

Nutritional biology of the weasel (*Mustela nivalis* L., 1766) in the light of the literature

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Abstract. In this literature review, we summarised and evaluated the results of studies on the feeding biology of the weasel, one of the least studied small mammal species in Europe. We provided an overview of the potential dietary spectrum of this species by summarizing studies conducted in 12 countries within the European distribution area. Among these dietary components, 35 genera from 16 orders and 42 species of animal diet were recorded. The combined results of eleven studies provided the basis for a statistical evaluation of dominance patterns, showing a predominant role for mammals (64.3–97.0%), with small rodents accounting for a significant proportion (87.3%). The second most important component was the bird taxon group (2.0–20.9%), while the third most important was the invertebrate taxon group (0.0–7.5%). Further components (e.g., consuming carcasses, eggs, fruits, etc.) may be considered alternative dietary sources for weasels. Although their dominance is not significant, they were frequent components of the weasel's diet, and their mention is therefore of particular importance. Among the studies published in the international literature, some authors also analysed the issue of seasonality. In our study, we provided a comprehensive picture of the variation in the dynamics of the proportions of the main dietary components for the "cold" and "warm" seasons. The dominant component in all seasons is the mammalian share ("warm" season 78.3%; "cold" season 92.5%), and within this the proportion of small rodents ("warm" season 65.2%; "cold" season 86.2%), reflected the less plasticity of the species in its diet choice due to its body size. The analysis conducted based on a summary of data from studies published in each country of the region indicates a lack of clustering within the dataset of dietary components, meaning that there is no statistically verifiable regularity in the proportions of components across each region of the distribution area.

Keywords: least weasel, dietary components, dietary spectrum, dietary niche breadth, seasonality.

Introduction

The weasel (*Mustela nivalis*) is the smallest predatory mammal of the family Mustelidae, within the genus *Mustela* (Tsinger 1959, Heidt 1972, Lanszki & Heltai 2007, Catalogue of Life 2025). The species-specific sexual dimorphism is most apparent in body size. Based on morphometric studies reported from the European distribution area, the extremes of adult male body weight range from 45 g (Čanádý 2016) to 290 g (Demirbaş & Baydemir 2013), similarly for body length, where the following extremes were recorded: 130.6 mm (Abramov & Baryshnikov 2000) and 382 mm (Douma-Petridou & Ondrias 1986 cited in Abramov & Baryshnikov 2000). In contrast, the body weight of females ranges from 26 g (Reichstein 1993 cited in Faragó 2012) to 73.3 g (Joensen 1969), while body length ranges from 114 mm to 214 mm (Székely 1972 cited in Faragó 2012). The weasel is a polytypical species (Zyll De Jong 1992), its area covers the entire Holarctic faunal range, including North Africa and most of Asia, and it occurs throughout Europe except Ireland and Iceland, and is also present in New Zealand, where it was introduced from Great Britain from the 1880s onwards to control populations of the European rabbit (*Oryctolagus cuniculus*) (Moors 1981, Zyll De Jong 1992, Sheffield & King 1994, Abramov & Baryshnikov 2000, King & Powell 2007). The common names for the species vary in its distribution, with the term „Least Weasel” being used in North America, northern and eastern Europe, and Asia, and „Common Weasel” in Great Britain, western and southern Europe, North Africa, and New Zealand (King & Powell 2007). In our study, we use the term least weasel to refer to *Mustela nivalis*. The habitat choice of the least weasel is largely determined by the abundance of

prey animals and the potential predation threat to it (Klemola et al. 1999, Brandt & Lambin 2007, Zub et al. 2008, Mougeot et al. 2019). It occurs in a wide range of habitat types, except large areas of contiguous woodland and sandy deserts, but its most favoured habitats are wooded habitats with a grove structure, tree and shrub rows, bushes and hedgerows, which provide good shelter from predation by raptors (Sheffield & King 1994, Faragó 2012). In the agricultural environment, it prefers woody habitats with linear vegetation structure (Magrini et al. 2009, Keszthelyi et al. 2024). In less disturbed areas, it prefers to settle in the burrows of its ground-dwelling prey animals, and thus also prefers meadows and pastures, fallows and alfalfa meadows (Beretzk 1939, 1944, Mougeot et al. 2019), and is known to have an urbanising character (Červinka et al. 2014, Vass & Bende 2024).

The conservation status and wildlife management of this small predator species vary across its distribution area. It is listed as a huntable mammal species in Russia (Url 1), not protected and even can be thinned in England and Scotland (Url 2), not protected in Ukraine (Akimova 2009) and Sweden (Url 3), not protected in Finland (Url 4), not protected in Poland (Atmeh et al. 2018), not protected in Denmark (Konradsen et al. 2024), protected in Hungary (Url 5), neither on the list of huntable nor protected species in Belarus (Url 6, 7), and classified as „Least concern” by The International Union for Conservation of Nature (IUCN) (McDonald et al. 2019). From a nutritional biology perspective, this species is understudied, and studies to understand its dietary composition within the Palearctic faunal range of its distribution are generally based on small sample sizes. The species is characterized by a broad dietary niche, as nutritional biology studies have detected plant (Goszczyński

1999, Mikheyev 2011), fungal (Mikheyev 2011), invertebrate (Korpimäki et al. 1991, Goszczyński 1999), and vertebrate taxa among its dietary components. Research indicates that the species' main diet consists of small rodent mammals, specifically *Microtus* and *Apodemus* spp. (Erlinge 1975, Elmeros 2006, Sidorovich et al. 2008). In addition to these, insectivores (*Talpa* and *Sorex* spp.) (Elmeros 2006), lagomorphs (Day 1968, Tapper 1979, McDonald et al. 2000), birds (*Perdix*, *Columba*, *Parus* spp.) and their eggs are also present in varying proportions in the diet composition (Krebs 1970, Tapper 1976, Korpimäki et al. 1991, Goszczyński 1999, Mikheyev 2011).

Our objective was to shed light on the role of the least weasel in wildlife management by understanding its dietary characteristics. It is trapped in many countries, but little scientific research is known on the extent and seasonality of actual bird and mammal consumption, making its conservation and wildlife management importance difficult to assess. Truly informed species management plans can only be formulated based on research in wildlife biology. A significant contribution to this is provided by our study, which summarizes the results of European nutritional biology.

Materials and methods

We compared the dietary components of this species based on the results of nutritional biology studies in eleven study areas – Russia (Parovshchikov 1963), Scotland (Moors 1975), Sweden (Erlinge 1975), England (Tapper 1979), Finland (Korpimäki et al. 1991), Poland (Goszczyński 1999), Great Britain (McDonald et al. 2000), Denmark (Elmeros 2006), Hungary (Lanszki & Heltai 2007), Belarus (Sidorovich et al. 2008), and Ukraine (Mikheyev 2011). In addition to the publications that provide a full dietary spectrum, the authors discuss the seasonality of dietary choices in publications from five countries (Scotland [Moors 1975], Sweden [Erlinge 1975], Finland [Korpimäki et al. 1991], Poland [Goszczyński 1999], Belarus [Sidorovich et al. 2008]).

The nutritional biological tests listed above are based on post-mortem examinations (stomach and bowel content analysis) and scats

analyses. In the analysis of stomach and bowel content, the alimentary (gastrointestinal) tract is cleaned by rinsing with water through a sieve with a 0.5 mm mesh, and then the individual alimentary components are separated using a stereomicroscope. They are then preserved in 70% alcohol until taxonomic determination (Goszczyński 1999, McDonald et al. 2000, Elmeros 2006). The contents of scat samples are identified after washing, like the one above. The results of stomach and bowel content analyses are reported together in studies from some distribution area countries (Table 1). Parovshchikov (1963), Moors (1975), Erlinge (1975), Tapper (1979), Korpimäki et al. (1991), Lanszki & Heltai (2007), Sidorovich et al. (2008), Mikheyev (2011) did not report detailed methodology for the preparation of samples for macroscopic analysis, and the analysis of dietary components was performed according to the identification keys developed by Day (1966). McDonald et al. (2000) and Elmeros (2006) used Teerink's (1991) identification key in addition to Day's (1966), as did Sidorovich et al. (2008) based on the latter. Goszczyński (1999) used the keys of Pucek (1981), Debrot (1982), and März (1987) for the identification of major components. Lanszki & Heltai (2007) used the identification method developed by Jędrzejewska & Jędrzejewski (1998) and Biró et al. (2005). Parovshchikov (1963) and Mikheyev (2011) did not report the methodology for the exact analysis of samples in their publication. The published studies report the identified dietary components to different taxonomic units, depending on the accuracy of identification; therefore, we aggregated the individual dietary components to make them comparable. Accordingly, we grouped each dietary component part into ten categories, which were: plant materials, other parts of plants/fungi, invertebrates, amphibians, reptiles, birds, bird eggs, mammals, other diet of animal origin (blood, carcass), and unidentified remains (Table 2). Since Mikheyev (2011) included fungi with the undefined plant part, this group was treated as a separate category in the analysis.

In addition to the above, we have compiled a taxon list of published dietary components from the distribution area to provide an overview of the predominant items. (Table 3). A summary assessment of the seasonality of dietary choice was conducted for two main periods: cold (September 1 to the last day of February) and warm (March 1 to August 31) by comparing results from five countries (Figures 5 and 6). Based on the results of our summarised studies in 11 countries (Table 1), the variables in Table 2, i.e., the aggregated dietary component taxon groups of plant (and fungi) and animal origin, formed the basis of the statistical analyses.

Table 1. Nutritional biological study based on digestive tract samples of the least weasel (*Mustela nivalis* L.) from the Palaearctic faunal range of 11 countries.

Country	Source	Method of testing and number of elements
Russia	Parovshchikov (1963)	Stomach n=45
		Scats n=213
Scotland	Moors (1975)	Scats n=264
		Bowel n=82
Sweden	Erlinge (1975)	Scats n=148
England	Tapper (1979)	Bowel n=687
Finland	Korpimäki et al. (1991)	Bowel n=7
		Scats n=171
Poland	Goszczyński (1999)	Scats n=195
		Stomach and Bowel n=13
		Prey found on the weasel trail n=5
Great Britain	McDonald et al. (2000)	Bowel n=458
Denmark	Elmeros (2006)	Stomach and Bowel n=132
Hungary	Lanszki & Heltai (2007)	Stomach and Bowel n=155
Belarus	Sidorovich et al. (2008)	Scats n=426
Ukraine	Mikheyev (2011)	Scats n=198

Table 2. The percentage of the aggregated dietary components of the analyzed studies. (Other parts of plants, fungi* - In his study, Mikheyev (2011) mentions fungi consumption together with plant diet, but does not separate the proportion of the two groups of species in terms of dietary components, so we refer to it as a separate category because of the unknown proportion of fungi consumption. By other plant parts, the author refers to the consumption of algae, moss, bark, sprouts, and leaves).

Source	Sample size	Dietary component (%)									
		Plant materials	Other parts of plants, fungi	Invertebrates	Amphibians	Reptiles	Birds	Bird eggs	Mammals	Diet of anim. orig. (carcass, blood)	Unidentified remains
Parovshchikov (1963)	258	0.8	0.0	1.6	4.3	0.0	5.3	0.0	86.4	1.6	0.0
Moors (1975)	346	0.0	0.0	0.0	0.0	0.0	13.5	2.3	84.2	0.0	0.0
Erlinge (1975)	148	0.0	0.0	0.0	0.0	1.0	2.0	0.0	97.0	0.0	0.0
Tapper (1979)	687	1.0	0.0	1.9	0.0	1.0	17.5	1.9	75.8	0.0	0.0
Korpimäki et al. (1991)	178	0.0	0.0	4.6	0.0	0.0	6.8	2.3	86.2	0.0	0.0
Goszczyński (1999)	213	2.8	0.0	7.5	0.8	0.0	17.1	2.8	64.3	0.4	4.3
McDonald et al. (2000)	458	0.3	0.0	0.0	0.3	0.3	4.0	0.9	93.9	0.3	0.0
Elmeros (2006)	132	0.0	0.0	3.8	0.0	0.0	2.4	0.0	92.9	0.8	0.0
Lanszki & Heltai (2007)	155	2.0	0.0	1.0	0.0	1.0	10.2	0.0	84.6	1.0	0.0
Sidorovich et al. (2008)	426	0.0	0.0	0.8	0.1	0.2	3.5	0.0	95.1	0.0	0.0
Mikheyev (2011)	198	9.6	1.8	1.3	1.1	0.3	20.9	0.0	65.3	0.0	0.0

Statistical analyses

The analyses were performed using R software version 4.3.1 (R Core Team 2023). Statistical methods, such as K-means clustering, can be combined with computational approaches, like bootstrapping, to validate the derived clusters (Field 2013, Everitt et al. 2011). To this end, we opted for three methods as sensitivity analyses that can offer stronger evidence in favor of either the null or the alternative hypothesis. First, the data matrix was subjected to clusterability analysis to determine if certain countries could be grouped. Hopkins' statistic was used to assess the clusterability of our dataset (Lawson & Jurs 1990), using the *clustertrend* R-package (Wright et al. 2023). In the next step, we used the visual method of assessing clusterability, the so-called Visual Assessment of Cluster Tendency (VAT) algorithm (Bezdek & Hathaway 2002). To that end, we employed a Pearson correlation-based distance method and visualized the data using a visual dissimilarity matrix. Regarding the gradient, low means "red", "white" means middle, and "blue" means high similarity between two countries. We used the R packages *cluster* (Maechler et al. 2021) and *factoextra* (Kassambara & Mundt 2020) to plot the matrix. As a third sensitivity analysis, we used the *gap statistic* (Tibshirani et al. 2001).

Results

Dietary spectrum of the least weasel, dietary niche breadth

A summary of dietary components published in nutritional biology studies from 1963 to 2023, based on the results of studies in 12 countries (Russia [Parovshchikov 1963], Ireland [Day 1968], England [Day 1968, Tapper 1976, Dunn 1977, Tapper 1979, King 1980], Sweden [Erlinge 1975], Scotland

[Moors 1975], Finland [Korpimäki et al. 1991], Poland [Jędrzejewski & Jędrzejewska 1993, Jędrzejewska & Jędrzejewski 1998, Goszczyński 1999], Great Britain [McDonald et al. 2000], Denmark [Elmeros 2006], Hungary [Lanszki & Heltai 2007], Belarus [Sidorovich & Pikulik 1997, Sidorovich et al. 2008], Ukraine [Mikheyev 2011, Dykyy et al. 2017, Martsiv & Dykyy 2023] and data for Europe [Sheffield & King [1994]] 42 species from 35 genera of 22 families of 16 orders were recorded as dietary components of animal origin. Fungi and plant dietary components were not identified in the studies carried out (Table 3). The names of each taxon in brackets (order/suborder: Insectivora; genus: *Clethrionomys*, *Sylvaeus*; *Terricola*; *Microtus*; species: *terrestris*) are given according to the latest taxonomic classification (Catalogue of Life 2025).

Spatial correlations of the proportions of the major dietary components

The Hopkins statistic produced a significant result, indicating the absence of clusterability within the dataset, i.e., suggesting spatial randomness of the data. Subsequently, we employed the following method involving a visual scrutiny of the ordered dissimilarity matrix to assess the potential for clustering among the countries (Figure 1). Consistent with the result from the Hopkins statistic, the ordered dissimilarity matrix failed to reveal any discernible patterns indicative of dataset clusterability (Figure 1).

Taxonomy						
Kingdom	Phylum/ Subphylum	Class/Subclass	Order/Suborder	Family	Genus	Species
Plantae	Tracheophyta	Magnoliopsida	Rosales	Rosaceae	Malus	<i>Malus domestica</i>
					Pyrus	<i>Pyrus communis</i>
Fungi	-	-	-	-	-	-
Animalia	Annelida	Clitellata	Crassicitellata/ Lumbricina	-	-	-
	Mollusca	-	-	-	-	-
	Arthropoda	Insecta	Hymenoptera	Vespidae	-	-
	Chordata/ Vertebrata	Teleostei	-	-	-	-
			Amphibia	Anura	Ranidae	Rana
		Squamata	-	Lacertidae	Lacerta	<i>Lacerta sp.</i>
			Aves	Columbiformes	Columbidae	Columba
		Falconiformes		-	-	-
		Galliformes*		Phasianidae	Perdix	-
		Charadriiformes		-	-	-
		Gruiformes		Gruidae	-	-
		Passeriformes		Corvidae	Garrulus	<i>Garrulus glandarius</i>
				Paridae	Cyanistes	<i>Cyanistes caeruleus</i>
	Parus				<i>Parus sp.</i>	
	Periparus		<i>Periparus ater</i>			
	Poecile		<i>Poecile palustris</i>			
	Turdidae		Turdus	<i>Turdus merula</i>		
	Sturnidae	Sturnus	<i>Sturnus vulgaris</i>			
	Passeridae	Passer	<i>Passer domesticus</i>			
	Sittidae	Sitta	<i>Sitta europaea</i>			
	Mammalia/ Theria	Rodentia/ Myomorpha	Cricetidae	Arvicola	<i>Arvicola amphibius (terrestris)</i>	
				Microtus	<i>Microtus agrestis</i>	
					<i>Microtus arvalis</i>	
					<i>Microtus (Terricola) subterraneus</i>	
					<i>Microtus oeconomus</i>	
					<i>Myodes (Clethrionomys) glareolus</i>	
					<i>Cricetus cricetus</i>	
					<i>Lemmus lemmus</i>	
					<i>Lemmus sibiricus</i>	
					<i>Lasiopodomys (Microtus) brandtii</i>	
				Muridae	Apodemus	<i>Apodemus (Sylvaemus) sylvaticus</i>
						<i>Apodemus (Sylvaemus) tauricus</i>
						<i>Apodemus agrarius</i>
						<i>Apodemus flavicollis</i>
					Micromys	<i>Micromys minutus</i>
					Mus	<i>Mus musculus</i>
				<i>Rattus norvegicus</i>		
Sciuridae				Sciurus	<i>Sciurus carolinensis</i>	
					<i>Sciurus vulgaris</i>	
				Tamias	<i>Eutamias sibiricus</i>	
Gliridae				Muscardinus	<i>Muscardinus avellanarius</i>	
Soricomorpha				Soricidae	Sorex	<i>Sorex spp.</i>
				Talpidae	Talpa	<i>Talpa europaea</i>
Erinaceomorpha, Afrosoricida (Insectivora)				-	-	-
Lagomorpha				Leporidae	Lepus	<i>Lepus timidus</i>
					Oryctolagus	<i>Oryctolagus cuniculus</i>
Carnivora/ Caniformia	Mustelidae	Mustela	<i>Mustela spp.</i>			
Artiodactyla	Cervidae	Capreolus	<i>Capreolus capreolus</i>			
		Alces	<i>Alces alces</i>			

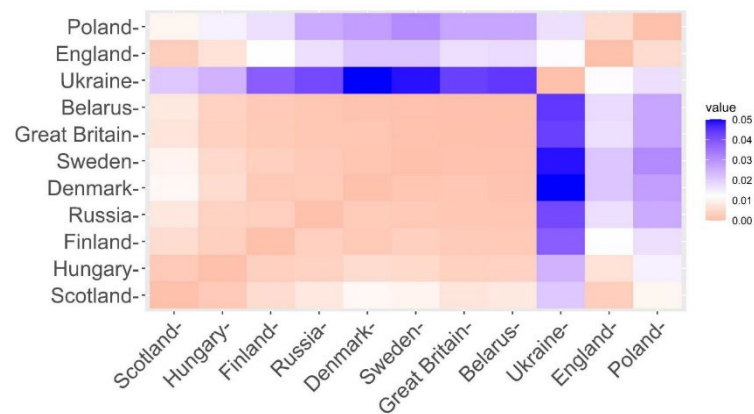


Figure 1. Ordered dissimilarity matrix using Pearson correlation-based distance method. The visual representation of this matrix unequivocally illustrates a dataset that lacks inherent clusterability, aligning consistently with the previously reported Hopkins statistic value of 0.03. In the graphical representation, proximate positioning of countries signifies similarity, with the utilization of a color scale. Specifically, regions of red coloration signify minimal distances between countries, indicative of similarity, while regions rendered in blue denote substantial distances between countries, suggesting dissimilarity.

As a third sensitivity analysis, we conducted an examination employing the *gap statistic*. The results indicated that the optimal number of clusters for the dataset is one, thus affirming the non-clusterable nature of the dataset. This finding aligns with the outcomes of the two preceding analyses. The two reduced dimensions, dimension 1 (Dim1) and dimension 2 (Dim2), account for 36.8% and 24.2% of the original data's variance, respectively, totaling 61% (Figure 2). This level of explained variance occupies a "gray zone," being neither definitively adequate nor inadequate for capturing the complexity of the original multi-dimensional dataset. As indicated above, the proportion of dietary components did not show any area-dependent variation based on the results

of the eleven studies we summarised. In all samples, mammals (64.3–97.0%), including small rodents (87.3%) (*Microtus* spp., *Clethrionomys* spp., *Apodemus* spp.), were the dominant component. Of these components, it was not possible to identify small mammals consumed by least weasels at the species level from the remains in all cases. The dominant taxa were: *Microtus*, *Apodemus*, and *Myodes* (*Clethrionomys*). In addition, the larger mammalian species and the blood were also present in the diet (e.g., *Alces alces*, *Capreolus capreolus*, *Mustelidae* spp.), but their presence was more indicative of carcass consumption (0.0–1.6%). In terms of dominance ratios, the next most dominant component in the set of components was birds (2.0–20.9%).

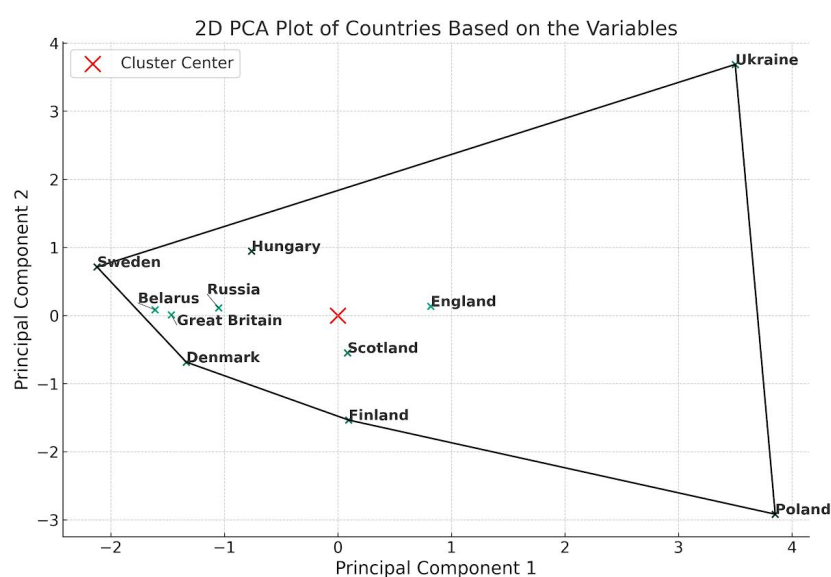


Figure 2. The 2-D plot presents the enhanced k-means clustering involving 1000 bootstrapping samples within a two-dimensional Euclidean space. Notably, within this visualization, the central red dot serves to denote the cluster's centroid, indicating the singular presence of one cluster. 61% of the total variance in the dataset can be explained by the two dimensions depicted.

Among the dominant dietary components, it is possible only for mammals and birds to establish dominance relations in the summary analysis. For both groups, to express dominance relations, we provide the dietary components at the order level (Figures 3 and 4). For birds, almost half of the analyzed studies provide taxonomic categories of order or below (Tapper 1979, Goszczyński 1999, McDonald et al. 2000, Elmeros 2006, Lanszki & Heltai 2007), while for mammals, Mikheyev (2011) does not provide taxonomic data. Accordingly, for the two main dietary groups mentioned, we report the proportion dynamics based on studies where dietary components are specified at the order level or higher. In birds, the order Passeriformes was the dominant order (86.3%), followed by Galliformes (9.5%) and Columbiformes (2.7%). Mammals were dominated by Rodentia (87.3%), followed by Lagomorpha (8.5%) and Eulipotyphla (3.8%)

(Figures 3, 4).

Egg consumption should also be mentioned about birds, but did not represent a dominant component (0.0–2.8%). Invertebrates were the third most significant component (0.0–7.5%). In the case of invertebrates, the authors typically did not report lower taxonomic categories, so detailed analysis of dominance relations is not possible. The following largest components in terms of weight are amphibians (0.0–4.3%) and reptiles (0.0–1.0%), which, together with the larger invertebrates, can also be considered as alternative dietary sources for least weasels. In addition to animal dietary components, plant and fungal dietary components were also detected during the analyses. Although the dominance ratios of these components are generally not significant based on the results of individual studies (0.0–9.6%), they are consistently present in the samples tested.

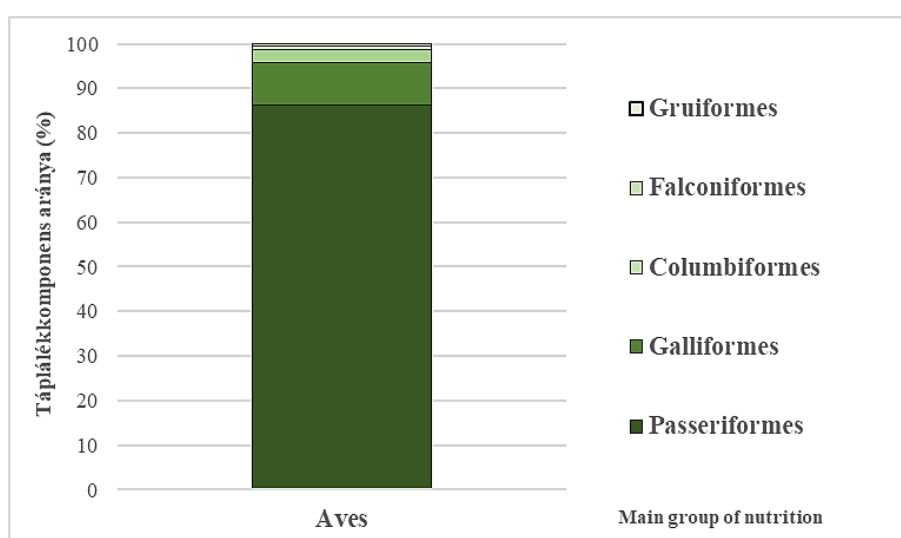


Figure 3. Rate dynamics of bird consumption of least weasels (*Mustela nivalis* L.) in the Palaearctic faunal range based on studies by Tapper (1979), Goszczyński (1999), McDonald et al. (2000), Elmeros (2006) and Lanszki & Heltai (2007).

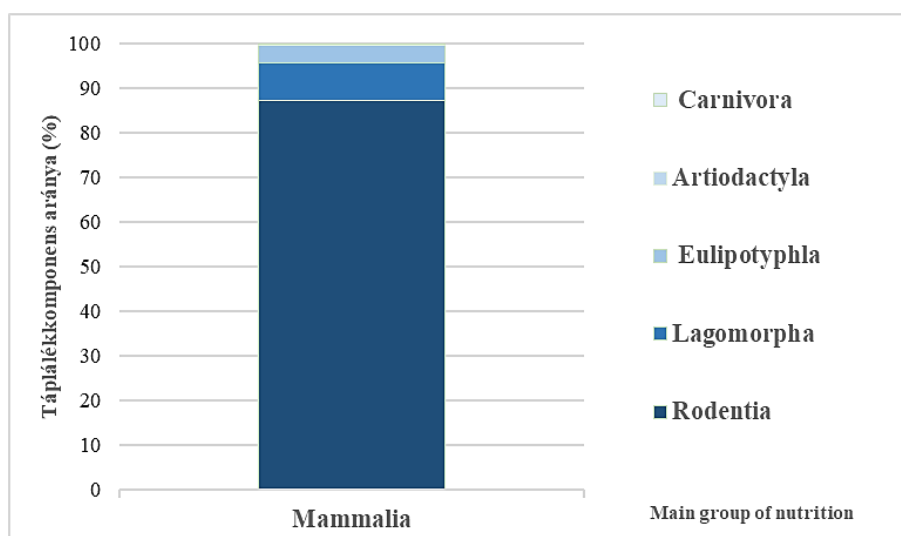


Figure 4. Mammalian consumption rate dynamics of least weasel (*Mustela nivalis* L.) based on the nutritional biology studies analysed.

Seasonality of dietary components

The authors of studies analyzing the seasonality of the dietary spectrum report a decrease in the variation of least weasel dietary components from warm to cold seasons (Figures 5, 6). The importance of Rodentia in the diet of least weasels is dominant in both warm and cold seasons, with an average seasonal shift of 21.0%, indicating that the role of Rodentia increases as the cold-season resource becomes scarcer. The second most dominant group, the birds, although represented in varying proportions in the samples collected in each country, can be considered as a component recorded throughout the year. Regarding the seasonal variation of this dietary component, the predominant share was observed during the warm season, averaging 12.5%, which then decreased to an average of 4.5% in the cold season. Egg predation is exclusively attributed to the warm period, and it is important to note that it represents a relatively small proportion, having been recorded in studies in Finland and Poland, with an average of only 4.7%. Although the share of Soricomorpha species is far below that of rodent prey of the same size class, they are permanently present in the dietary components, accounting for more than 10.0% of the total nutritional components during warm periods. However, their share over the entire period is low, at only 3.1%. The consumption of invertebrates, reptiles, and amphibians was also seasonal, but the proportion of these components was not high in the period from spring to frost. The highest proportion of these components was found in the Insecta group, but even in the warm period the combined proportion of these three main groups (Insecta, Amphibia, Squamata) did not exceed 4.8% on average, indicating that these components were less important in terms of quantity than in terms of frequency, as they are dietary components that are present continuously as

long as they are potentially available. In the cold period up to the beginning of frost, the combined proportion of these components was only 2.2%. Among the mammalian species with larger bodies (*Alces alces*, *Capreolus capreolus*, *Lepus timidus*), Lagomorpha was the dominant component. The dynamics of which showed that the warm period was the dominant period, with an average of 9.9% for the five countries combined, decreasing to 3.1% in the cold period. It is important to note that, in addition to possible predation among juveniles, carcass consumption may be of particular importance, but the extent of this cannot be realistically assessed from digestive tract studies. In mammal species with large body, carcass consumption as an alternative dietary source, especially when resources are scarce, reflects the adaptive dietary strategy of the least weasel, although the predominance of components clearly consumed as carcass clearly indicates that their presence can only be regarded an alternative dietary source, i.e., the species is an opportunistic carcass consumer, but we also know of records based on observation of predation of rabbits and deer by least weasels (Vass & Bende, 2024).

The consumption of components of plant origin did not differ significantly between the two periods. During the warm period, the proportion of this component was lower, at 3.4%, while in the cold period, it was 4.6%. Only in Poland were these vegetable components recorded, primarily in terms of fruit consumption. It can be concluded from the above that the composition of the dietary components indicates a wide spectrum; however, considering the dominance relationships, the components are actually concentrated in a narrow spectrum, adapting to the seasonal variation in the source supply of the Rodentia group and the potential supply of the area.

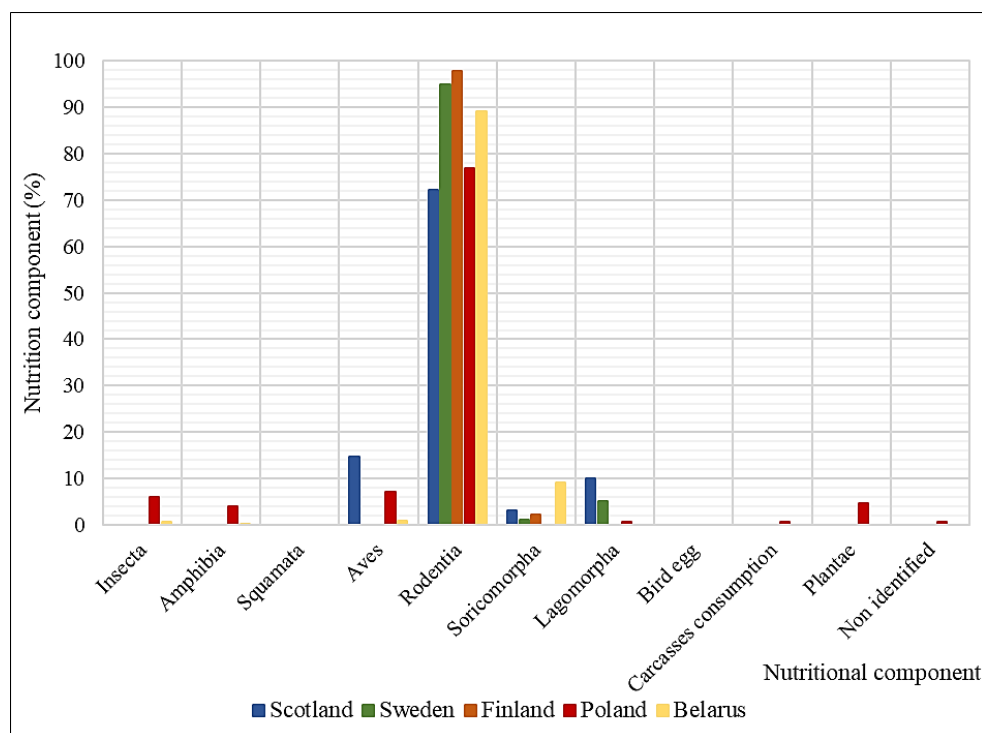


Figure 5. Diet choice of least weasels (*Mustela nivalis* L.) during cold season based on studies in five countries of the Palearctic faunal range.

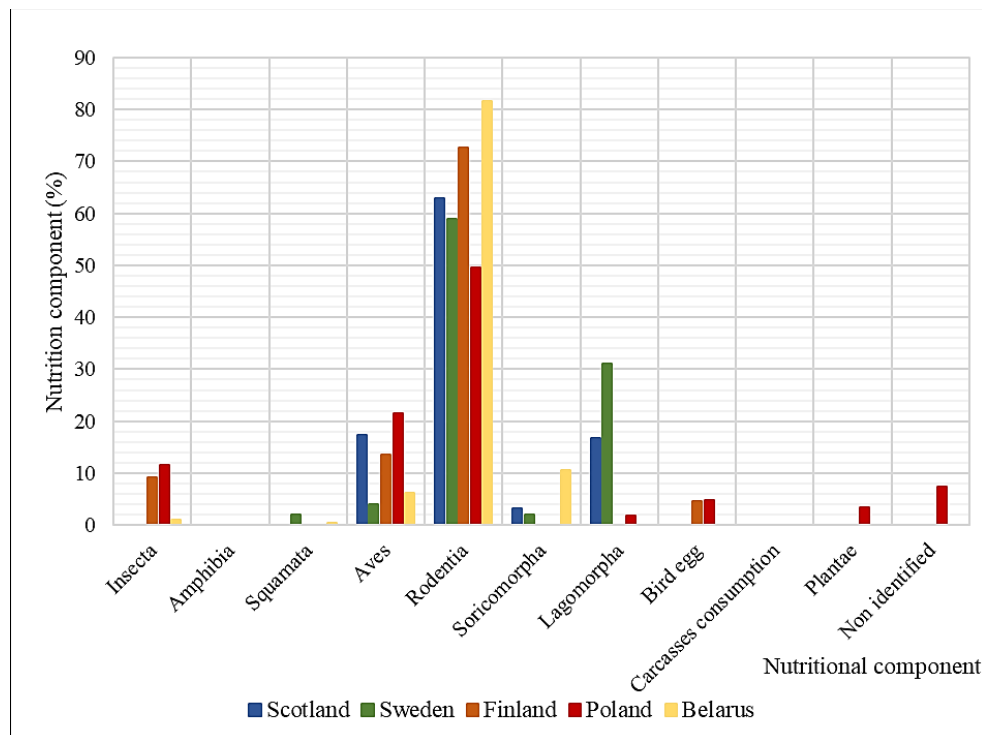


Figure 6. Diet choice of least weasels (*Mustela nivalis* L.) during warm season based on studies in five countries of the Palearctic faunal range.

Discussion

A summary of the nutritional biology literature from eleven countries in the area of the least weasel suggests that small rodents are the primary dietary group in the diet of this species. In addition to the studies analysed, the dominance of rodents is also confirmed by dietary ecology studies showing that small weasels contribute significantly to the mortality of their preferred small rodent populations through predation (Norrdahl & Korpimäki 1995) and control the cyclicity of their population changes (Korpimäki 1986, Hanski et al. 1991, Ylönen 1994, Ylönen et al. 2019). The dominance of rodents in the dietary composition can be explained partly by a specialist dietary strategy due to the least weasel's body size (Heidt 1972, Jędrzejewska & Jędrzejewski 1998, Sundell & Ylönen 2008) and partly by a reduction in the dietary niche overlap between competing predators that co-exist in the habitat (King & Moors 1979, Sidorovich et al. 2008). However, there are some places within the area, such as the UK, where small rodents were present in a lower proportion of the dietary composition (65.0% on average) compared to other countries in the distribution area. In these areas, the lower rodent abundance detected in the digestive tract was compensated for by a greater predation of birds (Tapper 1979) and rabbits (McDonald et al. 2000). Soricomorpha and Talpa species are a potential but not significant dietary source for least weasels, with dominance ratios of only 3.3% of mammalian predation, a similar proportion to this figure reported in several studies (Moors 1975, Lanszki & Heltai 2007). In some areas, this dietary source exceeds a dominance value of 9.0% (Elmeros 2006, Sidorovich et al. 2008), but these prey species are typically identified in the dietary composition in low proportions (McDonald et al. 2000) and not in all countries of

the distribution area (Goszczyński 1999). According to King (1980), least weasels completely ignore these small mammals despite their potential availability. According to Korpimäki & Norrdahl (1989), low shrew consumption can only be detected when the number of the main dietary shrew species is reduced, so that this small predator has an insignificant effect on the population dynamics of shrew species. The absence of shrew species can be explained by their defensive behaviour (Erlinge 1975) and the toxic secretion of their salivary glands (Dufton 1992, Ligabue-Braun et al. 2012, Rode-Margono & Nekaris 2015, Kowalski et al. 2022, 2024). The above is supported by the fact that the least weasel sometimes leaves the carcasses of shrews intact after capturing them (Rubina 1960, King 1980). However, there is a contrary report that the captive least weasel favoured shrews over voles (Erlinge 1975). *Talpa spp.* is present in low proportions in the diet of the least weasel (Sidorovich et al. 2008), although potential availability is also supported by the fact that the ectoparasite species range of least weasels and moles is sometimes similar, suggesting that least weasels may be in contact with moles and use their tunnels (Vásárhelyi 1948, King 1976, 1980). Low consumption rate of this prey is associated with the presence of toxins, as in *Sorex* species (Dufton 1992, Rode-Margono & Nekaris 2015). Predation pressure may be an indicator of toxin production, which some species use to ward off predators (Rode-Margono & Nekaris 2015).

The prey species of larger body size are typically selected by males and especially during periods of dietary scarcity (Erlinge 1975), which may be explained by the hypotheses of Moors (1980) that the prey distribution due to differences in body size is caused by the reduction of intraspecific competition and the specificity of polygyny. Moreover,

different body size is associated with various dietary strategies, contributing to the capture of other prey species (Erlinge 1975). Erlinge (1979), investigating the adaptive aspects of the sexual dimorphism of ermine, reports that fixed dietary allocation is associated with different habitat use and a larger range of activity of males. During the reproductive period of least weasels, males also tend to have a greater range of activity than females (King 1975, Pounds 1981, Macdonald et al. 2004), which may contribute to prey segregation as described above.

Bird consumption (9.37% on average) is reported in all the studies we analysed, but the proportion of this component in the diet composition varies between the countries of the distribution area. Predation pressure on birds increases when rodent availability is scarce, which, together with the proportion of birds detected, suggests that birds are the primary alternative dietary source for this small predator (Tapper 1979, Goszczyński 1999). Broekhuizen et al. (2007) also found that, in addition to low populations of least weasels, populations of songbirds such as *Calcarius lapponicus* and *Eremophila alpestris* showed an increase. The majority of studies based on digestive tract remains do not provide taxonomic data on birds (Parovshchikov 1963, Erlinge 1975, Moors 1975, Korpimäki et al. 1991, Sidorovich et al. 2008, Mikheyev 2011), but some of them can also determine least weasel bird consumption (Table 3) on orders (Passeriformes, Galliformes, Columbiformes, Gruiformes, Falconiformes [Tapper 1979, Goszczyński 1999, McDonald et al. 2000, Elmeros 2006, Lanszki & Heltai 2007, Remonti et al. 2007]), genus (*Columba* sp., *Parus* sp. [Goszczyński 1999]), or even species level (*Turdus merula* L., *Sturnus vulgaris* L. [Goszczyński 1999]; *Garrulus glandarius*, *Passer domesticus* [Mikheyev 2011]). This small predator may play an important role in the mortality of populations of the taxon Galliformes (Tapper 1976, Tapper et al. 1996, Vass & Bende 2024), and sometimes its predation on songbirds can be significant, Dunn (1977) attributes 20.8% of nest predation to least weasel predation and there is a relationship between nesting density and predation pressure on nesting birds, Krebs (1970) cites least weasel predation as a major cause of non-successful nesting with the Great tit (*Parus major*). Dyson et al. (2020) cite the taxon *Mustela* spp. (*M. erminea* or *M. nivalis*) as the most important nest predator of Anatidae nesting in the boreal forest. In his study, Moors (1981) found that least weasels and ermines introduced into New Zealand were responsible for about 77% of nest predations, making them a serious threat to the local avifauna.

The studies we summarised showed that the average share of bird eggs in the diet was only 0.92%. A similar dominance value is reported by McDonald et al. (2000), and higher values are reported by Tapper (1976), Korpimäki et al. (1991), Goszczyński (1999), among others, while other authors did not identify this component in their studies (Parovshchikov 1963, Erlinge 1975, Elmeros 2006, Lanszki & Heltai 2007, Sidorovich 2008, Mikheyev 2011). Bird eggs can also be considered an alternative dietary source due to their low proportion in the diet and, by definition, their occurrence during the warm season. However, the dominance values for this component should be treated with caution, as the absence of eggshells in the digestive tract content does not exclude nest predation with absolute certainty. Due to the sometimes

significant predation pressure, the inaccuracies in the detection of prey selection and egg consumption, the exact role of this species in small wildlife management is unknown and requires further nutritional biology studies, especially as the population dynamics of this small predator fluctuate in line with the gradation of small rodents, making it difficult to determine the true predation pressure in wildlife management.

Among the invertebrates, taxa Lumbricina (Day 1968), Insecta (Parovshchikov 1963, Day 1968, Korpimäki et al. 1991, Goszczyński 1999, Sidorovich et al. 2008, Mikheyev 2011), Mollusca (Mikheyev 2011), Diplopoda, Amphipoda, Arachnida (Strang et al. 2017) were detected in the dietary composition. The Lumbricina group can be detected in digestive samples by the presence of needle-thin bristles, as they are resistant to digestion and breakdown processes. However, the perforation of the sieves used to wash the samples is a factor influencing the successful detection of earthworm setae. According to the methodology, washing through a sieve with a hole size no greater than 0.21 mm enables the detection of needle-thin bristles with high reliability (Battisti et al. 2019). The methodology of the nutritional biology studies we examined utilized a sieve with a 0.5 mm hole size for washing through (McDonald et al. 2000, Elmeros 2006). Additionally, the possibility of confusion with small hair fragments and detached setae of *Rosa* sp. seeds is a potential source of error in identifying needle-thin bristles (Battisti et al. 2019). With regard to molluscs, it should be noted that the detection of this dietary taxon in faecal samples is sometimes difficult (Lanszki 2012). These methodological differences and possible inaccuracies may contribute to inaccurate quantification of the Lumbricina and Mollusca groups. Based on our results, the Insecta group constitutes the largest proportion of invertebrates, which is in agreement with the results of Strang et al. (2017), who reported that about 50.6% of invertebrates are Coleoptera, 22.3% Orthoptera and 12, 3% were represented by the insect orders Blattodea, and the taxa Lepidoptera, Hemiptera, Hymenoptera, Amphipoda, Isoptera, Diplopoda, Psocoptera and Arachnida together accounted for 14.8% of the invertebrate dietary component. Insects are an alternative dietary source for this species from spring to autumn (Goszczyński 1999, Martsiv & Dykky 2023), and Sidorovich et al. (2008) detected this taxon in the diet in lower proportions in the warm season, but also in the cold season. The low consumption values of the above-mentioned invertebrate taxa may be influenced by biological specificities such as seasonal availability and unavailability due to certain developmental stages. According to studies, the dietary groups above are also present in low proportions in the dietary composition of our target species during the period of their potential availability, suggesting that the species prefers the more advantageous prey for energy intake at this time.

Based on the literature data we summarised, amphibians and reptiles accounted for 0.6% and 0.34%, so these components also represent an alternative dietary source for least weasels. Similar dominance ratios for amphibians are reported in several literatures (Goszczyński 1999, McDonald et al. 2000, Sidorovich et al. 2008, Mikheyev 2011). Parovshchikov (1963) identified this component at a higher rate of 4.3%, while other studies did not detect amphibians as prey for least weasel (Erlinge 1975, Moors 1975, Tapper 1976,

Korpimäki et al. 1991, Tapper 1979, Elmeros 2006, Lanszki & Heltai 2007). Sidorovich et al. (2008) report that in their study the least weasel avoided wetlands to reduce interspecific competition, the absence of this habitat explains the low consumption rate of amphibians, and the absence of this dietary source is also confirmed by the presence of skin toxins in *Bufo* species that are more distant from water, as weasel-like predators (*Mustela lutreola*, *M. vison*, *Lutra lutra*), which consume amphibians in higher proportions than least weasels, have a lower proportion of toads compared to other frogs (Sidorovich & Pikulik 1997). Reptiles have a similar dominance in several studies (McDonald et al. 2000, Mikheyev 2011), some studies report a higher mass proportion (Erlinge 1975, Tapper 1979, Lanszki & Heltai 2007, Martsiv & Dykyy 2023), but many do not report reptile consumption of least weasels (Parovshchikov 1963, Moors 1975, Tapper 1976, Korpimäki et al. 1991, Goszczyński 1999, Elmeros 2006). Reptiles may emerge as an alternative dietary source when small mammal populations decline (Mougeot et al. 2019). Strang et al. (2017) also identified reptiles in the dietary composition of the least weasel and, as invertebrate, reptile and avian components played a larger role in the diet of this small predator than in other countries in their study, they attribute an opportunistic dietary strategy to this species, a claim supported by seasonal dietary data for least weasels from Martsiv & Dykyy (2023).

In addition to animal dietary sources, plant and fungal consumption also appears in the dietary composition, with a dominance value of 1.66%, as reported by several authors (Tapper 1979, Lanszki & Heltai 2007). Mikheyev (2011) provides a value of 11.4% for the consumption of plant parts and fungi. Dykyy et al. (2017) report that 19.0% of the species' diet is composed of plant material, and that least weasels prefer fruit for plant consumption. Remonti et al. (2007) identified 23.3% of plant material in the diet of *Mustela* sp. (*M. nivalis* and *M. erminea*) species, with these least weasel species preferring fruits of the taxa Rosaceae and Ericaceae. Martsiv & Dykyy (2023) described plant dietary sources in all seasons with the highest proportion in summer (45.5%). In contrast, some studies do not report data on plant or fungi consumption by least weasels (Erlinge 1975, Elmeros 2006, Sidorovich et al. 2008), so the presence of these components varied considerably between studies. This suggests that a reduction in the source of otherwise preferred dietary components and/or an increase in the supply of plant components (e.g., fruits, seeds) may result in a seasonally higher proportion of plant-derived dietary components in the diet of this species. The opportunistic dietary strategies of larger-bodied weasels were reported in several studies (Wise et al. 1981, Lodé 1994, Smith et al. 1995). In contrast, based on the analysis of dietary data, the diet of least weasels is characterised by a basically specialised strategy, as in some areas rodent consumption can be almost exclusive, especially during the cold season (Korpimäki et al. 1991, Jędrzejewska & Jędrzejewski 1998, Sidorovich et al. 2008), and their population dynamics are highly correlated with those of rodents and they are unable to survive on occasional buffer prey in the event of rodent population collapse (Jędrzejewska & Jędrzejewski 1998). The size and morphological characteristics of this species, its solitary hunting strategy mean that its prey animals are typically small, and it is

anatomically adapted to the capture of small rodents. If we consider the seasonal dynamics of the dietary composition and the dietary palette, along with its dominance relations detected during the warm season, then the characteristics of an opportunistic dietary strategy are evident (Gillingham 1984, Derting 1989), as indicated by the higher presence of alternative dietary sources mentioned above. An opportunistic dietary strategy may be an effective adaptive trait for this small predator, thereby reducing its dependence on small rodents. The sensitivity of the least weasel to cold and wet weather conditions, as evidenced by the time spent hunting, contributes to the higher small mammal consumption detected during the cold season. Studies indicate that during the summer period, hunting occurs almost every day and the daily predation rate fluctuates around the daily energy requirement, while during the winter period, the number of days spent in predation is one third lower. In this case, the daily catch rate only slightly exceeded the energy requirement, and the lost predation time was compensated by prey storage during the cold period (Jędrzejewska & Jędrzejewski 1989, Sidorovich et al. 2008). This behaviour can also be interpreted as an energy-efficient behaviour, which represents an adaptation to the cold season. In winter, snow cover restricts rodent movements to a single corridor, which may even increase the predation efficiency of least weasels preying under a snow cover (Ylönen et al. 2019). In summary, we conclude that the preference for periodically lower proportions of dietary components in addition to a dominant dietary component reflects the adaptive, plastic dietary strategy of the least weasel, which can be interpreted as an important adaptive trait, but our study also highlighted that the role of these components can only be uncertainly assessed in many cases. A realistic assessment of the role of the least weasel in conservation and wildlife management is essentially possible through a better understanding of its nutritional characteristics, which, in the light of our results, also justifies the need for further studies.

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