in the orchards and plantations, a few *M. musculus* were present in 2018 and 2021, but none in 2019, 2020 and 2022.

The proportion of *M. musculus* varied significantly between habitats ($G = 592.1$, $p < 0.0001$)—it was the dominant species on the farms, accounting for 36.5% of all small mammals caught in site No 3 and 95.5% in site No 9 (Figure 1). The species was not numerous in kitchen gardens and homesteads. The only habitat where the relative abundance of *M. musculus* was high were farms, where RA was 100–300 times higher than in most natural habitats (Table 2).

3.2. Stable Isotope Ratios of House Mouse in Anthropogenic Habitats

The central position of the *M. musculus* stable isotope ratio in the most natural habitats—meadows, gardens and plantations—was the highest according to both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The ranges of hair $\delta^{15}\text{N}$ values of mice trapped in kitchen gardens and homesteads were very narrow, while the ranges of hair $\delta^{15}\text{N}$ values of mice trapped on farms and orchard plantations were more than three times wider (Table 3). The wider range reflects the greater variety of foods of animal origin in the diet. Ranges of $\delta^{13}\text{C}$ values across these habitats did not differ that much.

Table 3. Central position (mean \pm SE) and ranges of hair stable isotope ratios of *M. musculus*.

Habitat	N	$\delta^{13}\text{C}$, ‰			$\delta^{15}\text{N}$, ‰		
		Mean \pm SE	Min–Max	Range	Mean \pm SE	Min–Max	Range
Orchard and plantation	10	-16.55 ± 1.53	-24.09 – -11.42	12.67	10.84 ± 1.49	6.42–18.40	11.98
Kitchen garden	3	-23.28 ± 3.11	-28.51 – -17.75	10.76	7.29 ± 0.76	5.93–8.55	2.62
Homestead	5	-21.79 ± 1.70	-26.88 – -17.19	9.69	8.20 ± 0.67	6.49–9.67	3.18
Farm	86	-23.42 ± 0.29	-27.21 – -13.89	13.32	8.37 ± 0.26	4.72–16.41	11.69

Normality of distribution was confirmed in all habitats except for hair $\delta^{13}\text{C}$ values of farm mice ($D = 0.22$, $p < 0.001$); kitchen garden and homestead mice samples were pooled.

The cumulative influence of season, habitat, available food source, animal gender and age was significant for the distribution of both $\delta^{13}\text{C}$ ($F_{14.88} = 5.13$, $p < 0.0001$) and $\delta^{15}\text{N}$ ($F_{14.88} = 3.80$, $p < 0.0001$) values, explaining 36.2% and 27.8% of the variation, respectively.

At univariate level, season (Hotelling's $T^2 = 0.17$, $p < 0.05$) and available food source ($T^2 = 0.18$, $p < 0.05$) were the only significant factors, in both cases $\eta^2 = 0.08$. The influence of habitat ($T^2 = 0.13$, $p < 0.08$) was on the trend level. Two other categorical factors, gender ($T^2 = 0.02$) and age ($T^2 = 0.02$), and continuous predictors, body mass ($T^2 = 0.001$) and body condition ($T^2 = 0.02$), all were not significant.

Correlation between body mass and $\delta^{15}\text{N}$ was not significant, that with $\delta^{13}\text{C}$ —significant, but weak ($r = -0.23$, $p < 0.02$), explaining only 5.3% of $\delta^{13}\text{C}$ variance. Correlations of body mass index with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were both positive, though weak ($r = 0.26$ and 0.25 , respectively, $p < 0.02$), explaining 6.5% and 6.4% of variance, respectively.

Average hair $\delta^{13}\text{C}$ values of mice from farms were significantly lower than those in orchards (Tukey's HSD, $p < 0.001$), kitchen gardens and homesteads (both $p < 0.05$). Habitat separation of *M. musculus* according to $\delta^{15}\text{N}$ values was not expressed (Figure 2a).

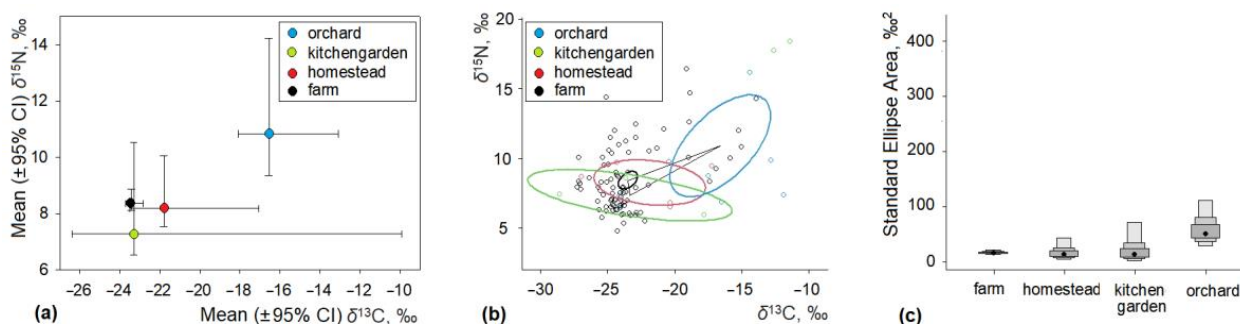


Figure 2. Position of *M. musculus* in isotopic space according to hair sample stable isotope ratios in the gradient of anthropogenic disturbance of habitats, from orchards to farms (a), ellipses, representing isotopic niche width areas of the mice from different habitats (b), and SEA density plots, representing the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th and 95th (shown from dark to light) credibility intervals for different habitats (c).

For comparison in niche size of *M. musculus*, we calculated standard ellipse areas (SEA). Isotopic niches based on standard ellipses show at least partial overlap in all groups representing different habitats (Figure 2b). Individuals from orchards and kitchen gardens had variation that is more considerable according to SEA (Figure 2c) to compare with the farms and homesteads.

When mice were trapped in natural habitats, their hair $\delta^{13}\text{C}$ values were significantly higher than in all other cases (HSD, $p < 0.001$). When the food source included livestock feed indoors, the mice hair $\delta^{15}\text{N}$ values were the lowest ($p < 0.001$). As shown by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, *M. musculus* had similar diets when they could obtain food from both natural and anthropogenic sources, which was assumed to be the case for mice trapped in outbuildings or when human food was readily available, as in the case of mice indoors close to the source of human foods (Figure 3a).

These differences were reflected in the trophic niches of *M. musculus*. The ellipse areas were completely separated when mice fed in the orchards on the natural foods, compared to when food was received in farms (Figure 3b). Individuals that consumed food from natural sources had significantly more variable isotope values, as shown in Figure 3c, with both estimated TA and SEA being the highest.

If mice were able to obtain natural food and human food at the same time, as was the case for *M. musculus* trapped at various buildings in the kitchen garden, homesteads and residential buildings on both farms, the ellipses overlapped (Figure 3b), but the variation was much smaller (Figure 3c). The lowest dietary variation and the smallest ellipse area were found for *M. musculus* using livestock feed.

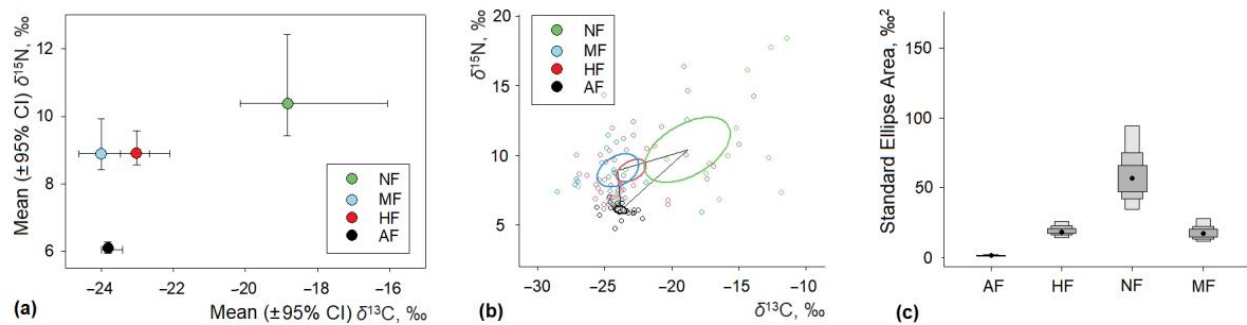


Figure 3. Position of *M. musculus* in isotopic space according to hair sample stable isotope ratios in the gradient of available food sources (a), ellipses, representing isotopic niche width areas of the mice, according to available food sources (b), and SEA density plots, representing the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th and 95th (shown from dark to light) credibility intervals, according to available food sources (c). NF—mice foods originated from natural sources, MF—mice foods from natural and anthropogenic sources; HF—human foods available; AF—livestock, rabbits and poultry feed available.

3.3. Intraspecific Differences of Isotopic Ratios in House Mice

Analysing pooled sample, no gender- or age-based differences were found in the isotopic space of *M. musculus* (Figure 4). This means that males and females (Figure 4a) and adults, subadults and juveniles (Figure 4b) most probably consumed similar food sources according to their isotopic data. Lower $\delta^{13}\text{C}$ values were found in the hair of adult mice, although the difference was at trend level (Tukey's HSD, $p < 0.07$). Meanwhile, nitrogen isotopic values of juveniles and subadults tend to be higher.

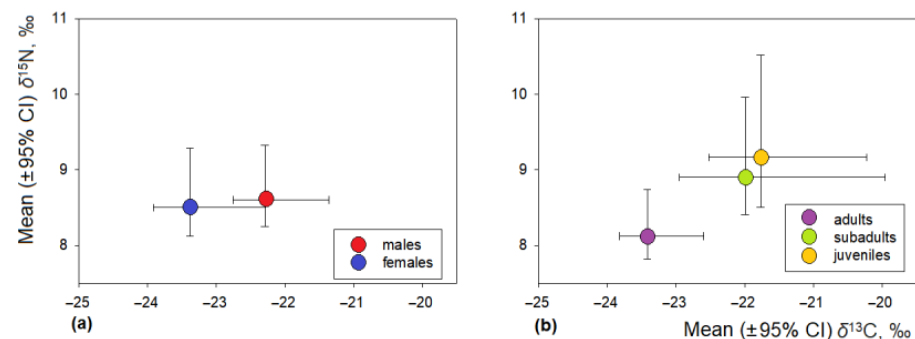


Figure 4. Intraspecific differences of the isotopic space of *M. musculus*: (a)—gender-based; (b)—age-based.

3.4. Seasonal Differences of Isotopic Ratios in House Mice

The isotopic space of *M. musculus* showed some seasonal aspects (Figure 5). The highest hair $\delta^{15}\text{N}$ values were found in autumn and significantly exceeded the winter (HSD, $p < 0.02$) and spring ($p < 0.005$) values. The highest $\delta^{13}\text{C}$ values were also characteristic to autumn season (Figure 5a) and exceeded the summer ones ($p < 0.01$).

Standard ellipse areas of *M. musculus* overlapped in winter and spring, but were fully separated in autumn and summer (Figure 5b) showing that these seasonal dietary niches were different in some extent. SEA density plots (Figure 5c) showed that in autumn standard ellipse area was considerably larger indicating the wider range of consumed resources in autumn, to compare with the other seasons.

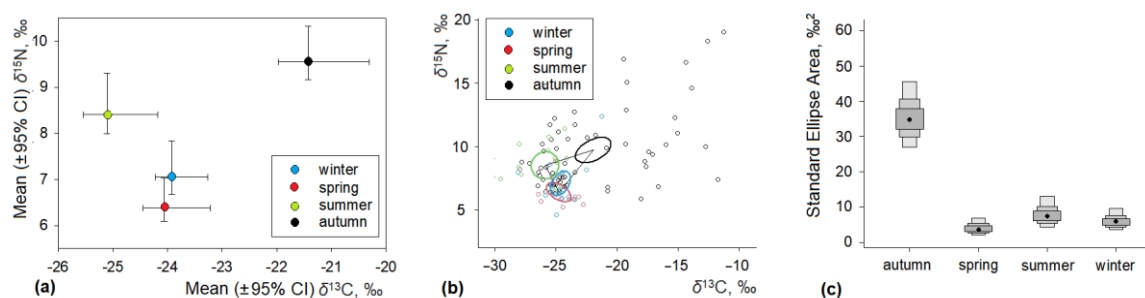


Figure 5. Seasonal position of *M. musculus* in isotopic space according to hair sample stable isotope ratios (a), ellipses, representing isotopic niche width areas of the mice, trapped at different seasons (b), and SEA density plots, representing the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th and 95th (shown from dark to light) credibility intervals, according to the seasons (c).

4. Discussion

M. musculus is widely distributed in Lithuania [11,12], though no permanent feral populations exist [12–14,17]. However, no studies of species diet have been conducted thus far. Our results from stable isotope analysis of their hair showed that the diet of *M. musculus* was highly variable, depending mainly on the season and their food source and, to a lesser extent, on the habitat in which the mice were trapped. No intraspecific (age or gender based) differences were found.

We presume that *M. musculus* can change foraging strategies according to the habitat, in particular depending on the degree of anthropogenic impact. We found that *M. musculus* dietary niches overlap in different habitats as long as mice have access to human food. Therefore, we believe this being an evidence that *M. musculus* prefers food of anthropogenic origin, which is abundant and available throughout the year. Niches diverge when they forage outdoors on natural foods compared to farms where mice have access to livestock feed. The hair $\delta^{15}\text{N}$ values of mice from farms were lowest, while the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were the highest in the most natural outdoor habitats. When *M. musculus* were using livestock feed, variation of their diet was minimal.

Living close to humans supports *M. musculus* with nearly unlimited and rich food resources [8], though commensalism in the anthropogenic environments is not sufficiently analysed [55], particularly how species diets are adapted under concurrence with the other small mammals. Interspecific competition limits success of *M. musculus* in outdoor habitats, and possibilities to become crop pests [56]. Initiating this study, we expected house mice to be dominant species in homesteads and kitchen gardens [57], however it appeared only on the third year of the investigation and was not numerous (see Table 2).

Interaction with the similar species inevitably involve competition for resources [3, 5,8,22,26,29,58]. This may be a reason limiting permanent feral *M. musculus* populations, as there are scarce human foods [59]. Competition with other small mammals may lead to the extinction of *M. musculus* following the displacement of humans [60]. Coexistence with *Microtus* voles has had a negative effect on the rate of mice population increase [61]. Other species coexisting with *M. musculus* in our latitudes were the bank vole (*Clethrionomys glareolus*) and the yellow-necked mouse (*Apodemus flavicollis*), which are often synoptically registered in agricultural and commensal habitats [62–64].

Differences in use of resources and comparisons of the diets of co-habiting species can help to identify their niches [22]. Most interesting is comparison of the isotopic position of *C. glareolus* (Table 4) and *M. musculus* (see Table 3) from our study sites, as both are omnivorous [52,57] and were found living synoptically in commensal habitats. The central positions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between these two species differ in orchards ($t = 11.3$, $p < 0.001$; $t = 8.4$, $p < 0.001$, respectively) and in homesteads ($t = 4.8$, $p < 0.001$; $t = 1.71$, $p = 0.10$), with both mean values for *C. glareolus* being lower. Another characteristic feature is the

significantly lower range of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *C. glareolus* in all habitats compared. Thus, *M. musculus* most possibly had a much wider dietary niche with higher consumption of foods of animal origin.

Table 4. Central position (mean \pm SE) and ranges of stable isotope ratios in the hair of *C. glareolus*, living synoptically in the investigated habitats, according to [52,57].

Habitat	N	$\delta^{13}\text{C}$, ‰			$\delta^{15}\text{N}$, ‰		
		Mean \pm SE	Min–Max	Range	Mean \pm SE	Min–Max	Range
Homestead	56	-25.91 ± 0.11	-27.90 – -23.98	3.92	5.94 ± 0.26	2.44–10.70	8.26
Kitchen garden	5	-25.40 ± 0.28	-27.43 – -24.57	2.86	6.14 ± 0.26	4.78–7.06	2.28
Orchard and plantation	155	-23.63 ± 0.08	-26.00 – -28.55	2.55	5.84 ± 0.16	-1.62 – -11.30	2.28

Our results show, that the diet of *M. musculus* expanded during the autumn, endorsed by the highest distribution of individual stable isotope values, with an increase in the consumption of food of animal origin in cases of the higher nitrogen stable isotope values (see Figure 5). Other authors also point to changes in the diet, such as the importance of plants in spring and the increased consumption of invertebrates in autumn [5]. Various insects, earthworms and caterpillars are included in the opportunistic diet of *M. musculus* on the islands, such consumption threatening invertebrate communities [65]. In some cases, diet of *M. musculus* have been mostly carnivorous [22].

We did not find strong correlations of the body mass or body condition with the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Most possibly, correlation of ^{13}C enrichment with body mass [45] works only for larger mammalian herbivores.

The high ecological plasticity of *M. musculus* allows the species change its diet seasonally and according to habitat characteristics, in particular, but not exclusively, the degree of anthropization of the environment. Flexibility in reproductive strategies [66,67], habitat use [68], switching between agricultural and commensal habitats [69], spatial distribution [70], dispersion and migrations [71], together with behavioural adaptability [19,72] make *M. musculus* irresistible in nearly all environments [17,68,73–75]. However, we had only limited number of *M. musculus* trapped in orchards and homesteads.

5. Conclusions

After assessing the dietary niche of the house mouse (*Mus musculus*) in the gradient of natural to fully commensal habitats, that is, in the meadows, orchards, kitchen gardens, homesteads and farms, we found that:

1. The main factors, responsible for the diet variation are the season and the source of available food.
2. The dietary niches of mice eating natural food in orchards were completely separated from those of mice eating livestock feed on farms, the latter having the lowest dietary variation.
3. Based on isotopic data, all mice (males, females, adults, subadults and juveniles) were likely to consume similar diets.
4. *M. musculus* has much wider dietary niche and consumes more foods of animal origin than the other synoptically living omnivore, the bank vole.

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Data Availability Statement: Due to ongoing investigation and preparation of Ph.D. thesis, data of this study are available from the second author upon reasonable request.

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