Reproductive output of the striped field mouse across European agroecosystems and other biotopes: dominance of temporal over habitat effects

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Abstract:
Reproductive trait variation shapes small mammal population dynamics and persistence under environmental change, so clearer characterization of its temporal, spatial, and habitat-related patterns in agroecosystems would improve assessment of population processes in human-modified landscapes. We analysed long-term reproductive data for the striped field mouse (*Apodemus agrarius*) from central and northern Europe, collected over multiple decades in Slovakia and Lithuania, to test the effects of temporal factors (year, month), spatial context (region), habitat type, and biological traits (female body size and body condition) on litter size and breeding seasonality. The impact of these factors on litter size was assessed utilizing Generalized Linear Models (GLMs), augmented by nonparametric tests. Mean litter size was slightly higher in Lithuania than in Slovakia (6.87 ± 0.14; median 7 vs. 6.33 ± 0.06; median 6). Northern populations exhibited greater temporal variability with longer and less synchronised breeding seasons. Litter size increased with female body size, but not body condition. The effects related to the habitat, including those among agroecosystems, were weak and inconsistent. Temporal factors accounted for most of the observed variation. Embryo resorption rates were similar between regions (~ 10–20%), indicating comparable levels of prenatal mortality. The absence of reduced litter size in agricultural or other anthropogenic habitats likely contributes to the species' persistence and ongoing range expansion. This highlights the importance of long-term datasets for evaluating population dynamics in the context of environmental change.

Keywords: *Apodemus agrarius*, temporal variability, reproductive output, breeding seasonality.

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Reproductive output of striped field mouse populations

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Abstract

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Introduction

Reproduction is key to understanding population dynamics and life-history evolution in small mammals. Traits such as litter size, breeding frequency, and phenology vary with environmental conditions (Speakman 2008, Merritt et al. 2003, Gliwicz and Taylor 2002). Breeding activity is synchronized with favourable seasons because reproductive physiology responds to photoperiod and temperature (Bronson and Heideman 1994). Local biotic and abiotic factors shape population-specific reproductive patterns (Lin and Batzli, 2001, Batzli 1992). Along climatic gradients, populations in more seasonal or northern environments typically exhibit shorter and more synchronized intra-annual breeding periods within a given year, whereas populations in milder regions may reproduce over longer periods. These patterns describe variation in reproductive phenology within years and should be distinguished from inter-annual population fluctuations driven by stochastic or cyclic dynamics (Bronson 2009, Merritt et al. 2003). Because reproduction is energetically costly, especially during gestation and lactation, females must balance reproductive investment with survival (Speakman 2008). Consequently, fecundity is often linked to habitat quality, energy availability, and female body size, with larger individuals generally achieving higher reproductive output (Fokidis et al. 2007, Glazier and Eckert 2002).

Reproductive indices influence small mammal population dynamics because population persistence depends on reproductive output rather than survival (Krebs 2013). Metrics such as litter size, pregnancy rate, breeding frequency and breeding season length are sensitive indicators of demographic change. In agroecosystems, these indices are particularly informative because land use, management intensity, and climatic variability mainly affect the timing and intensity of reproduction (Zejda et al. 2023, De la Peña et al. 2003, Batzli 1992).

From a life-history perspective, reproductive indices show how energy is spent on reproduction, growth and survival in different environments (Stott et al. 2024, Heldstab 2021). These traits can change to deal with different environments, which helps populations to adapt. Datasets collected over a long time help to spot short-term changes and long-term patterns, and predict how populations will respond to changes in climate and habitat (Merritt et al. 2003, Batzli 1992). These datasets are important for understanding how populations are controlled and how communities respond to environmental change (Culhane et al. 2022, Singleton et al. 2007).

The striped field mouse (*Apodemus agrarius* Pallas, 1771) is one of the most widespread small mammals in the temperate zone of Eurasia. The distribution of the species extends from Central and Eastern Europe through Siberia to the Far East and northern China, with isolated populations documented in Central Europe and the Balkans (Petrosyan et al., 2023). Historically associated with floodplains and open habitats, *A. agrarius* has undergone substantial range expansion since the 19th–20th centuries, driven by agricultural development, land clearing, and more recently climate warming and landscape change (Petrosyan et al. 2023, Khlyap et al. 2021). This expansion has been rapid and ongoing across Central and Northern Europe, including Slovakia and Lithuania, where the species is increasingly occupying agricultural and other human-modified habitats (Tulis et al. 2025, Balčiauskas and Balčiauskienė 2024, Tulis et al. 2016, Herzig-Straschil et al. 2003).

Within its native range, *A. agrarius* is predominantly associated with humid lowland environments, including river valleys, wetlands, and floodplain forests. However, it is also frequently observed in farmlands and disturbed habitats (Balčiauskas and Balčiauskienė 2024, Dimitrov et al. 2015, Horváth et al. 2005). The species is frequently encountered in heterogeneous landscapes combining natural and anthropogenic elements, including agricultural mosaics, early-successional habitats, and forest–field edges. There has been an increasing incidence of sightings in urban and suburban environments across its European range (Dwużnik et al. 2017, Pieniążek et al. 2017, Horváth et al. 2005).

Apodemus agrarius is a species that is characteristic of Central and Eastern European farmland and is closely associated with open agricultural habitats, ruderal vegetation, and ecotones between crops and semi-natural landscape elements (Shevchyk et al. 2023, Tõnisalu and Väli 2022, Kozakiewicz et al. 1999). Populations frequently persist in heterogeneous agricultural landscapes where arable fields are interspersed with grassy margins, wetlands, forest strips, and fallows (Markovska 2022, Heroldová et al. 2007, Zejda et al. 2023, De la Peña et al. 2003). Simultaneously, simplified monocultures and intensive management tend to reduce habitat suitability and demographic stability. As a granivorous rodent, *A. agrarius* may provide ecosystem services such as weed seed removal and supporting predator diets. However, it is important to note that the species' high reproductive output may also contribute to crop damage and pathogen transmission (Shevchyk et al. 2023, Tõnisalu and Väli 2022, White et al. 2012, De la Peña et al. 2003).

Laboratory and field studies indicate that *A. agrarius* can reproduce under a wide range of environmental conditions. Female specimens of this species are capable of producing multiple litters per year, typically with three to six offspring, and that the gestation period lasts approximately 18–21 days (Vukicevic-Radić et al. 2004). The period of peak breeding activity is typically from spring to autumn, although this timing and duration vary geographically and may be prolonged in milder climates or urban environments (Pieniążek et al. 2017, Baláž et al. 2012, Yoon et al. 1997, Stanko 1992, Andrzejewski et al. 1978). The litter size, which is most commonly assessed as the number of embryos in utero, typically ranges from three to nine embryos across populations (Balčiauskas et al. 2022, Baláž et al. 2012, Andrzejewski et al. 1978). Consequently, uterine embryo counts provide a standardised metric of reproductive output, thus facilitating comparisons among populations experiencing divergent environmental conditions, particularly in species undergoing rapid range expansion (Balčiauskas and Balčiauskienė 2024, Tulis et al. 2016, Bazhenov et al. 2015).

Despite the numerous studies conducted on the biology and distribution of *A. agrarius*, long-term comparative analyses of reproductive traits across regions and habitat types remain limited. In particular, the relative contributions of temporal variability and habitat characteristics to reproductive output in agricultural landscapes are not yet sufficiently understood. The present study addresses this gap by analysing multi-decadal reproductive data from populations in Lithuania and Slovakia, evaluating spatial and temporal variation in litter size and breeding seasonality, and assessing the roles of environmental factors and female body characteristics.

This study aimed to quantify the long-term spatial and temporal variation in the reproductive traits of *A. agrarius* across northern and central European populations that are exposed to different climates and habitats. Using multi-decadal reproductive data from Lithuania and Slovakia, we compared uterine embryo counts, breeding season length, and parity among populations inhabiting heterogeneous agricultural and semi-natural landscapes. Specifically, we assessed the following: (i) differences in reproductive parameters among populations, (ii) the relationship between female body size, condition, and reproductive output, and (iii) the relative contributions of temporal factors (year and month) and habitat categories to reproductive variability. This study evaluates how reproductive performance responds to spatial and temporal heterogeneity in agroecosystem contexts by integrating long-term demographic data across regions.

Materials and methods

Study site

We analysed the reproductive data of *A. agrarius*, collected via snap trapping in two European regions that represent central and northern populations (Fig. 1). Samples from Slovakia represented Central European populations, and samples from Lithuania represented Northern European populations. For brevity, these regions are referred to by country name. The Slovakian data span the period from 1987 to 2017, and the Lithuanian data span the period from 1984 to 2024.

The territory of Slovakia (47.73–49.62° N, 16.83–22.57° E; 49,036 km2) experiences significant variations in altitude, ranging from 94–2,655 m, with mean January temperatures ranging from –1 to 2 °C and July temperatures ranging from 18–21 °C (Slovak Hydrometeorological Institute 2024). The region's ecosystems are diverse, with forests (37.8%), agricultural land (28.6%), and grasslands (21.1%) constituting the dominant land cover types. Smaller shares of wetlands (0.4%) and inland waters (1.4%) are also present (Černecký et al. 2020). Lithuania (53.90–56.45° N, 20.93–26.85° E; 65,286 km^2) is predominantly low-lying, with mean January temperatures ranging from –3.7 to –0.9 °C and July temperatures ranging from 17.4 to 18.9 °C (Lietuvos Hidrometeorologijos Tarnyba 2024). In 2024, the predominant land use was agricultural land (51.6%), forests (32.9%), water bodies (4.1%), and wetlands (1.5%) (Land Resource 2024). Both regions have undergone processes of agricultural intensification and land-use restructuring in recent decades; however, the overall composition of their habitats remains dominated by agricultural and forested landscapes.

Small mammal trapping in both countries covered diverse habitats that were often poorly described or inconsistent with broad schemes such as EUNIS, CORINE, and IUCN. Based on the available descriptions, we classified the habitats into the following nine categories: forests, scrublands, wetlands, grasslands, riparian areas located within 50 meters of water, mixed (mosaics of different habitat patches) or fragmented habitats, disturbed sites (natural or anthropogenic), agricultural land, and commensal habitats (e.g., farms and buildings). Mixed or fragmented habitats were defined as mosaic landscapes composed of adjacent habitat patches (e.g., forest edges, grassland–forest transitions, heterogeneous farmland). Disturbed habitats included sites that had been significantly modified by natural or anthropogenic disturbance, such as landfills or cormorant colonies. This grouping supports consistency with other studies and broader representativeness.

Trapping and sample size

Small mammals were mainly collected using standard snap-trapping methods, which are commonly utilised in the context of long-term monitoring programmes. Snap traps (7 x 14 cm) were arranged in lines of 25 traps, with a spacing of 5 m, and one or more lines per habitat. The traps were baited with brown bread soaked in crude sunflower oil and left for three days, checked once or twice daily. The baits were replaced after precipitation had fallen or when they had been consumed.

The analysed sample comprised 333 adult females out of 3,823 dissected *A. agrarius* in Lithuania and 542 out of 7,114 in Slovakia. Sample sizes have increased over time, a phenomenon that has been particularly pronounced in Slovakia during the 1980s–2000s and in Lithuania during the 1980s–2010s. This coincided with the observed range expansion of the species in Slovakia (Tulis et al. 2025, 2016) and with the increasing abundance and use of commensal habitats in Lithuania (Balčiauskas and Balčiauskienė 2024).

The number of reproductive females varied between regions and seasons (Table S1). Sampling was seasonally uneven, with peaks in autumn in Lithuania and in spring and summer in Slovakia. In some years, no pregnant females were captured despite considerable trapping effort (Table S2). Habitat distribution also differed between countries (Table 1): most females in Lithuania were captured in meadows, whereas in Slovakia they were most frequent in mixed and agricultural habitats.

In Slovakia, long-term ecological and parasitological research were mainly due to the solution and financial support of several VEGA and APVV projects; in recent years these were mainly APVV-0108-06, APVV-0267-10, VEGA 2/0043/09, and VEGA 1/0390/12. Research on small mammals has been carried out on the basis of several exemptions, e.g., 297/108/06-3.1 of 7 March 2006, 6743/2008-2.1 of 29 July 2008, 4874/2011-2.2 of 18 May 2011, and 4559/2015–2.3. In Lithuania, this study is in accordance with Lithuanian legislation (the Republic of Lithuania Law on the Welfare and Protection of Animals No. XI-2271, “Requirements for the Housing, Care and Use of Animals for Scientific and Educational Purposes”, approved by Order No B1-866, 31 October 2012 of the Director of the State Food and Veterinary Service (Paragraph 4 of Article 16) and European legislation (Directive 2010/63/EU) on the protection of animals), and was approved by the Animal Welfare Committee of the Nature Research Centre (protocol nos. GGT-7, GGT-8, and GGT-9).

Small mammal processing

All captured females were measured post-mortem, including body mass (Q, to the nearest 0.1 g) and body length (L, to the nearest 0.1 mm), in accordance with standardized procedures (Blackwell et al. 2006). Necropsies were performed either immediately after trapping in field laboratory conditions or later in laboratory facilities after freezing the specimens. Standard small-mammal dissection protocols were applied in both countries, including examination of reproductive organs to determine pregnancy, embryo number, resorptions, placental scars and other reproductive indicators. Body condition index (BCI) was calculated as the ratio of body mass to body length, and was used as an indicator of individual condition (Balčiauskas et al. 2025). This ratio enables comparisons to be made across age, sex and habitat categories. Embryo mass was excluded from female body mass in all analyses.

Females were classified into age and reproductive categories based on external and reproductive characteristics observed during necropsy. Those with an open vagina, developed mammae, placental scars or embryos in utero were classified as adults. Subadults were defined as having a closed vagina and undeveloped mammary glands, while juveniles were identified by their small body size, thread-like vagina and incomplete fur development (Adamczewska-Andrzejewska 1973, Pelikán 1965). The same age-classification criteria were applied in Lithuania and Slovakia (Balčiauskas et al. 2022, Baláž et al. 2012, Pelikán, 1965).

Reproductive output was quantified as the number of embryos present in the uterus. Embryos that were distinctly smaller than the others within the same pregnancy were classified as resorbed. Reliable macroscopic identification of resorption was only possible when normally developed embryos were at least 4 mm in length (Pelikán 1967).

Some country-specific differences occurred in the assessment of reproductive parameters. In Lithuania, healthy and resorbed embryos, placental sites and *corpora lutea* were recorded, enabling the estimation of actual and potential litter size, as well as the number of litters per year. In Slovakia, however, only healthy and resorbed embryos were consistently counted, while the presence or absence of placental sites was noted and corpora lutea were not recorded. Consequently, breeding disorders in Slovakia could be assessed only as resorption rates (i.e. intrauterine losses after implantation, as defined by Pelikán 1967), whereas in Lithuania, both resorption and non-implantation rates were evaluated. Therefore, all cross-country comparisons rely exclusively on parameters measured consistently in both datasets.

Throughout this manuscript, the term “litter size” refers specifically to the number of embryos in the uterus (uterine embryo counts). However, we use the term “litter size” for consistency with the terminology commonly used in the cited literature.

Data processing and statistical analyses

The normality of uterine embryo count distributions was assessed using the Anderson–Darling test, which is sensitive to deviations at the tails of the distribution. Litter size distributions were normal in Lithuania ($K^2 = 2.51$, $p = 0.285$), for both primiparous ($K^2 = 2.34$, $p = 0.30$) and multiparous ($K^2 = 2.86$, $p = 0.24$) females. However, they deviated significantly from normality in Slovakia (all $K^2 > 48$, $p < 0.01$).

Due to the discrete nature of uterine embryo counts, several Generalised Linear Model (GLM) error structures were evaluated, including Gaussian, Poisson and negative binomial distributions as an extension of ordinary linear regression (DataCamp 2025). Although the data were count data, the embryo counts were biologically bounded (range 1–14), approximately symmetrical (skewness ≈ 0.55) and under-dispersed relative to a Poisson distribution (variance ≈ 3.0 versus mean ≈ 6.5). No zero inflation was detected. The Poisson and negative binomial models produced identical qualitative results, with the same significant predictors and unchanged effect directions. Residual diagnostics further indicated that the assumptions of the Gaussian model were adequately satisfied. Therefore, the Gaussian GLM was retained as it provided an appropriate and interpretable representation of the data.

Litter size was used as the dependent variable, with year, month, habitat group and parity as categorical predictors and body mass, body length and BCI as continuous covariates. Outliers were retained and no missing values were imputed. The significance of the predictors was evaluated using Fisher's F-test. Effect sizes were expressed as partial eta-squared (η^2) and observed power (OP) was calculated for $\alpha = 0.05$.

As climatic variables were not consistently available for all sampling years and sites, temporal predictors (year and month) were used as integrative proxies. These proxies were used to capture inter-annual climatic variability and seasonal environmental conditions affecting reproduction.

To complement the model-based analyses, nonparametric tests were applied where appropriate. Differences between regions were tested using the Mann–Whitney U test with continuity correction and differences related to habitat were assessed using the Kruskal–Wallis H test. To enable comparison with previous studies, both parametric and nonparametric summary statistics are provided in Tables S3–S7 Student's t-tests were used for pairwise comparisons of means and chi-squared tests for proportions (Tibco 2025). Statistical significance was accepted at $p < 0.05$. All analyses were performed using Statistica for Windows, version 8.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Variability of the body parameters in adult females of *Apodemus agrarius*

In general, adult *A. agrarius* females in Slovakia were significantly larger, but of lower body condition, compared to those in Lithuania (Table 2). All differences between countries are highly significant: average Q in Lithuania was less by 3.7% ($t= 2.8$, $p< 0.01$), average L by 9.0% ($t=17.8$, $p<0.0001$), and average BCI was bigger by 20.4% ($t=20.3\%$, $p<0.0001$).

Body size parameters revealed distinct regional variations over several decades (Fig. 2). Body mass did not differ between countries in the 1980s ($t = 0.14$, $p = 0.886$); however, females in Slovakia were significantly heavier in the 1990s ($t = 4.28$, $p < 0.001$) and 2000s ($t = 2.37$, $p = 0.018$). Conversely, females in Lithuania were heavier in the 2010s ($t = 3.06$, $p = 0.0025$). Body length was significantly greater in Slovakia in all decades (all $p < 0.001$), whereas BCI was consistently higher in Lithuania, with strong, highly significant differences in every decade (all $p < 0.0001$). Overall, Slovakian females were structurally longer, Lithuanian females exhibited better body condition consistently, and the direction of body mass differences shifted over time.

Habitat-related differences in body parameters were further evaluated using one-way ANOVA separately for each region (Table S3). In Lithuania, habitat had no significant effect on body mass or body length of adult females, whereas BCI differed significantly among habitats ($F_{8,299} = 3.08$, $p = 0.002$). In Slovakia, significant habitat-related differences were detected for body mass ($F_{7,529} = 2.74$, $p = 0.008$) and body length ($F_{7,487} = 4.99$, $p < 0.001$), while variation in BCI among habitats was not statistically significant ($F_{7,485} = 1.76$, $p = 0.094$). Within each region, however, body parameters showed overlapping ranges and comparable mean values across different habitats, indicating limited differentiation in adult female morphology specific to particular habitats.

Relation of litter size to body parameters

In both the Lithuanian and Slovakian *A. agrarius* populations examined, litter size was positively correlated with female body size, indicating that larger females tended to produce larger litters (Fig. 3). In the Lithuanian sample, litter size showed significant positive correlations with both body size measures (Q: $r = 0.22$, $p < 0.001$; L: $r = 0.28$, $p < 0.001$), but not with BCI ($r = -0.08$, $p = 0.18$). Similar patterns were observed in the Slovakian population (Q: $r = 0.25$, $p < 0.001$; L: $r = 0.28$, $p < 0.001$; BCI: $r = -0.03$, $p = 0.54$). In both countries, Q and L were strongly inter-correlated (LT: $r = 0.66$; SK: $r = 0.71$). Body condition was negatively associated with body length in both datasets (LT: $r = -0.52$; SK: $r = -0.34$).

Spatial and temporal variability in litter size

The litter size of *A. agrarius* was significantly larger in Lithuania than in Slovakia, as evidenced by both the median uterine embryo count (7 vs. 6; Mann–Whitney adjusted $z = 2.86$, $p < 0.005$) and the mean value (6.87 ± 0.14 vs. 6.33 ± 0.06; $t = 4.24$, $p < 0.0001$). Lithuanian populations also exhibited greater inter-annual variability, whereas Slovakian populations showed more stable litter sizes across decades, with a few exceptions (Fig. 4; Table S4).

GLM explained 25% of litter size variation in Lithuania ($F_{51,216} = 2.74$, $p < 0.001$, $R^2 = 0.25$) and 20% in Slovakia ($F_{44,448} = 3.74$, $p < 0.001$, $R^2 = 0.20$). In both regions, temporal factors (year and month) accounted for the largest proportion of explained variance, whereas habitat and parity had no significant effects (Table 3). Body mass and body length contributed modestly to variation in Lithuania but not in Slovakia.

Seasonal patterns also reflected regional variations in the timing of reproduction (Fig. 5). In Lithuania, reproduction occurred over a longer period, from March to December, with greater month-to-month variability. By contrast, the Slovakian breeding season was shorter and more synchronised, spanning April to October. Despite these differences in season length and synchrony, both regions exhibited an increase in litter size around midsummer.

Given the sample size and the observed effect size, there was over a 90% chance that the influence of the year and month truly existed in Lithuania. These factors explained 19% and 9.5%, respectively, of the variability in *A. agrarius* litter size. Body size and body condition explained 2.5–4.0% of the variability with a 64–84% chance of observation. In Slovakia, two analysed time factors explained litter size variability with a 100% chance (Table 3). The temporal variation of litter size in two regions is presented graphically in Fig. 5.

The Lithuanian population of *A. agrarius* exhibited greater temporal variability in litter size than the Slovakian population, which showed a more stable and synchronised pattern across the years (see Fig. 5a and 5b). In Lithuania, litter size fluctuated markedly from year to year, whereas in Slovakia, variation was limited.

Seasonal and monthly analyses revealed consistent regional differences in reproductive timing (Figures 5c–f; Tables S5–S6). In Lithuania, reproduction occurred over a longer period, from March to December, with litter size generally remaining high throughout the year and peaking in midsummer. In Slovakia, the breeding season was shorter and more synchronised, spanning April to October. Litter size increased towards summer and declined in autumn. Despite differences in season length and variability, both regions showed an increase in litter size at midsummer.

There were significant differences in the composition of multiparous and primiparous females between regions: in Lithuania, multiparous females accounted for 9.6% of reproducing females, whereas in Slovakia, this figure was 41.4% ($\chi^2 = 100.5$, $p < 0.0001$). In both regions, multiparous females produced slightly larger litters than primiparous females, although the magnitude and statistical significance of this effect differed between countries. In Lithuania, the median litter size increased from 7 for primiparous females to 7.5 for multiparous females and the mean litter size increased from 6.83 ± 0.15 to 7.56 ± 0.49; however, these differences were not statistically significant (Mann–Whitney adjusted $z = 1.37$, $p = 0.17$; $t = 1.22$, $p = 0.22$). By contrast, Slovakia exhibited a significant parity effect, with the median litter size rising from 6 to 7 ($z = 3.92$, $p < 0.005$) and the mean litter size increasing from 6.19 ± 0.07 to 6.52 ± 0.09 (t = 2.90, $p < 0.005$). Despite these differences, the absolute increase in mean litter size was greater in Lithuania (0.74 offspring) than in Slovakia (0.33 offspring).

Litter size stability across habitats

In Lithuania, median uterine embryo counts varied by habitat. Higher median values were observed in wetlands, riparian areas and mixed habitats, while lower values were observed in forests, agricultural areas, disturbed areas and commensal habitats (Fig. 6a; Table S7). However, substantial overlap among quartile ranges indicated that there were no significant habitat-related differences in litter size (Kruskal–Wallis H = 0.0, p = 1.0).

In Slovakia, litter size was more uniform across habitat categories, with median values generally ranging from six to seven embryos and narrow interquartile ranges (Fig. 6b). No habitat-related differences were detected, and reproductive output remained stable across all habitat types.

Overall, habitat effects on litter size were not significant in either region. Lithuanian populations exhibited greater variability in embryo counts across habitats, whereas Slovakian populations demonstrated more consistent reproductive output, which is consistent with the GLM results indicating limited influence of habitat on litter size.

Embryo resorptions and non-implantations

The proportion of litters with resorbed embryos was observed at the same frequency in both countries: 10.4% in Lithuania and 9.2% in Slovakia ($\chi^2 = 0.09$, p = 0.77). Similarly, 20.9% of embryos were lost due to resorptions in affected pregnancies in Lithuania, and 19.5% were lost in Slovakia ($\chi^2 = 0.05$, p = 0.82). These results suggest comparable levels of prenatal mortality and reproductive stress in the two regions, indicating that the overall frequency and intensity of embryo resorption are consistent across both populations.

In Lithuania, non-implantation was registered in 17.9% of litters, resulting in a loss of 26.4% of embryos in affected pregnancies.

Discussion

Building on earlier research from former Czechoslovakia (North Bohemia and current Slovakia) into the reproduction of *A. agrarius* (Stanko 2014, Baláž et al. 2012, Pelikán 1966), this study integrates long-term datasets from Central and Eastern Slovakia with comparable data from Lithuania, thus providing a multi-decadal and cross-regional perspective. This broader framework reveals how climatic and geographic gradients shape reproductive variability across Europe, enabling temporal drivers to be evaluated alongside spatial differences.

Consistency of findings with broader patterns

The observed reproductive patterns are consistent with the documented range expansion of *A. agrarius*, which has been closely linked to agricultural development, land clearing and, more recently, climate warming (Petrosyan et al. 2023, Khlyap et al. 2021). Over the past century, the species has markedly expanded across Central and Northern Europe. This includes a 135% increase in its range in Slovakia, as well as increasing abundance and synanthropy in Lithuania (Tulis et al. 2025, Balčiauskas and Balčiauskienė 2024, Tulis et al. 2016, Herzig-Straschil et al. 2003). Predictive models suggest further northeastward expansion under ongoing environmental change (Bazhenov et al. 2015). In this context, the longer and less synchronised breeding season, as well as the higher temporal variability, observed in northern populations, are consistent with a flexible reproductive strategy that enables the species to persist and spread across heterogeneous and human-modified landscapes. This strategy is potentially supported by behavioural flexibility during colonization (Jánošíková et al. 2025).

Inter-population differences in reproductive output

Differences in reproductive output between populations were consistent across analyses, with northern (Lithuanian) populations of A. *agrarius* producing significantly larger and more variable litters than central (Slovak) populations. This higher reproductive potential in the north was primarily expressed through greater temporal variability and less synchronised reproduction rather than uniformly higher mean litter sizes. In both regions, multiparous females produced larger litters than primiparous females; however, the effect was stronger in Lithuania, further indicating greater reproductive flexibility. In contrast, Slovak populations produced smaller but more consistent litters, reflecting a more temporally constrained and synchronised breeding pattern.

Such geographic variation in reproductive traits is commonly associated with environmental gradients in temperature, season length and resource availability, which influence breeding strategies and energy allocation (Ims 1997, Bronson 1985). Similar north–south differences in reproductive effort have been documented in other small mammals, where shorter or more seasonal breeding periods are offset by adjustments in reproductive output (Yoccoz et al. 2000, French et al. 1975). Therefore, cross-regional comparisons are essential for interpreting reproductive variation in species experiencing contrasting climatic regimes (Merritt et al. 2003, Lin and Batzl, 2001, Bronson and Heideman 1994). Long-term, multi-regional datasets are particularly valuable for species undergoing rapid range expansion, such as *A. agrarius*, because they allow persistent regional differences in reproductive strategies to be distinguished from short-term annual variability. This provides insight into how temporal plasticity may facilitate continued spread (Balčiauskas and Balčiauskienė 2024, Petrosyan et al. 2023, Tulis et al. 2016, Bazhenov et al. 2015, Herzig-Straschil et al. 2003).

Temporal drivers of reproductive variability

Clear regional differences in reproductive timing suggest that temporal factors primarily influence reproductive variability in *A. agrarius*. The northern population reproduced over a longer, less synchronised period (March–December), whereas the central population had a shorter, more synchronised breeding season (April–October) with a pronounced summer peak. These contrasting patterns suggest that northern populations have greater temporal flexibility and that central populations are subject to stronger seasonal constraints, which is consistent with the broader dominance of year and month effects observed in the statistical models.

Sampling differed between countries, with Lithuania peaking in autumn and Slovakia in spring-summer. This seasonal imbalance in sampling effort could potentially affect the apparent strength of temporal effects, as peak reproductive periods may be unevenly represented between regions. For example, sampling in Lithuania during autumn may overrepresent late-season reproduction, whereas sampling in Slovakia during spring and summer may emphasise early and peak breeding phases.

However, even as these effects were statistically accounted for. the month and year were also intrinsically linked to the seasonal distribution of sampling effort, meaning they cannot be considered fully independent of the sampling structure. Consequently, uneven seasonal sampling between countries may have influenced the estimated strength of temporal effects, so the models cannot completely separate biological reproductive phenology from sampling design. Nevertheless, temporal predictors remained consistently important across analyses, suggesting that temporal variation likely reflects genuine biological patterns to some extent. Due to the retrospective and heterogeneous nature of the dataset, these results should be interpreted with caution. Direct climatic variables were not included due to a lack of consistent long-term data. Instead, temporal predictors likely integrate climatic and environmental variability influencing reproductive phenology in small mammals.

Such differences likely reflect climatic and energetic constraints on reproduction. In less seasonal environments, milder temperatures and prolonged resource availability relax energetic limitations and weaken synchronizing cues, resulting in extended, less synchronized breeding seasons (Bronson 2009, Bronson and Heideman 1994). Conversely, stronger seasonality restricts reproduction to a narrower favourable window, promoting tighter synchrony (Merritt et al. 2003, Batzli 1992). The climatic effects on reproductive phenology in mammals are well documented, and increasing seasonality or climatic variability tends to reinforce synchrony. However, climate warming may extend breeding periods and advance their onset (Findlay-Robinson et al. 2023, Iler et al. 2021). Together, these patterns demonstrate that the reproductive timing of *A. agrarius* primarily adjusts to temporal environmental cues, which could have consequences for population dynamics and community interactions in the context of ongoing climate change.

Body size and body condition effects

Within each region, the number of uterine embryos was positively related to female body size (mass and length), indicating that larger individuals invest more heavily in reproduction within a given ecological context. This pattern is consistent with mammalian allometry, whereby structural size reflects long-term resource acquisition and constrains physiological capacity for gestation and lactation (Speakman 2008, Bronson 1985, Tuomi 1980).

Our results show a positive relationship between female body size and litter size, consistent with the broader morphological patterns described for *A. agrarius* across Central and Northern Europe. In a large-scale analysis across Slovakia, Lithuania and Estonia, body size increased along a northward climatic gradient, consistent with Bergmann's rule, while appendage length decreased following Allen's rule (Balčiauskas et al. 2025). These geographic patterns indicate that morphology responds strongly to climatic gradients. The relationship between structural size and reproductive output observed in the present study supports the interpretation that environmental conditions affecting growth and body size may indirectly influence reproductive performance.

As structural size reflects lifetime energy expenditure, it often provides a more reliable prediction of reproductive potential than short-term measures of body condition (Bronson and Heideman 1994). The medium-strength correlations observed here are consistent with life-history theory, which links body size to reproductive output and competitive ability in small mammals (Glazier and Eckert 2002).

However, between-region comparisons revealed that Lithuanian *A. agrarius* females were structurally smaller yet produced more embryos than Slovakian females, highlighting the importance of environmental effects on reproductive output. Although BCI was not a significant predictor within regions, Lithuanian females consistently exhibited a higher average BCI, indicating a better energetic status. This suggests that, while body size limits reproductive investment within populations, environmental factors, such as habitat quality and longer breeding seasons, can increase overall reproductive output between populations by enhancing energy reserves and ovulation rates (Speakman 2008. Fokidis et al. 2007, Glazier and Eckert 2002). Life-history adjustments are important at northern or expanding range margins, where increased fecundity may compensate for stronger seasonality or higher juvenile mortality rates. Overall, these results suggest that structural size places relative limits on reproduction, while environmental conditions influence absolute reproductive performance across regions.

Absence of habitat effects

Within its native range, *A. agrarius* is typically associated with humid lowland habitats such as river valleys, wetlands, and floodplain forests. However, it also occupies farmlands, disturbed areas, and increasingly urban environments (Balčiauskas and Balčiauskienė 2024, Dimitrov et al. 2015). This species thrives in landscapes that combine natural and human-made elements, often dominating early successional or reforested sites (Horváth et al. 2005). Its success in agricultural and urban habitats reflects a generalist strategy characterized by high tolerance of anthropogenic disturbance, strong mobility and maintenance of gene flow across fragmented landscapes via green corridors (Baláž et al. 2012, Gortat et al. 2015). Urban populations are often dense and stable, exhibiting traits consistent with local adaptation, such as increased body mass and extended breeding seasons compared to rural populations (Balčiauskas and Balčiauskienė 2024, Dwużnik et al. 2017, Pieniążek et al. 2017, Babińska-Werka et al. 1979). Across its expanding range, population performance is often more closely linked to climatic variability than to habitat type per se, with abundance responding positively to spring precipitation and negatively to summer rainfall (Okulova et al. 2011). While individuals in contaminated environments may exhibit reduced body size or developmental stability, high ecological plasticity enables *A. agrarius* to persist and continue to expand across diverse human-modified landscapes (Andrzejewski et al. 1978, Mitter et al. 2015).

Consistent with this ecological flexibility, habitat-related differences in litter size were generally weak in the present study. Slightly larger litters occurred in Lithuanian wetlands and mixed habitats, whereas Slovak populations exhibited relatively uniform reproductive output across habitat types. This contrasts with patterns observed in many other small mammals, where habitat quality strongly influences reproductive performance through its effects on food availability, cover and energetic constraints (Lin and Batzli 2001, Stenseth et al. 1985). Experimental and field studies demonstrate that optimal habitats promote higher litter sizes and breeding intensity, whereas habitat fragmentation or resource limitation can modify reproductive strategies or sex ratios (Sullivan et al. 2023, Aars et al. 1995). While habitat-related variation in litter size has been reported in *A. agrarius* locally, particularly along altitudinal gradients or in resource-rich sites (Baláž et al. 2012), the limited expression of this variation in the present study suggests that reproduction in this species is largely buffered against local habitat variation. Instead, flexibility in reproductive timing and energy allocation appears to maintain relatively stable reproductive output across habitats, reinforcing the predominance of temporal over habitat effects.

Reproductive stability and disturbances

The embryo resorption rate in *A. agrarius* was similar in the central (Slovak) and northern (Lithuanian) populations (approximately 10–20%), indicating comparable levels of prenatal mortality and reproductive stress, despite regional differences in climate and habitat. However, compared with earlier Slovak data, breeding disturbances appear to be more frequent. Pelikán (1967) reported affected litters in only 6.06% of cases, with embryo resorption occurring in just 1.07% of embryos. Nevertheless, consistent with previous findings of weak habitat-related variation in reproductive traits (Stanko 2014, Baláž et al. 2012), *A. agrarius* demonstrates high ecological flexibility. In small mammals, reproductive stability is often maintained through physiological adjustments that balance energetic costs against environmental constraints (Speakman 2008), despite population dynamics being shaped by the combined effects of resources, predation and climate (Batzli 1992). The persistence of relatively stable reproductive output across regions therefore supports the view that rodents can buffer reproductive processes against moderate environmental fluctuations (Wan et al. 2022).

Maximum embryo counts violate the 'one-half rule'.

In rodents, litter size usually follows the 'one-half rule', whereby the average litter size is approximately half the number of mammae, and the maximum litter size is close to the total number of nipples (Holcová Gazárková and Adamík 2025, Gilbert 1986). While this pattern is widespread, it is not absolute and deviations have been documented in several taxa (Sherman et al. 1999), including the desert woodrat (*Neotoma*), where litter sizes exceed the number of nipples (Cameron 1973). In *A. agrarius*, which has 12 mammae (Stewart et al. 2020), reported litter sizes across its range vary from one to ten (Wilson et al. 2017), with occasional extreme values. Historical studies from Slovakia documented frequent large litters, including multiple cases of nine embryos and one case of ten embryos (Pelikán 1965, 1967), while later studies still recorded rare cases of nine embryos (Baláž et al. 2012). In Lithuania, maximum litter sizes of up to 12 embryos have been reported (Likevičienė 1959, Prūsaitė 1988). Therefore, the few large litters observed here are rare but biologically plausible outliers within the documented upper limits of reproductive variability in this species. In one exceptional case, all 14 of the embryos had fully developed and had not been resorbed by the time of birth. Their combined mass was approaching that of the female, which indicates an extremely high level of reproductive investment.

The mean *A. agrarius* litter sizes reported historically for Slovakia (6.64 between 1953 and 1963, Pelikán 1966; 6.40 between 1986 and 1990; Stanko 1992) and Lithuania (8.2 in the early 1950s; Likevičienė 1959) are higher than those observed in the present study (6.33 and 6.87, respectively). These differences may reflect ecological or methodological variation and could potentially be linked to species expansion dynamics (Tulis et al. 2025, Balčiauskas and Balčiauskienė 2024, Tulis et al. 2016), although we will not speculate further on this. Embryo counts are widely regarded as reliable indicators of reproductive potential as implanted embryos closely reflect ovulation and early gestational success with limited subsequent resorption (Loeb and Schwab 1987) and correspond well to realised litter sizes in rodents (Silva et al. 2015, Innes 1978). Although they represent potential rather than actual birth litter size, embryo counts provide a robust and comparable measure of reproductive investment in long-term ecological studies.

Study limitations and potential biases

Sampling effort varied across countries, decades, seasons, and habitats due to the retrospective nature of the material and its collection through multiple independent projects. Such unevenness could influence temporal or habitat-related patterns, however, we minimized this risk by using models that explicitly incorporated year, month, body size, and habitat. This adjustment accounts for differences in sampling distribution.

Methodological differences between Lithuania and Slovakia, mainly the more detailed assessment of *corpora lutea*, placental sites, and non-implantations in Lithuania, could introduce bias if one dataset underestimates early reproductive failure or potential fecundity. However, our cross-regional analysis relies solely on parameters measured consistently in both countries: the number of embryos and resorption rates. Embryo counts are widely accepted as reliable indicators of realized reproductive investment, and they are robust to moderate methodological variation (Silva et al. 2015, Loeb and Schwab 1987, Innes 1978). Both datasets applied identical criteria for distinguishing healthy and resorbed embryos.

Conclusions

Following a review of data spanning over four decades, we can conclude that *A. agrarius* has exhibited consistent core reproductive traits alongside flexible responses to environmental changes. This indicates that its ecological success and ability to persist and expand in the face of current climate and land use dynamics are based on reproductive plasticity.

In line with this pattern, there was no significant difference in reproductive output among habitat types. Agricultural habitats were not found to be associated with smaller litter sizes or greater reproductive variability. This suggests that agroecosystems in the regions studied can support reproductive performance that is comparable to that of other habitat types.

However, the longer breeding season, larger litters and greater inter-annual variability observed in Lithuania suggest that there is higher reproductive plasticity at the northern range margin. These traits likely contribute to the species' continued expansion across northern Europe, reflecting adaptive responses to changing climatic and habitat conditions.

As ethical and legal restrictions on the capture and dissection of small mammals increase, access to detailed reproductive data is declining rapidly. This makes the present study especially relevant, as it provides valuable long-term insights into reproductive variation that would be difficult to obtain under current research regulations.

References

Aars, J., Andreassen, H.P., Ims, R.A., 1995. Root voles: litter sex ratio variation in fragmented habitat. J. Anim. Ecol. 64(4): 459-472. doi:10.2307/5649

Adamczewska-Andrzejewska, K.A., 1973. Growth, variations, and age criteria in *Apodemus agrarius* (Pallas, 1771). Acta Theriol. 18(19): 353-394.

Andrzejewski, R., Babińska-Werka, J., Gliwicz, J., Goszczyński, J., 1978. Synurbization processes in population of *Apodemus agrarius*: I. Characteristics of populations in an urbanization gradient. Acta Theriol. 23(20): 341-358.

Babińska-Werka, J., Gliwicz, J., Goszczyński, J., 1979. Synurbization processes in a population of *Apodemus agrarius*. II. Habitats of the striped field mouse in town. Acta Theriol. 24(30): 405-415.

Baláž, I., Ambros, M., Tulis, F., 2012. *Biology and Distribution of the Species of the Family Muridae (Rodentia) in Slovakia. Part 2: Apodemus flavicollis, A. sylvaticus, A. uralensis, A. agrarius*. Constantine the Philosopher University, Nitra, Slovakia.

Balčiauskas, L., Balčiauskienė, L., 2024. Striped field mouse invading human-modified environments of Lithuania during last five decades. Land 13(10): 1555. doi:10.3390/land13101555

Balčiauskas, L., Csanády, A., Stanko, M., Timm, U., Balčiauskienė, L., 2025. Morphological variation in the striped field mouse across three countries. Animals 15(3): 452. doi:10.3390/ani15030452

Balčiauskas, L., Stirkė, V., Balčiauskienė, L., 2022. Rodent fertility in commercial orchards in relation to body mass and condition. Agric. Ecosyst. Environ. 329, 107886. doi:10.1016/j.agee.2022.107886

Batzli, G.O., 1992. Dynamics of small mammal populations: a review, in: McCullough, D.R., Barrett, R.H. (Eds.), *Wildlife 2001: Populations*. Springer, Dordrecht, pp. 831-850. doi:10.1007/978-94-011-2868-1_63

Bazhenov, Y.A., Pavlenko, M.V., Korablev, V.P., Kardash, A.I., 2015. Current distribution of the striped field mouse (*Apodemus agrarius* Pallas, 1771) in Eastern Transbaikalia. Russ. J. Biol. Invasions 6(1): 1-5. doi:10.1134/S2075111715010026

Blackwell, G.L., Bassett, S.M., Dickman, C.R., 2006. Measurement error associated with external measurements commonly used in small-mammal studies. J. Mammal. 87(2): 216-223. doi:10.1644/05-MAMM-A-215R1.1

Bronson, F.H., 1985. Mammalian reproduction: an ecological perspective. Biol. Reprod. 32(1): 1-26. doi:10.1095/biolreprod32.1.1

Bronson, F.H., 2009. Climate change and seasonal reproduction in mammals. Philos. Trans. R. Soc. B 364(1534): 3331-3340. doi:10.1098/rstb.2009.0140

Bronson, F.H., Heideman, P.D., 1994. Seasonal regulation of reproduction, in: Knobil, E., Neill, J.D. (Eds.), *The Physiology of Reproduction*. Raven Press, New York, pp. 541-583.

Cameron, G.N., 1973. Effect of litter size on postnatal growth and survival in the desert woodrat. J. Mammal. 54(2): 489-493. doi:10.2307/1379133

Culhane, K., Sollmann, R., White, A.M., et al., 2022. Small mammal responses to fire severity mediated by vegetation characteristics and species traits. Ecol. Evol. 12(5): e8918. doi:10.1002/ece3.8918

Černecký J., Gajdoš P., Špulerová J., Halada Ľ., Mederly P., Ulrych L., Rybanič R., 2020. Ecosystems in Slovakia. J. Maps 16(1): 28–35. doi:10.1080/17445647.2019.1689858

DataCamp, 2025. GLM in R: Generalized Linear Model. Available from https://www.datacamp.com/tutorial/generalized-linear-models [30 September 2025].

De la Peña, N.M., Butet, A., Delettre, Y., Paillat, G., Morant, P., Le Du, L., Burel, F., 2003. Response of the small mammal community to changes in western French agricultural landscapes. Landsc. Ecol. 18(3): 265-278. doi:10.1023/A:1024438602714

Dimitrov, H., Chassovnikarova, T., Markov, G., 2015. Craniometrical description of striped field mouse (*Apodemus agrarius* Pallas, 1771) in Bulgaria. J. BioSci. Biotechnol. 2(2): 131-138.

Dwużnik, D., Gortat, T., Behnke, J.M., et al., 2017. Comparison of helminth community of *Apodemus agrarius* and *A. flavicollis* between urban and suburban populations. Parasitol. Res. 116(11):, 2995-3006. doi:10.1007/s00436-017-5609-5

Findlay-Robinson, R., Deecke, V.B., Weatherall, A., Hill, D.L., 2023. Effects of climate change on life-history traits in hibernating mammals. Mammal Rev. 53(2): 84-98. doi:10.1111/mam.12308

Fokidis, H.B., Risch, T.S., Glenn, T.C., 2007. Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. Anim. Behav. 73(3): 479-488. doi:10.1016/j.anbehav.2006.08.010

French, N.R., Stoddart, D.M., Bobek, B., 1975. Patterns of demography in small mammal populations, in: *Small Mammals: Their Productivity and Population Dynamics*. Cambridge University Press, London, pp. 73-102.

Gilbert, A.N., 1986. Mammary number and litter size in Rodentia: the “one-half rule”. Proc. Natl. Acad. Sci. U.S.A. 83(13): 4828-4830. doi:10.1073/pnas.83.13.4828;

Gliwicz, J., Taylor, J.R., 2002. Comparing life histories of shrews and rodents. Acta Theriol. 47(Suppl. 1), 185-208.

Glazier, D.S., Eckert, S.E., 2002. Competitive ability, body size and geographical range size in small mammals. J. Biogeogr. 29(1): 81-92. doi:10.1046/j.1365-2699.2002.00646.x

Gortat, T., Rutkowski, R., Gryczyńska, A., et al., 2015. Anthropopressure gradients and population genetic structure of *Apodemus agrarius*. Conserv. Genet. 16(3): 649-659. doi:10.1007/s10592-014-0690-0

Heldstab, S.A., 2021. Latitude, life history and sexual size dimorphism correlate with reproductive seasonality in rodents. Mammal Rev. 51(2): 256-271. doi:10.1111/mam.12231

Heroldová, M., Zejda, J., Tkadlec, E., 2007. Structure and diversity of small mammal communities in agricultural landscape. Agric. Ecosyst. Environ. 120(2–4): 206-210. doi:10.1016/j.agee.2006.10.001

Herzig-Straschil, B., Bihari, Z., Spitzenberger, F., 2003. Recent changes in the distribution of the field mouse (*Apodemus agrarius*). Ann. Naturhist. Mus. Wien, Ser. B 105, 421-428.

Holcová Gazárková, A., Adamík, P., 2025. Mammae numbers and litter sizes in an arboreal rodent fit the one-half rule. Ecology 106(9): e70195. doi:10.1002/ecy.70195

Ims, R.A., 1997. Determinants of geographic variation in growth and reproductive traits in the root vole. Ecology 78(2): 461-470. doi:10.1890/0012-9658(1997)078[0461:DOGVIG]2.0.CO;2

Iler, A.M., CaraDonna, P.J., Forrest, J.R., Post, E., 2021. Demographic consequences of phenological shifts. Annu. Rev. Ecol. Evol. Syst. 52(1): 221-245. doi:10.1146/annurev-ecolsys-011921-032939

Innes, D.G., 1978. A reexamination of litter size in some North American microtines. Can. J. Zool. 56(7): 1488-1496. doi:10.1139/z78-206

Jánošíková, R., Tulis, F., Baláž, I., Eccard, J.A., Mazza, V., 2025. Range expansion during recolonization. Behav. Ecol. 36(4): araf053. doi:10.1093/beheco/araf053

Khlyap, L.A., Dinets, V., Warshavsky, A.A., Osipov, F.A., Dergunova, N.N., Petrosyan, V.G., 2021. Aggregated occurrence records of the invasive striped field mouse. Biodivers. Data J. 9, e69159. doi:10.3897/BDJ.9.e69159

Kozakiewicz, M., Gortat, T., Kozakiewicz, A., Barkowska, M., 1999. Effects of habitat fragmentation on four rodent species. Landsc. Ecol. 14(4): 391-400. doi:10.1023/A:1008132720570

Krebs, C.J., 2013. *Ecology: The Experimental Analysis of Distribution and Abundance*, 6th ed. Pearson, San Francisco, CA, USA.

Land Resource Monitoring Information System, 2024. Available from https://zisis.lt/en/ [20 December 2024].

Lietuvos Hidrometeorologijos Tarnyba, 2024. Available from https://www.meteo.lt/klimatas/lietuvos-klimatas/klimato-duomenys/ [20 December 2024].

Likevičienė, N., 1959. *Lietuvos TSR peliniai graužikai*. Ph.D. Thesis, Vilnius University, Vilnius, Lithuania.

Lin, Y.-T.K., Batzli, G.O., 2001. Influence of habitat quality on vole population dynamics. Ecol. Monogr. 71(2): 245-275. doi:10.1890/0012-9658(2001)071[0245:TIOHQO]2.0.CO;2

Loeb, S.C., Schwab, R.G., 1987. Estimation of litter size in small mammals. J. Mammal. 68(3): 671-675. doi:10.2307/1381601

Markovska, O., 2022. Small mammals in natural and agricultural lands of Slobozhanshchyna (eastern Ukraine): results of a five-year-long survey. GEO&BIO 23: 143-153. doi:10.15407/gb2312

Merritt, J.F., Lima, M., Bozinovic, F., 2003. Seasonal regulation in fluctuating small mammal populations. Oikos 94(3): 505-514. doi:10.1034/j.1600-0706.2001.940312.x

Mitter, G., Sumasgutner, P., Gamauf, A., 2015. Niche partitioning of three *Apodemus* species. Ann. Naturhist. Mus. Wien, Ser. B 117: 37-46.

Okulova, N.M., Kalinkina, E.V., Mironova, T.A., et al., 2011. Ecology of the striped field mouse in forest-steppe. Povolzh. Ekol. Zh. 2: 174-184 (in Russian).

Pelikán, J., 1965. Reproduction and population structure of *Apodemus agrarius*. Zool. Listy 14(4): 317-332.

Pelikán, J., 1966. Comparison of birth rates in four *Apodemus* species. Zool. Listy 15(2): 125-130.

Pelikán, J., 1967. Resorption rate in embryos of four *Apodemus* species. Zool. Listy 16(4): 325-342.

Petrosyan, V., Dinets, V., Osipov, F., Dergunova, N,. Khlyap, L. 2023. Range Dynamics of Striped Field Mouse (Apodemus agrarius) in Northern Eurasia under Global Climate Change Based on Ensemble Species Distribution Models. Biology 12(7):1034. doi:10.3390/biology12071034

Pieniążek, A., Sokół, M., Kozakiewicz, M., 2017. Ecological characteristics of two rodent species in urban environments. Nat. Resour. 8(2): 69-80. doi:10.4236/nr.2017.82005

Prūsaitė, J. (Comp.), 1988. *Fauna of Lithuania. Mammals*. Mokslas, Vilnius, Lithuania.

Sherman, P.W., Braude, S., Jarvis, J.U.M., 1999. Litter sizes and mammary numbers of naked mole-rats. J. Mammal. 80(3): 720-733. doi:10.2307/1383241

Shevchyk, L., Grod, I., Holiney, H., Kravets, N., 2023. Rodents of the family Muridae of Ternopil Region. Theriol. Ukrainica 26: 43-53. doi:10.53452/TU2605

Silva, M.P.L., Leite, Y.L.R., Costa, L.P., 2015. Litter size and embryo implantation in neotropical rodents. Oecol. Aust. 19(1): 183-194. doi:10.4257/oeco.2015.1901.12

Singleton, G.R., Brown, P.R., Jacob, J., Aplin, K.P., 2007. *Rodent Outbreaks: Ecology and Impacts*. International Rice Research Institute, Los Baños, Philippines.

Slovak Hydrometeorological Institute, 2024. Available from http://www.shmu.sk [29 December 2024].

Speakman, J.R., 2008. Physiological costs of reproduction in small mammals. Philos. Trans. R. Soc. B 363(1490): 375-398. doi:10.1098/rstb.2007.2145

Stanko, M., 1992. Bionomics and ecology of Apodemus-agrarius pall (Rodentia, Muridae) on east Slovak lowlands. 1. breeding. Biologia 47(2): 173-182.

Stanko, M., 2014. *Striped Field Mouse (Apodemus agrarius) in Slovakia*. Institute of Parasitology, Slovak Academy of Sciences, Slovakia.

Stenseth, N.C., Gustafsson, T.O., Hansson, L., Ugland, K.I.. 1985. On the evolution of reproductive rates in microtine rodents. Ecology, 66(6): 1795-1808. doi:10.2307/2937375

Stewart, T.A., Yoo, I., Upham, N.S., 2020. Coevolution of mammae number and litter size. bioRxiv preprint. doi:10.1101/2020.10.08.331983

Stott, I., Salguero-Gómez, R., Jones, O.R., et al., 2024. Life histories are not just fast or slow. Trends Ecol. Evol. 39(9): 830-840. doi:10.1016/j.tree.2024.06.001

Sullivan, T.P., Sullivan, D.S., Boonstra, R., Krebs, C.J., Vyse, A., 2023. Population regulation in the deer mouse. Mammal Res. 68(1): 37-51. doi:10.1007/s13364-022-00659-x

TIBCO Software Inc., 2025. Data Science Textbook. Available from https://docs.tibco.com/data-science/textbook [15 January 2025].

Tõnisalu, G., Väli, Ü., 2022. Edge effect in rodent populations. Eur. J. Wildl. Res. 68(3): 34. doi:10.1007/s10344-022-01580-z

Tulis, F., Ambros, M., Baláž, I., Žiak, D., Sládkovičová, V.H., Miklós, P., 2016. Expansion of the striped field mouse in Slovakia. Folia Oecol. 43(1): 27-35.

Tulis, F., Jánošíková, R., Ambros, M., et al., 2025. Five-decade expansion of striped field mouse. Mammal Res. 70: 465-475. doi:10.1007/s13364-025-00810-4

Tuomi, J., 1980. Mammalian reproductive strategies: a generalized relation of litter size to body size. Oecologia 45(1): 39-44. doi:10.1007/BF00346705

Wan, X., Yan, C., Wang, Z., Zhang, Z., 2022. Sustained population decline of rodents is linked to accelerated climate warming and human disturbance. BMC Ecol. Evol. 22(1): 102. doi:10.1186/s12862-022-02056-z

White, T.A., Lundy, M.G., Montgomery, W.I., et al., 2012. Range expansion in an invasive small mammal: influence of life-history and habitat quality. Biol. Invasions 14(10): 2203-2215. doi:10.1007/s10530-012-0225-x

Wilson, D.E., Lacher, T.E., Mittermeier, R.A. (Eds.), 2017. *Handbook of the Mammals of the World: Rodents II*. Lynx Edicions, Barcelona, Spain.

Yoccoz, N., Hansson, L., Ims, R., 2000. Geographical differences in size, reproduction and behaviour of bank voles in relation to density variations. Pol. J. Ecol. 48: 63-72.

Yoon, M.-H., Jung, S.-J., Oh, H.-S., 1997. Population structure of Korean striped field mouse. Korean J. Biol. Sci. 1(1): 53-61. doi:10.1080/12265071.1997.9647348

Zejda, J., Heroldová, M., Jánová, E., 2023. T Transformation of the Agricultural Landscape and its Influence on Small Terrestrial Mammal Communities in Central Europe. Available from http://dx.doi.org/10.2139/ssrn.4982782 [10 May 2025]

Table 1. Distribution of the *Apodemus agrarius* sample in two European regions, represented by Lithuania and Slovakia, by habitat.

Country	Agricultural	Meadow	Commensal	Forest	Mixed	Disturbed	Riparian	Shrub
LT	42	182	40	29	7	14	8	2
SK	118	11	34	33	224	23	57	42

Table 2. Basic statistics on the body size and condition of *Apodemus agrarius* in two European regions, represented by Lithuania (1984–2024) and Slovakia (1987–2017).

Country	Body mass, g		Body length, mm		BCI	
	avg±SE	Min–max	avg±SE	Min–max	avg±SE	Min–max
LT	26.0±0.27	12.8–44.9	94±0.38	71.6–112	3.12±0.03	1.85–4.97
SK	26.9±0.22	15.5–46.0	103±0.29	83.0–121	2.48±0.02	1.56–5.37

Table 3. Factors, influencing litter size of *Apodemus agrarius* in two European regions, represented by Lithuania and Slovakia (univariate tests of significance, η^2 indicates effect sizes, and OP indicates observed powers).

Factor	Lithuania				Slovakia			
	F	p	η^2	OP	F	p	η^2	OP
Q	5.45	< 0.025	0.025	0.64	0.06	0.80	0.000	0.06
L	8.74	< 0.002	0.039	0.84	0.88	0.35	0.002	0.16
BCI	6.80	< 0.01	0.031	0.74	0.19	0.66	0.000	0.07
Year	1.59	< 0.05	0.186	0.99	2.07	< 0.002	0.111	1.00
Month	2.51	< 0.01	0.095	0.93	8.90	< 0.001	0.106	1.00
Habitat	1.42	0.20	0.044	0.60	0.61	0.74	0.01	0.26
Parity	0.09	0.77	0.000	0.06	0.06	0.81	0.000	0.06

Figure captions

Figure 1. Position of the countries (inset) and sampling sites in central and northern populations, represented by Slovakia and Lithuania. CORINE land use class 2 is shown as background (https://www.eea.europa.eu/data-and-maps/figures/corine-land-cover-1990-by-country/legend). System of coordinates: ETRS_1989_LAEA; Projection: Lambert_Azimuthal_Equal_Area; WKID: 3035 Authority: EPSG. Map lines do not necessarily depict accepted national boundaries.

Figure 2. Region-based differences in the body mass (Q, g), body length (L, mm), and body condition index (BCI) of adult *Apodemus agrarius* females. Lithuania (LT, green) represents Norther Europe, Slovakia (SK, magenta) – Central Europe. The boxplots show the mean (central symbol), the standard error (box), and the standard deviation (whiskers). Significant differences are marked by asterisk.

Figure 3. Relationship between body parameters and litter size in adult *Apodemus agrarius* females in two European regions, represented by Lithuania (a) and Slovakia (b).

Figure 4. Decadal variation in the litter size of *Apodemus agrarius* in two European regions, represented by Lithuania (LT, green) and Slovakia (SK, magenta). Boxplots show median (central symbol), 25%–75% quartiles (box), and minimum–maximum (whiskers) of uterine embryo counts for each decade from the 1980s to the 2010s.

Figure 5. Temporal variation in *Apodemus agrarius* litter size in two European regions, represented by Lithuania (a,c,e) and Slovakia (b,d,f). Boxplots show median (central symbol), 25%–75% quartiles (box), and minimum–maximum (whiskers) of uterine embryo counts for each.

Figure 6. Variation in *Apodemus agrarius* litter size in different habitats in two European regions, represented by Lithuania (a) and Slovakia (b). Boxplots show median (central symbol), 25%–75% quartiles (box), and minimum–maximum (whiskers) of uterine embryo counts for each.

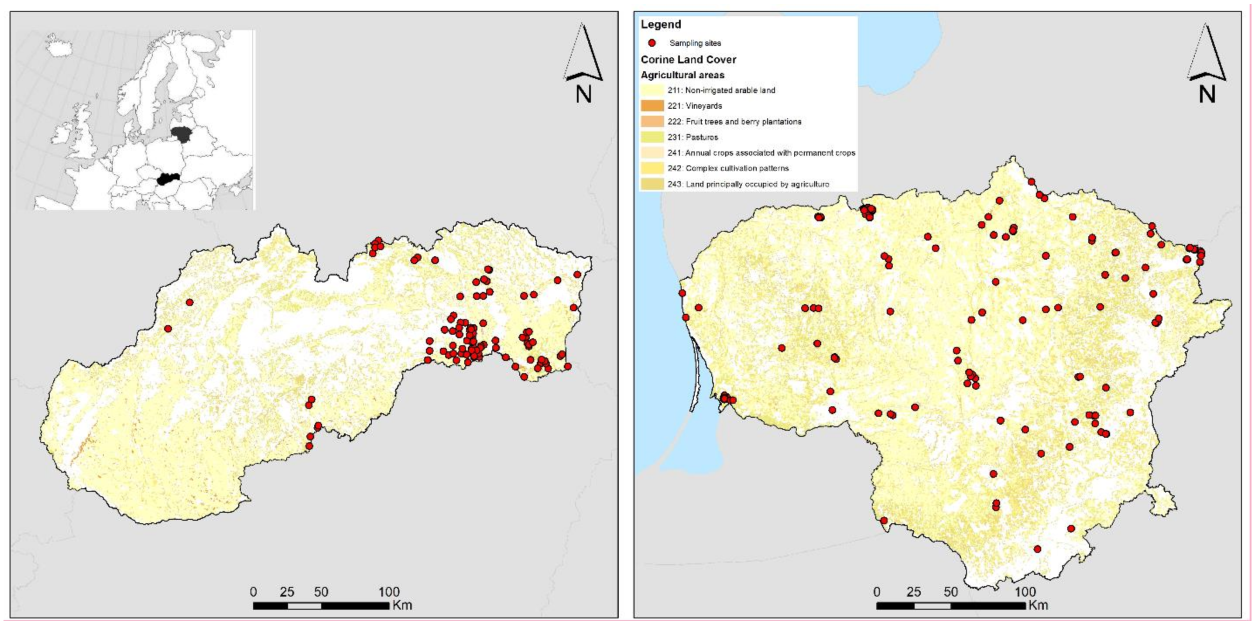


Figure 1.

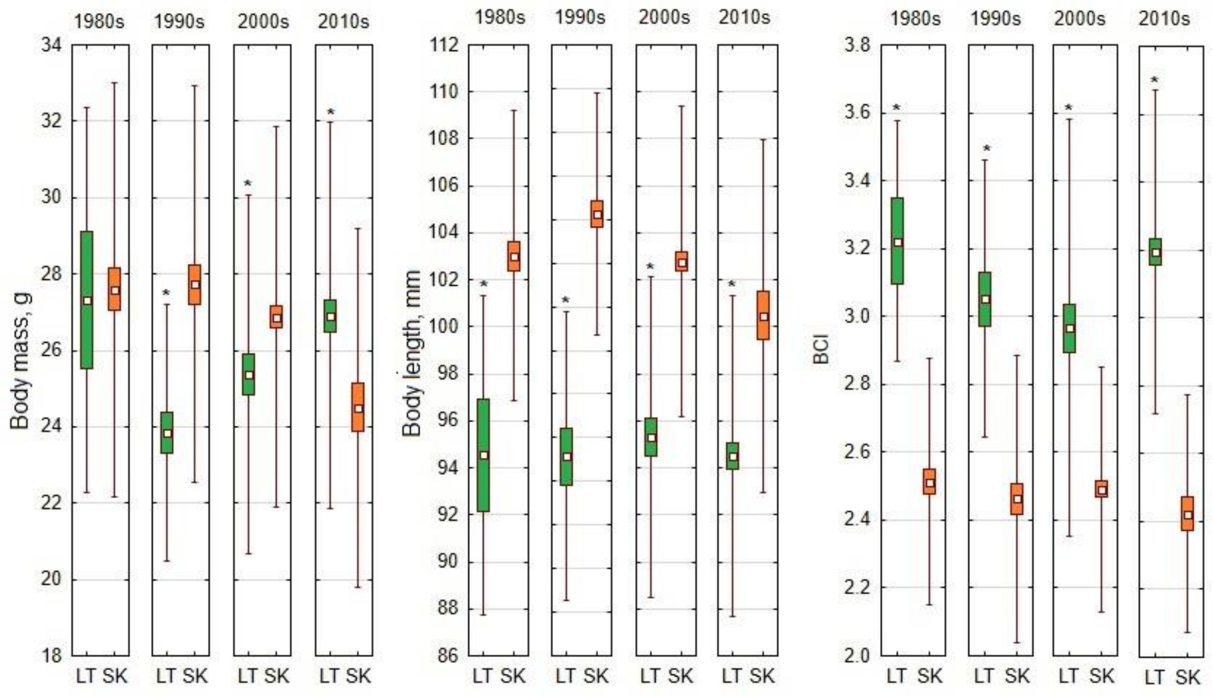
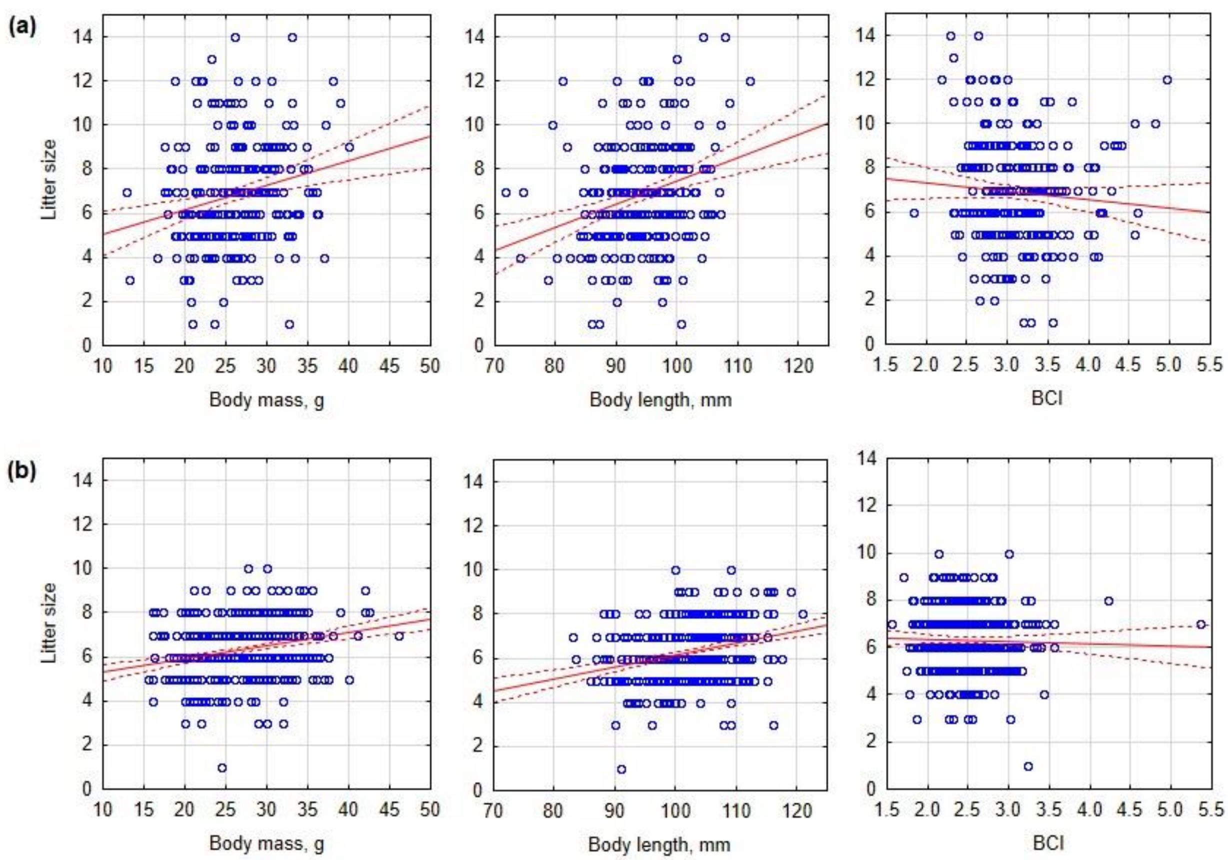


Figure 2.


(a)
(b)
Litter size
Body mass, g
Body length, mm
BCI
0
2
4
6
8
10
12
14
10
15
20
25
30
35
40
45
50
70
80
90
100
110
120
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5

698 Figure 3.

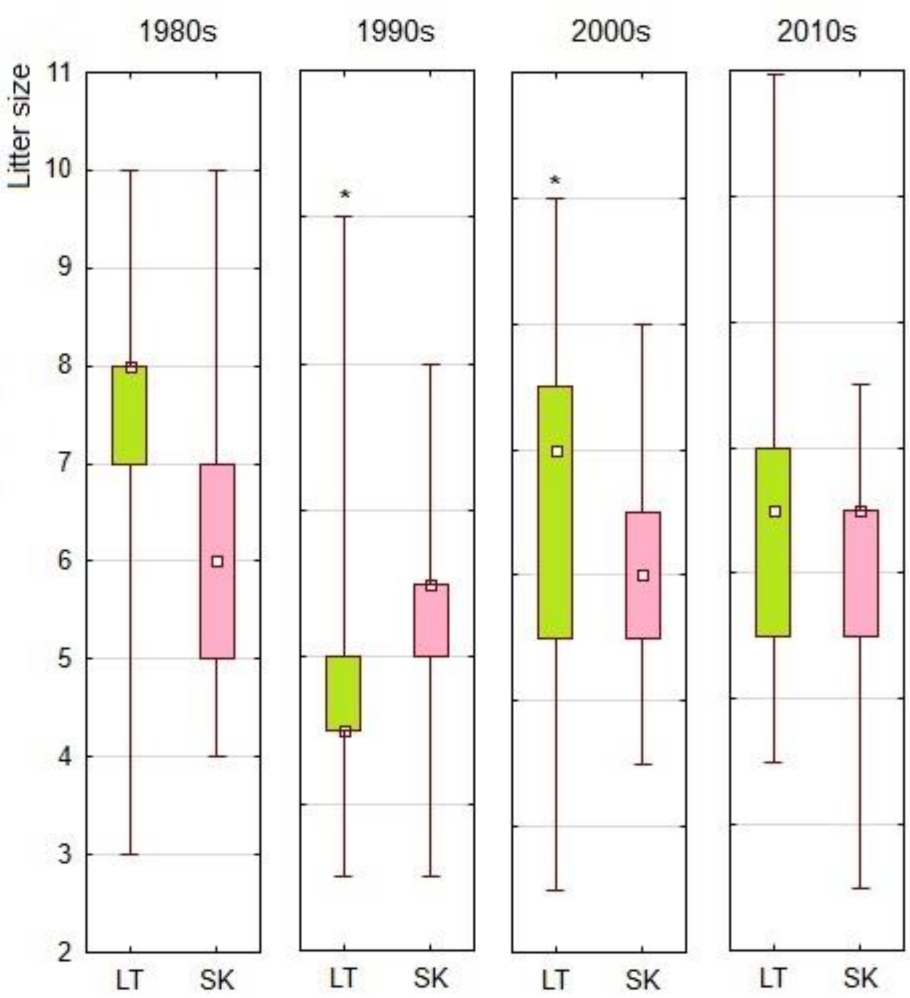

1980s
1990s
2000s
2010s
Litter size
11
10
9
8
7
6
5
4
3
2
*
*
LT
SK
LT
SK
LT
SK
LT
SK

Figure 4.

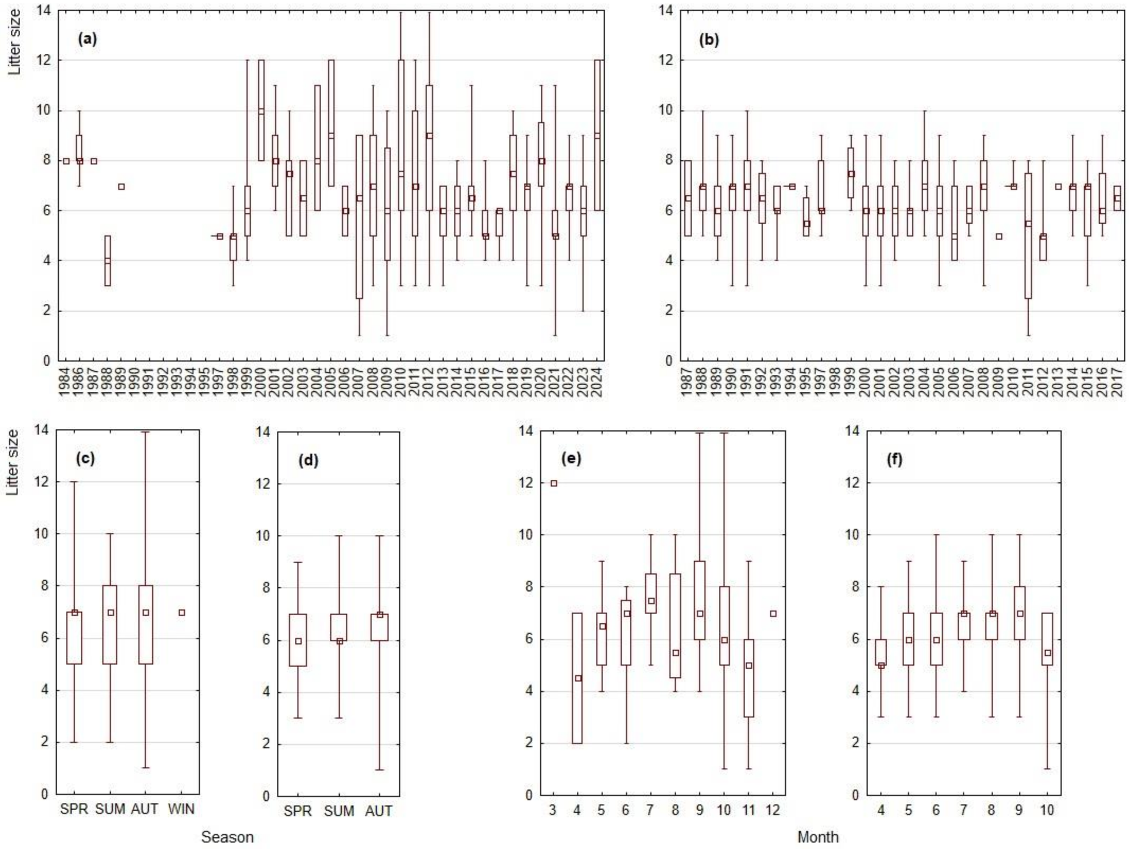


Figure 5.

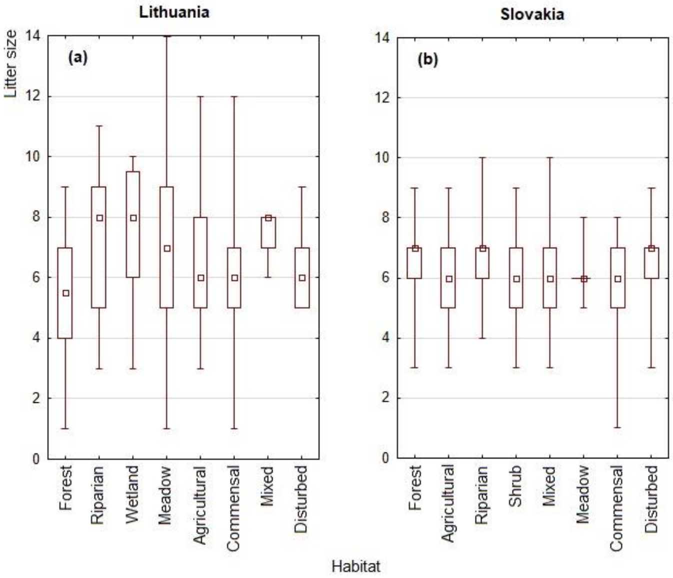


Figure 6.

Figure 1

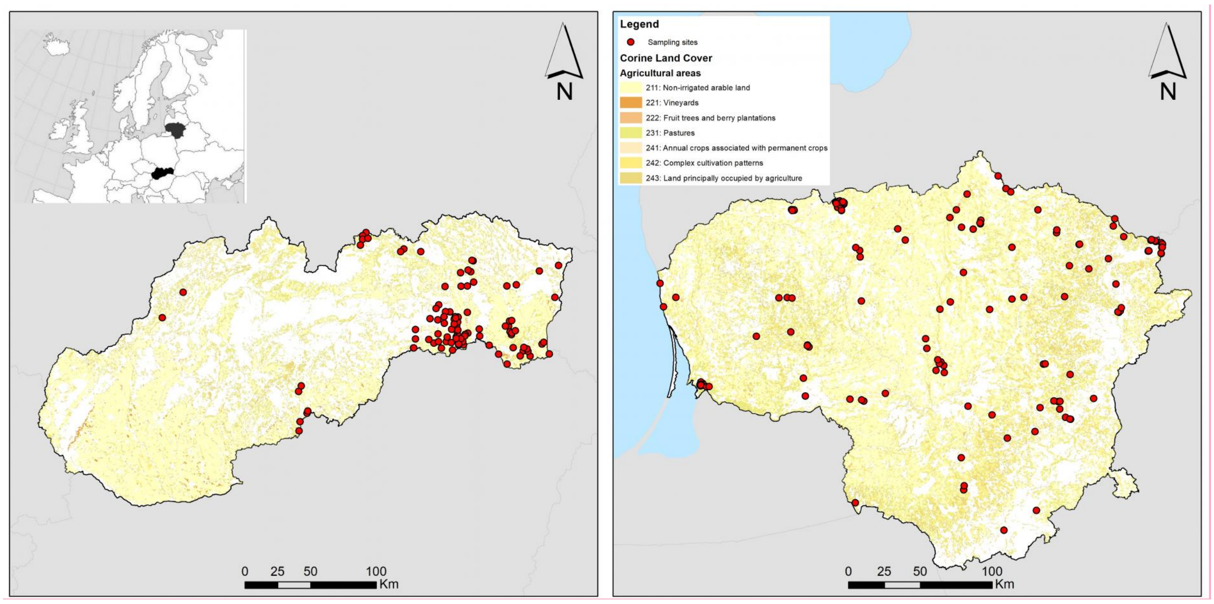


Figure 1

Figure 2

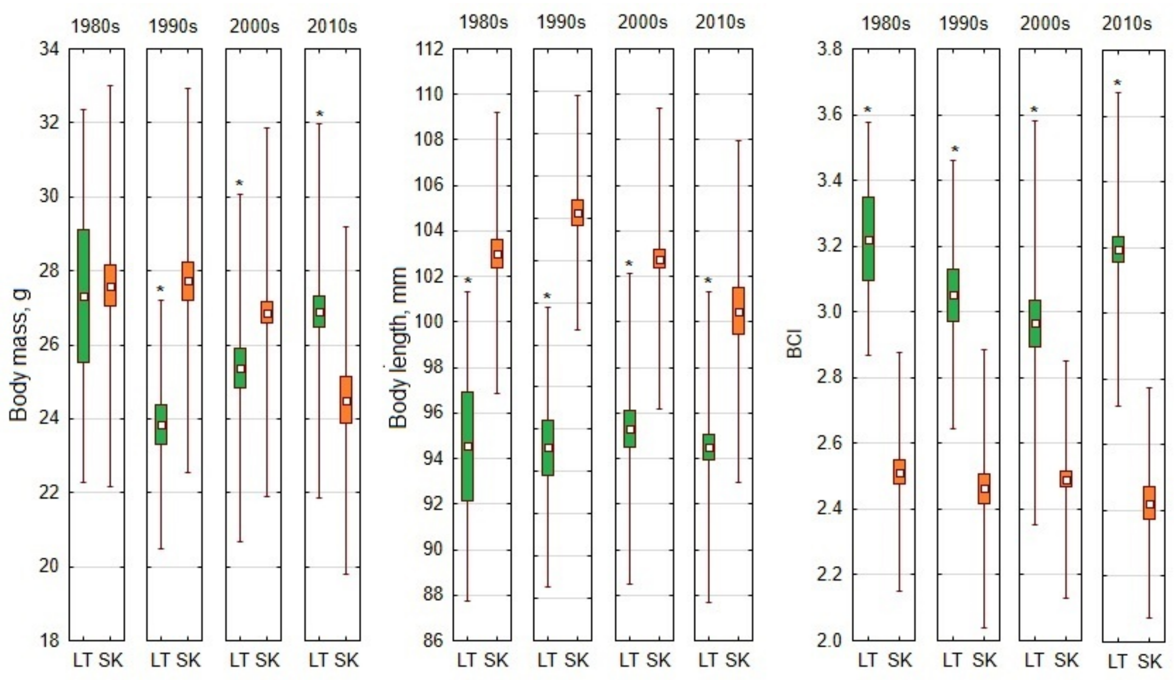


figure 2

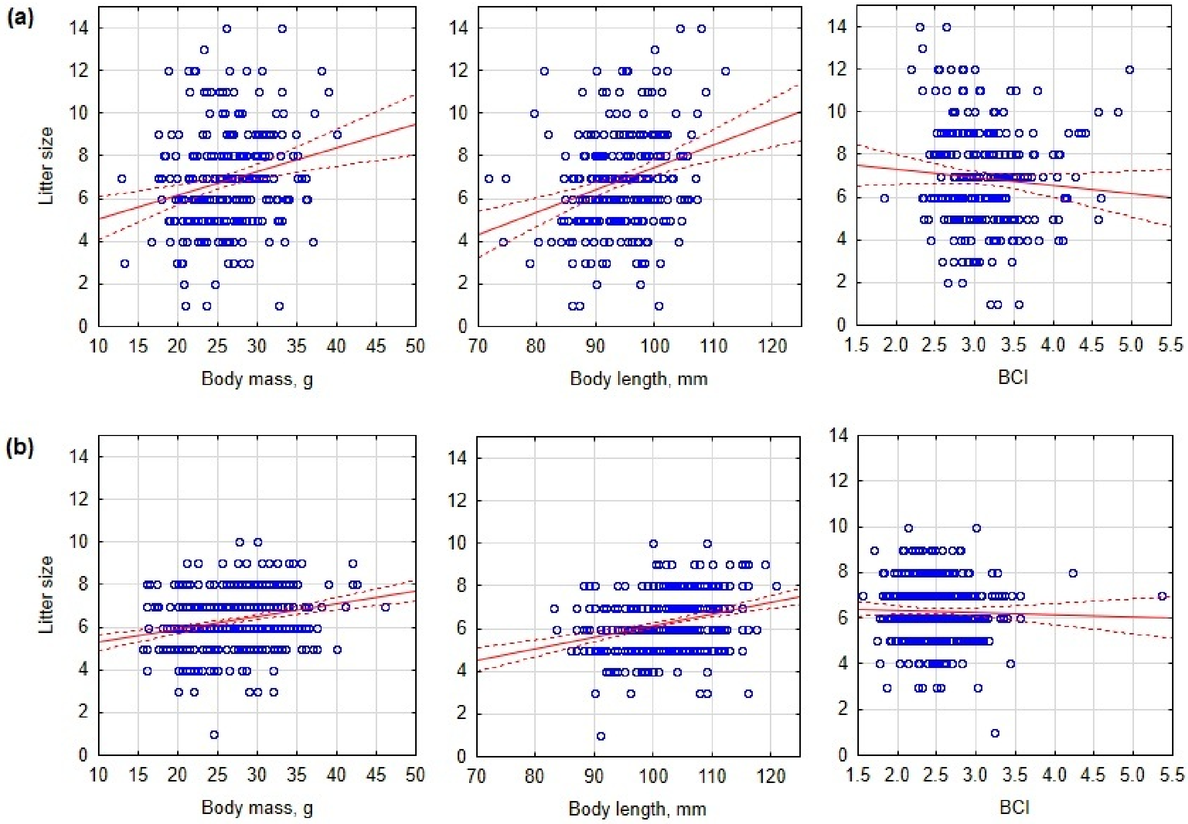

(a)
Litter size
0
2
4
6
8
10
12
14
Body mass, g
10
15
20
25
30
35
40
45
50
Body length, mm
70
80
90
100
110
120
BCI
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
(b)
Litter size
Body mass, g
Body length, mm
BCI

Figure 3

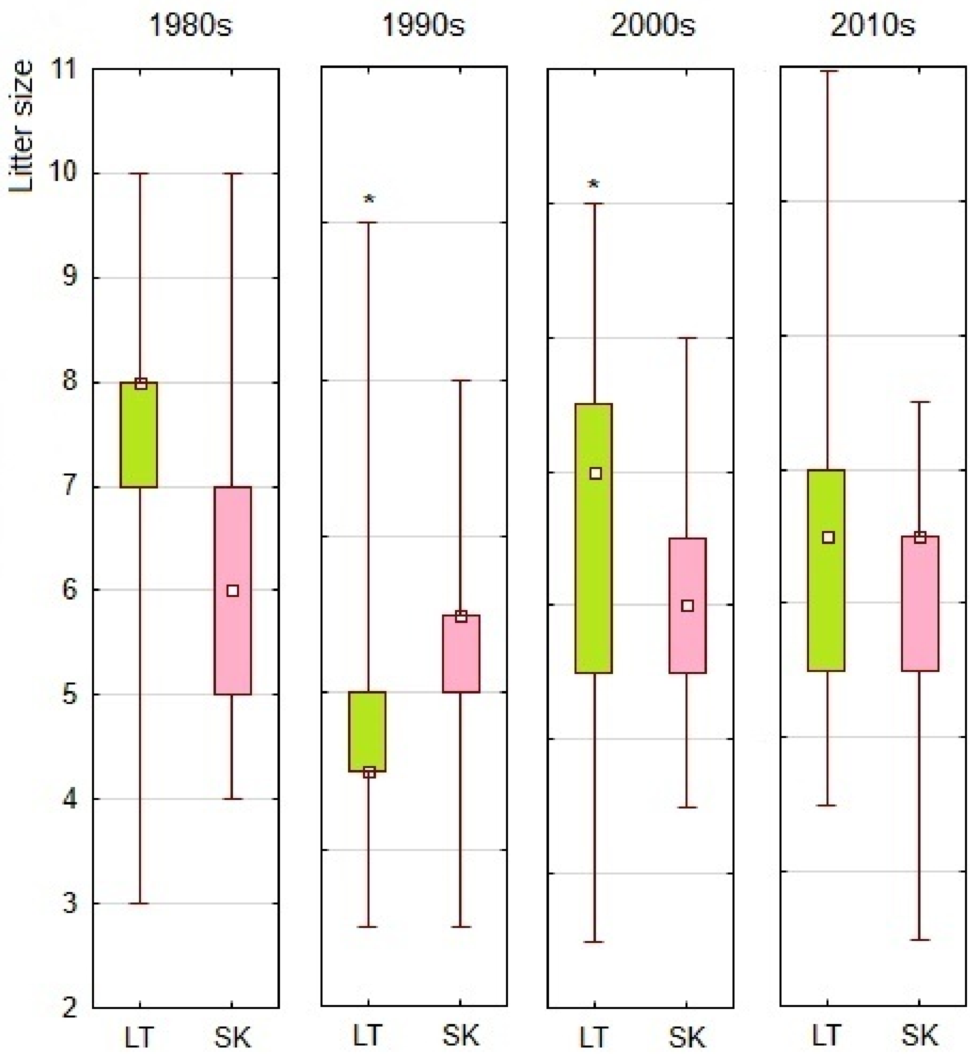

1980s
1990s
2000s
2010s
Litter size
11
10
9
8
7
6
5
4
3
2
*
*
LT
SK
LT
SK
LT
SK
LT
SK

Figure 4

Figure 5

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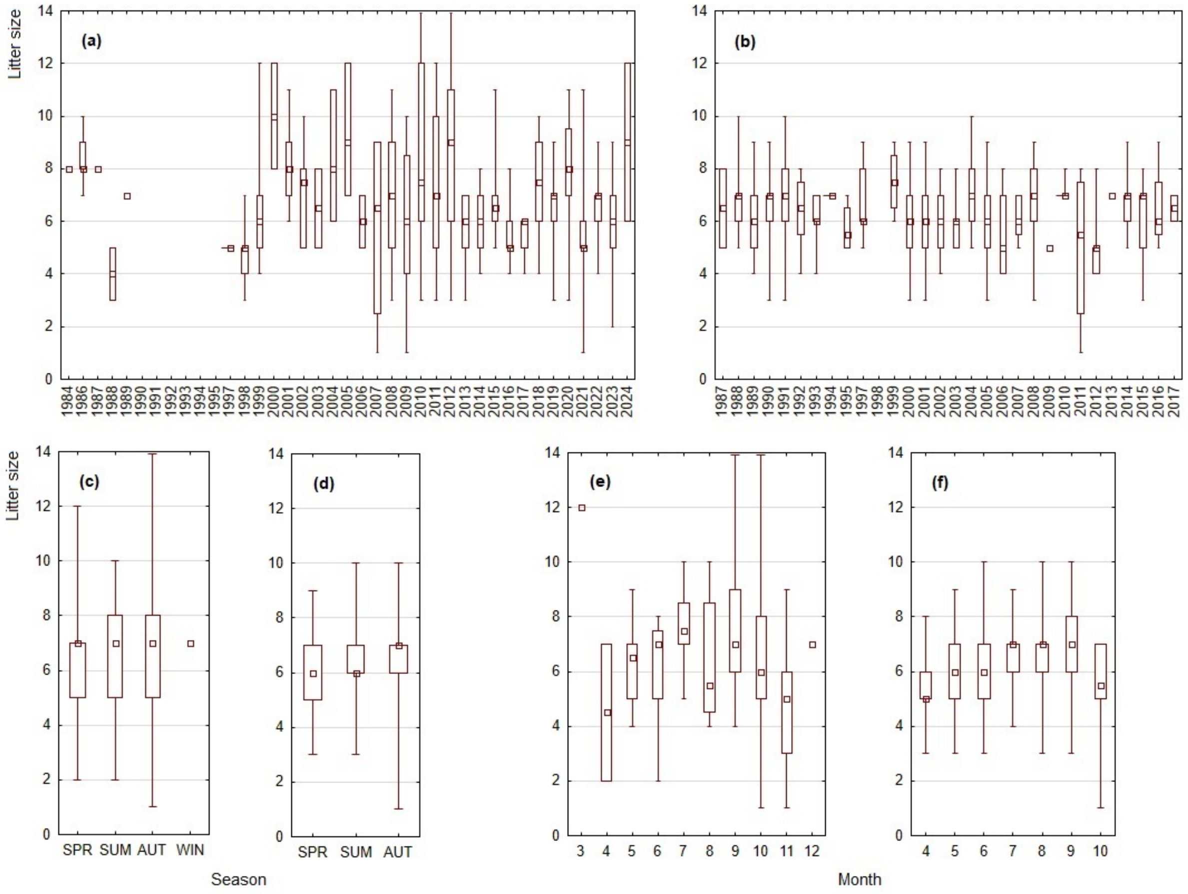

Figure 5

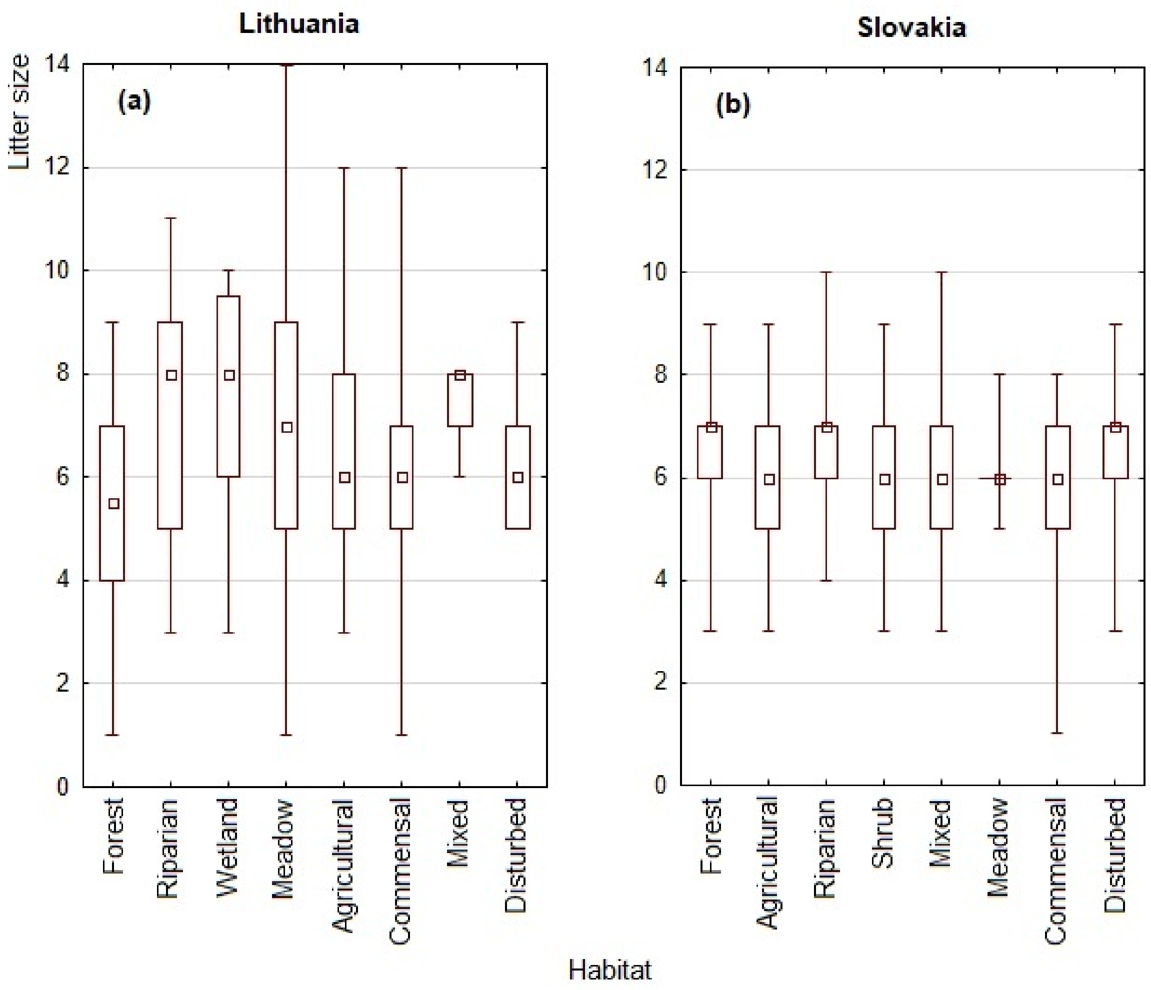
Lithuania
Slovakia
Litter size
(a)
(b)
0
2
4
6
8
10
12
14
Forest
Riparian
Wetland
Meadow
Agricultural
Commensal
Mixed
Disturbed
Forest
Agricultural
Riparian
Shrub
Mixed
Meadow
Commensal
Disturbed
Habitat

Figure 6

Manuscript body

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