Agriculture, Ecosystems and Environment 329 (2022) 107886

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Rodent fertility in commercial orchards in relation to body mass and body condition

Linas Balčiauskas [*], Vitalijus Stirkė, Laima Balčiauskienė

Nature Research Centre, Akademijos 2, LT, 08412 Vilnius, Lithuania

ARTICLE INFO

Keywords:
Rodents
Litter size
Pregnancy disruption
Body condition
Agrolandscape
Lithuania

ABSTRACT

Although rodents are recognized as pests, they are still an important part of agricultural ecosystems. In 2018–2020, we snap-trapped small mammals in Lithuania in 18 commercial orchards (apple and plum orchards, currant and raspberry plantations) and in adjacent control habitats. We aimed to discover whether the litter size of the six most abundant rodent species depended on season, on female body mass and/or on fitness. Litter size in common and root voles was smaller in habitats with a higher intensity of agricultural practices. Compared to summer, observed litter size in autumn significantly decreased in common voles (from 5.6 to 4.8) and yellow-necked mice (from 5.8 to 4.6). In autumn, litter size and female body mass was positively correlated in all rodent species, while in summer this was characteristic to root voles ($r = 0.67$, $p < 0.05$, 45% of variation of the litter size explained) and yellow-necked mice ($r = 0.53$, $p < 0.005$, 27% respectively) only. Female body condition index and litter size correlations were weak. Potential litter size exceeded the observed rate and breeding failures were observed in all species, with the highest percentage in root, bank and common voles.

1. Introduction

Rodents are an important part of agricultural ecosystems, such as commercial orchards, which may serve as reserves for biological diversity (Balčiauskas et al., 2019). They are, however, widely recognized as pests and treated accordingly (Stenseth et al., 2003; Fischer and Schröder, 2014). Data on rodents in agricultural landscapes (Fischer et al., 2011; Janova and Heroldova, 2016) are mainly related to cereal crop areas (Heroldová and Tkadlec, 2011). Rodent research in commercial orchards is scarce (Sullivan et al., 1998; Bertolino et al., 2015; Riojas-López et al., 2018; Suchomel et al., 2019), while that in the Baltic countries is represented only by a pilot study on small mammal diversity in the orchards (Balčiauskas et al., 2019). Data on rodent reproduction in orchards are even scarcer (Somoano et al., 2016, 2017).

The usual breeding season of the yellow-necked mouse (*Apodemus flavicollis*), field vole (*Microtus agrestis*) and bank vole (*Clethrionomys glareolus*) in Lithuania is April–September, while that of striped field mouse (*Apodemus agrarius*) is April–October (Prūsaitė, 1988), of common vole (*Microtus arvalis*) March–October (Mažeikytė, 1993; Balčiauskas, 2005) and of root vole (*Microtus oeconomus*) April–November (Balčiauskas et al., 2012). However, winter breeding of *A. flavicollis* has also been confirmed (Balčiauskienė et al., 2009c). The reproduction capability of various rodent species is an important factor, as it defines the ability to withstand negative factors, including poison treatment (Tobin and Fall, 2004; Werner and Griebeler, 2011), and the ability to recover in numbers and to re-occupy territories after severe disasters or poisoning (Brakes and Smith, 2005). Therefore, we focused our study on the reproduction of the most abundant rodent species in the commercial orchards of Lithuania (northern Europe) in relation to body mass and body condition of adult females.

In general, mammal litter size is related to environmental resources, latitude, selection (r- or K-selection) type (Millar, 1977; Glazier, 1985; Sikes and Ylönen, 1998), body size (Western, 1979; Fokidis et al., 2007) and cyclicity of abundance (Stenseth et al., 1985). In rodents, climate change may also have an influence to litter size (McLean et al., 2019). Species with large litters have more foods available, or are subjected to greater risks when obtaining additional energy in the lactation period (Glazier, 1985). Rodent litter size, therefore, is greater in optimal habitats than in suboptimal ones (Stenseth et al., 1985). Litter size in iteroparous mammals is usually higher at the beginning of the reproduction period, spring and summer (Tkadlec and Krejčová, 2001). This is an adaptive mechanism, as offspring born in autumn may not survive in winter (McLean et al., 2019).

Many life history variables are correlated with body size, the latter

* Corresponding author.
E-mail addresses: linas.balciauskas@gamtc.lt (L. Balčiauskas), vitalijus.stirke@gamtc.lt (V. Stirkė), laima.balciauskiene@gamtc.lt (L. Balčiauskienė).

https://doi.org/10.1016/j.agee.2022.107886
Received 21 February 2021; Received in revised form 24 January 2022; Accepted 24 January 2022

influencing many aspects of the biology of the species (Ernest, 2003; Sibly and Brown, 2007; Eccard and Rödel, 2011; Werner and Griebeler, 2011). The statement of S.K.M. Ernest (2003) that "life history characteristics will show minor variation with environmental conditions (resource availability, climate, competitive environment, and predation pressure), a general life history for each species was sought to average over minor differences in local populations" is disputable in terms of litter size, as a variety of publications show different litter sizes (Stenseth et al., 1985; Innes and Millar, 1994; Yoccoz and Ims, 1999; McLean et al., 2019). Therefore, databases on litter size in various species (Ernest, 2016) occupying different habitats are important for wide-scale analyses. The data presented in this paper cover a gap regarding the reproduction of various small mammal species in orchards. Previously, the relationship between body condition and reproduction in orchard habitats was analysed only in water voles (*Arvicola amphibius*) (Evsikov et al., 2008; Somoano et al., 2016).

Our work with small mammals in commercial orchards was initiated with the aim of finding a reference species for the risk assessment of plant protection products in Lithuania, i.e. it was related to the Sustainable Plant Protection Transition (Sustainable Plant Protection Transition: A global health approach SPRINT, 2020). After recognizing the fact that the diversity of small mammals in the commercial orchards is comparable to that in the natural habitats (Balčiauskas et al., 2019), we further investigated the diet and biology of these animals. The aim of this study was to analyze the reproduction data of the six most abundant small mammal species in commercial orchards and to find whether there were relationships between litter size, female body mass and body condition (this used as a proxy for fitness). Specifically, we tested whether there were differences in litter size depending on the crop type, crop age and intensity of agricultural activities. This is the first publication on the reproduction of small mammals in agricultural habitats in the Baltic region.

2. Materials and methods

This study was conducted in Lithuania (North Europe) in 2018–2020, snap-trapping small mammals in commercial orchards and berry plantations. Climate in the territory is transitional between continental and maritime: average air temperatures are −4.9 °C in January and 17.2 °C in July. Rainfall averages from 570 mm to 902 mm annually depending on the location, and snow cover lasts 65–105 days (Holmberg, 2000; LHMT, Lithuanian Meteorological Service, 2021).

We analyzed body condition and reproductive parameters (number of registered litters, litter size and pregnancy disruptions) in the most numerous small mammal species in the orchards and adjacent control habitats (meadows or forests).

2.1. Study sites

Eighteen study sites with 20 trapping locations were selected across Lithuania, representing apple and plum orchards, as well as currant, raspberry and highbush blueberry plantations, with various intensities of agricultural practices. Agricultural practices used at the sites included the application of plant protection agents and rodenticides, the mowing of grass (and subsequent removal of the cut grass), the mulching of the areas between the rows of plants and scarification of the soil between the rows. We defined high intensity as the frequent application of two or more of the measures, while medium intensity was using two measures during the crop season, once or several times, and low intensity as only grass mowing (Table 1). In the absence of other agricultural practices, grass mowing was the only factor that had the possibility to influence small mammals in the control habitats (Balčiauskas et al., 2019).

2.2. Small mammal trapping

Small mammals were trapped using snap traps set in 1–4 lines. Line consisted of 25 traps, each set 5 m apart as in (Balčiauskas et al., 2019). In 15 out of 18 sites, lines were positioned in a row, while in three smallest sites – parallel to each other with distance no less than 20 m between. Traps were baited with bread crust soaked in raw sunflower oil, set for three days, and checked once per day. The bait was changed after rain or when consumed. The total trapping effort was 25,503 trap days.

Table 1
Number of studied sites with different characteristics of habitats.

Crops	N	Crop age[a]			Intensity[b]			Control habitat[c]		
		O	MD	Y	H	M	L	MM	NM	FE
Apple	11	9	1	1	6	2	3	8	2	1
Plum	2		1	1		1	1	1	1	
Currant	3		3			1	2	3		
Raspberry	3		2	1	1	1	1	1	1	1
Highbush blueberry	1		1		1			1		

[a] Age of the orchard: O—old, MD—medium, Y—young.
[b] Intensity of agricultural practices on site: L—low, M—medium, H—high.
[c] Control habitat: MM—mowed meadow, NM—non-mowed meadow, FE—forest edge.

Trapping was conducted in the first half of summer (2–28 June in 2018, 5–29 June and 3–4 July in 2019, and 2–25 June in 2020) and in the first half of autumn (3–20 September and 1–11 October in 2018, 17–27 September and 2–12 October in 2019, 24–30 September and 1–15 October in 2020).

Species of mice and bank voles were identified according external characters. Specimens of *Microtus* voles were identified according differences of their teeth. Juveniles, subadults and adults were identified based on body weight, the status of the sex organs and atrophy of the thymus, the latter of which decreases with animal age (Balčiauskas et al., 2012). The reproductive status of males was judged under dissection from the appearance and size of the genitals, scrotal testes show male being adult, while full epididymis shows active spermatogenesis. After breeding, the testes and related glands become slumped, slate-coloured, and diminish in size (Balčiauskas et al., 2012).

Reproductive activity was defined as the percentage of males having spermatogenesis and the percentage of pregnant females (visible embryos) or reproducing females, being in the onset of pregnancy (open vagina, sealed vagina, impregnated). In both cases, this was assessed in relation to the total number of adult animals of the respective gender, separately in summer and in autumn.

Breeding failures were evaluated as the percentage of pregnancies with non-implanted or resorbed embryos from all registered pregnancies. The numbers of embryos, *corpora lutea* and the numbers of fresh placental scars were counted under dissection. The observed litter size was defined as the number of viable (non-resorbing) embryos or fresh placental scars, while potential litter size as the numbers of *corpora lutea*, as in Balčiauskas et al., (2012, 2019). We treated the difference between the numbers of *corpora lutea* and the numbers of placental scars as non-implantation, while the difference between the numbers of embryo and *corpora lutea* as embryo resorption. We also directly counted resorbed embryos, with the latter being smaller and darker than the rest of the embryos in the uterus or already partially disintegrated (Balčiauskas et al., 2012).

Body condition index C, based on body weight in g (Q) and body length in mm (L), was calculated according to Moors (1985) and used as individual fitness indicator. The weight of the uterus with embryos was excluded (Sibly and Brown, 2007).

The study was approved by the Animal Welfare Committee of the Nature Research Centre, protocol No GGT-7 and was conducted in accordance with Lithuanian (the Republic of Lithuania Law on the Welfare and Protection of Animals No. XI-2271) and European legislation (Directive 2010/63/EU) on the protection of animals. Snap trapping was justifiable, as we studied reproduction parameters and collected tissues and internal organs for analysis of pathogens, stable isotopes and chemical elements (not covered in this publication). In Lithuania, permission to snap trap small mammals is not required.

2.3. Data analysis

We applied main effects ANOVA to the litter size to test the possible cumulative influence of categorical predictors—species, season, crop type and intensity of agricultural practices. Hotelling's T^2 was used for multivariate testing. Differences were evaluated by Student's t test and Tukey HSD. The confidence level was set as $p < 0.05$ (we interpret $p < 0.10$ as indicating the trend, which is non-significant). We tested the dependence of litter size from the body condition index and body mass using the Pearson correlation coefficient and linear regression, separately for summer and autumn seasons. Differences in the reproductive activity were assessed by χ^2 test. Calculations were done in Statistica for Windows, ver. 6.0 (StatSoft, Inc., Tulsa, OK, USA).

3. Results

We trapped 1450 individuals of small mammals, and identified 11 species. Common shrew (*Sorex araneus*), pygmy shrew (*Sorex minutus*), house mouse (*Mus musculus*), harvest mouse (*Micromys minutus*) and *A. amphibius* were not numerous, totaling only 3.9% of all trapped individuals. No small mammals were trapped in the studied highbush blueberry plantation for two years, therefore this habitat was not studied in 2020. Gender and age distribution of the six most numerous species is presented in Table 2.

We registered 279 reproductive females among these six rodent species in 2018–2020, 19 being in the onset of first pregnancy (open vagina, impregnated), 254 in first pregnancy (embryos visible) or after the first litter (*corpora lutea* and/or placental scars present), and six after the first litter and being pregnant with a second litter. In total, 65 cases of breeding failures were registered, 58 cases being embryo non-implantation and eight cases being embryo resorbtion.

Seasonally, breeding activity in both males and females was higher in the summer months in all rodent species (Fig. 1). The decrease in proportion of pregnant females in the autumn months was best expressed in *M. agrestis* ($\chi^2 = 6.64$, df = 1, p = 0.01), *M. arvalis* ($\chi^2 = 5.10$, $p < 0.05$) and *A. agrarius* ($\chi^2 = 4.24$, $p < 0.05$), while this trend was not significant in *A. flavicollis* ($\chi^2 = 3.10$, p = 0.07) and *M. oeconomus* ($\chi^2 = 2.49$, p = 0.11).). The proportion of pregnant females in *C. glareolus* was low in both summer and autumn (31.3% and 18.2%, respectively, NS). The loss of reproductive activity among males in autumn was strongest in *A. flavicollis* and *C. glareolus* ($\chi^2 = 49.31$ and $\chi^2 = 12.97$, respectively, both $p < 0.001$), while males of *M. arvalis* were reproductively active in both seasons.

Table 2
Gender and age distribution in the most numerous rodent species from the commercial orchards (ad – adults, sub – subadults, juv – juveniles).

Species	Males			Females			Total
	Ad	Sub	Juv	Ad	Sub	Juv	
Yellow-necked mouse (*Apodemus flavicollis*)	99	64	38	60	76	47	374[a]
Striped field mouse (*A. agrarius*)	38	64	81	29	16	112	346[a]
Common vole (*Microtus arvalis*)	41	32	114	132	17	98	436[a]
Root vole (*M. oeconomus*)	8	4	5	17	2	6	42
Field vole (*M. agrestis*)	7	4	2	14	2	2	31
Bank vole (*Clethrionomys glareolus*)	22	23	38	27	12	19	164[a]

[a] Ages and genders of a few individuals were not identified due to corpse damage by insects, slugs or other mammals

3.1. Rodent body condition

The body condition of rodents significantly differed between species (ANOVA, F = 8.30, df = 5, $p < 0.001$), the same also being true for adult females (F = 4.06, df = 5, $p < 0.005$). A gender-based difference in body condition index, C, was significant in *A. agrarius* only, the females being in better condition than males (t = 2.05, df = 330, $p < 0.05$). In general, we found mice to be in better body condition than voles (Tukey unequal HSD, $p < 0.01$). The highest body condition index was characteristic to *A. flavicollis* in general, and also to adult females of this species. Body condition among voles did not differ (Table 3).

3.2. Litter size of the most numerous rodent species in the commercial orchards

Differences of potential litter size among the six most numerous rodent species were not significant (ANOVA, $F_{5,204} = 1.31$, p = 0.26), with the highest average fecundity found in *A. agrarius* and *M. oeconomus* (Table 4). Minimum and maximum potential litter size fluctuated widely in all species. However, variation of observed litter size was species dependent ($F_{5,252} = 2.59$, p = 0.026), with the highest litter size observed in *A. agrarius*. Though potential litter size exceeded observed sizes in all species, the difference was significant in *M. arvalis* only. The highest percentage of breeding failures was characteristic to *M. oeconomus*, *C. glareolus* and *M. arvalis* (Table 4).

3.3. Litter size of small mammals: seasonal differences

We found that the observed litter size decreased in autumn in all rodents from the commercial orchards. A significant decrease in observed litter size was found in *M. arvalis* (t = 2.87, df = 125, $p < 0.005$) and *A. flavicollis* (t = 2.29, df = 47, $p < 0.05$), while an insignificant tendency of decrease was characteristic to *M. oeconomus* (t = 1.92, df = 14, $p < 0.10$). In the other species, the litter size decrease was not expressed (Fig. 2).

A decrease of potential litter size in autumn was found in *M. arvalis* (t = 2.94, df = 108, $p < 0.005$), *A. flavicollis* (t = 3.12, df = 31, $p < 0.00$) and *M. oeconomus* (t = 2.54, df = 14, $p < 0.05$), while a tendency of decrease was characteristic to *C. glareolus* (t = 1.76, df = 18, $p < 0.10$).

3.4. Influence of the habitat, habitat age and intensity of agricultural practices

The observed and potential litter sizes were not dependent on habitat (Hotelling's $T^2 = 0.023$, $F_{8,404} = 0.60$, p = 0.78), therefore we did not provide data on litter size according to crop type or comparisons between crop habitats to control ones. However, we did find a trend in the orchards and berry plantations of an increase in observed litter size in young-aged habitats in *M. arvalis* (ANOVA, $F_{2,99} = 2.54$, p = 0.08). In *A. flavicollis*, litter size was significantly larger in old aged habitats ($F_{1,29} = 2.11$, $p < 0.05$). The other three small mammal species, *M. oeconomus*, *M. agrestis* and *C. glareolus*, did not reproduce in habitats other than old ones (Fig. 3A).

A decrease in observed litter size in the areas with a higher intensity of agricultural practices in the orchards and plantations was registered for *M. oeconomus* ($F_{1,6} = 5.67$, $p < 0.05$), the trend of decrease was characteristic for *M. arvalis* (ANOVA, $F_{2,99} = 2.96$, p = 0.056), while a decrease in *C. glareolus* was not significant. In *A. flavicollis*, litter size was similar irrespective of intensity of agricultural practices. The observed trend of litter size increase in *A. agrarius* and *M. agrestis* along with intensity of agriculture was not significant (Fig. 3B).

3.5. Female body mass, body condition and litter size

In summer, litter size was significantly correlated with female body

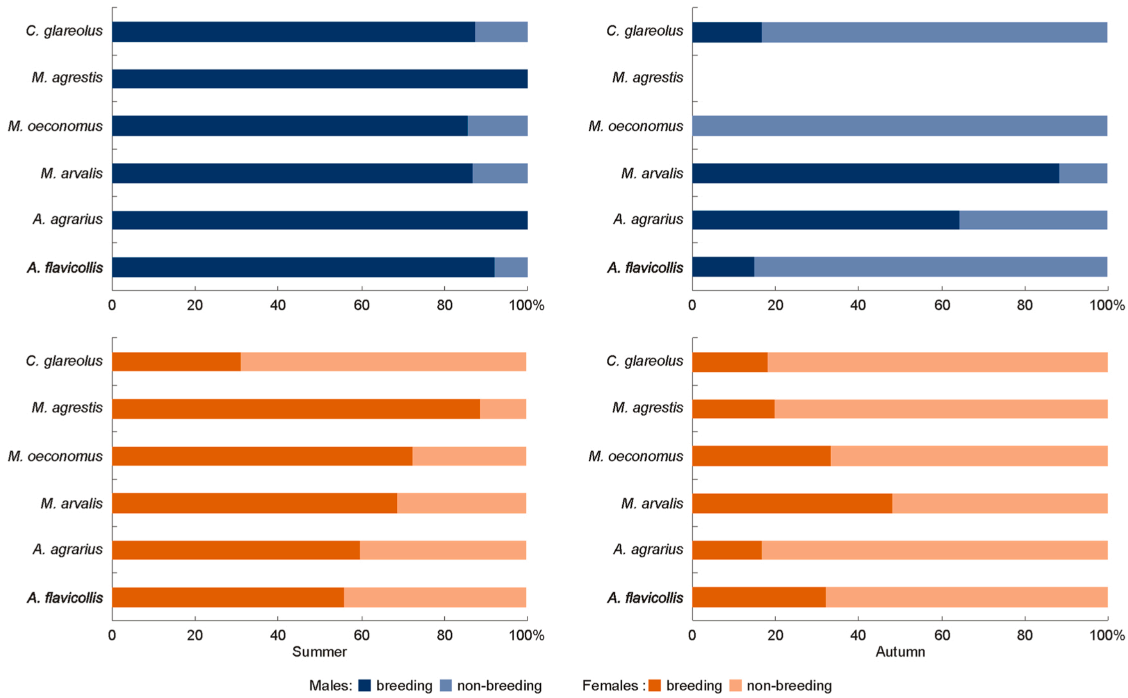

Fig. 1. Proportion of breeders in the most numerous rodent species in the commercial orchards in summer and autumn.

Table 3
Body condition indexes of the most numerous rodent species. N is shown in Table 2. Significance of differences between species is shown by letter subscripts.

Species	All individuals		Adult females	
	average ± SE	Min–max	average ± SE	Min–max
Apodemus flavicollis	3.40 ± 0.03^{A}	2.45–5.06	3.54 ± 0.06^{a}	2.65–4.63
Apodemus agrarius	3.38 ± 0.03^{A}	2.30–5.07	3.34 ± 0.08^{b}	2.61–4.59
Microtus arvalis	3.25 ± 0.02^{B}	2.07–4.98	3.23 ± 0.05^{b}	2.07–4.98
Microtus oeconomus	3.01 ± 0.06^{B}	2.14–4.16	3.05 ± 0.09^{b}	2.26–3.54
Microtus agrestis	3.29 ± 0.09^{B}	2.27–4.47	3.43 ± 0.16^{b}	2.27–4.47
Clethrionomys glareolus	3.24 ± 0.04^{B}	1.86–4.53	3.35 ± 0.12^{b}	2.09–4.34

^{AB} $p < 0.01$, ^{ab} $p < 0.05$

mass in *M. oeconomus* ($r = 0.67$, $p < 0.05$, body mass explained 45% of variation of the litter size) and *A. flavicollis* ($r = 0.53$, $p < 0.005$, 27% of litter size variation explained). Positive correlations in *A. agrarius* ($r = 0.39$) and *C. glareolus*, as well as negative correlations in *M. arvalis* and *M. agrestis*, were weak and not significant (Fig. 4A).

In autumn, litter size and female body mass were positively correlated in five rodent species (Fig. 4B). In *M. oeconomus*, *M. agrestis* and *C. glareolus*, the correlations were weak ($r = 0.26$–0.29) and not significant, while litter size and female body mass in *A. agrarius* was not correlated. The strongest correlations were found in *A. flavicollis* ($r = 0.58$, $p < 0.005$, body mass explained 34% of variation of the litter size) and *M. arvalis* ($r = 0.36$, $p < 0.001$, 13% of litter size variation explained by female body mass).

In general, female body condition index and litter size correlations were weak. In summer, the exceptions were *M. oeconomus* ($r = 0.47$) and *C. glareolus* ($r = -0.36$), though both were not significant (Fig. 5A).

In autumn, strong positive correlations between body condition index and litter size were found in *C. glareolus* ($r = 0.64$, $p < 0.05$, 42% of litter size variation explained) and *M. agrestis* ($r = 0.75$, NS). Positive correlations in *A. flavicollis* and *M. arvalis* were weak and not significant. A strong negative correlation between body condition index and litter size in *M. oeconomus* ($r = -0.75$) was also not significant. In *A. agrarius*, litter size and female body condition index was not correlated (Fig. 5B).

3.6. Minimum body mass of reproducing individuals and timing of reproduction

In *A. flavicollis*, the minimum body mass of reproducing males was 18.1 g, while individuals under 25 g accounted for 1% of all adult animals. In females of this species, the minimum body mass of a fertilized female was 20 g, with individuals under 25 g accounting for 3.3% of all adults. In *A. agrarius*, the minimum body mass of reproducing males was 15.6 g, with individuals under 20 g accounting for 21.1% of all adult animals. For females, the respective numbers were 12.8 g (embryos of 6 days) and 13.8%.

In *M. arvalis*, the minimum body mass of reproducing males was

Table 4
Reproduction parameters in the most numerous rodent species in the commercial orchards (LS – litter size).

Species	Observed			Potential			Failures (% of cases)
	N	LS±SE	Min–max	N	LS±SE	Min–max	
Apodemus flavicollis	49	5.33 ± 0.25	2–10	33	5.91 ± 0.35	2–10	12.2
Apodemus agrarius	28	6.21 ± 0.31	3–9	20	6.35 ± 0.35	4–9	21.4
Microtus arvalis	127	5.08 ± 0.15^{A}	2–10	110	5.55 ± 0.15^{B}	2–10	29.1
Microtus oeconomus	16	5.81 ± 0.50	2–11	16	6.31 ± 0.53	2–11	43.8
Microtus agrestis	14	5.00 ± 0.36	3–7	11	5.55 ± 0.39	3–7	14.3
Clethrionomys glareolus	24	5.58 ± 0.29	3–8	20	5.85 ± 0.29	4–8	29.2

^{AB} $p < 0.05$

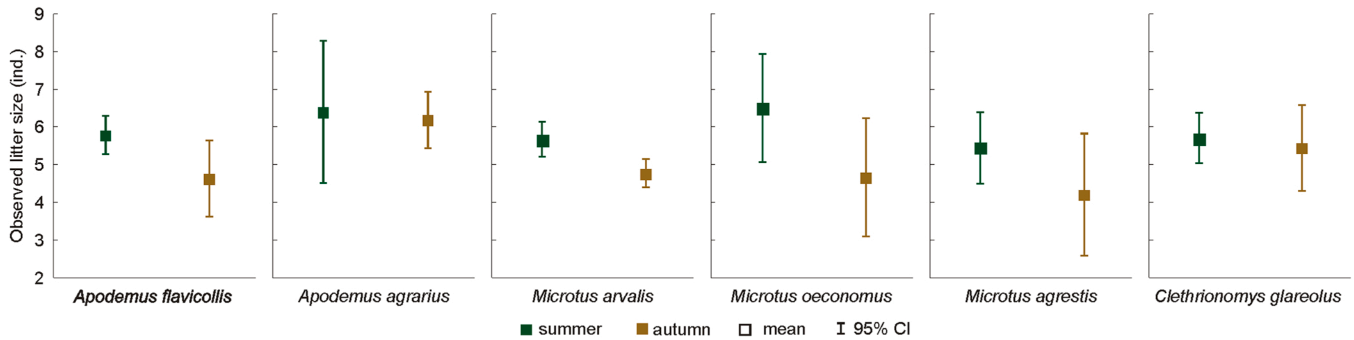

Fig. 2. Seasonal decrease of the observed litter size in rodents in the commercial orchards.

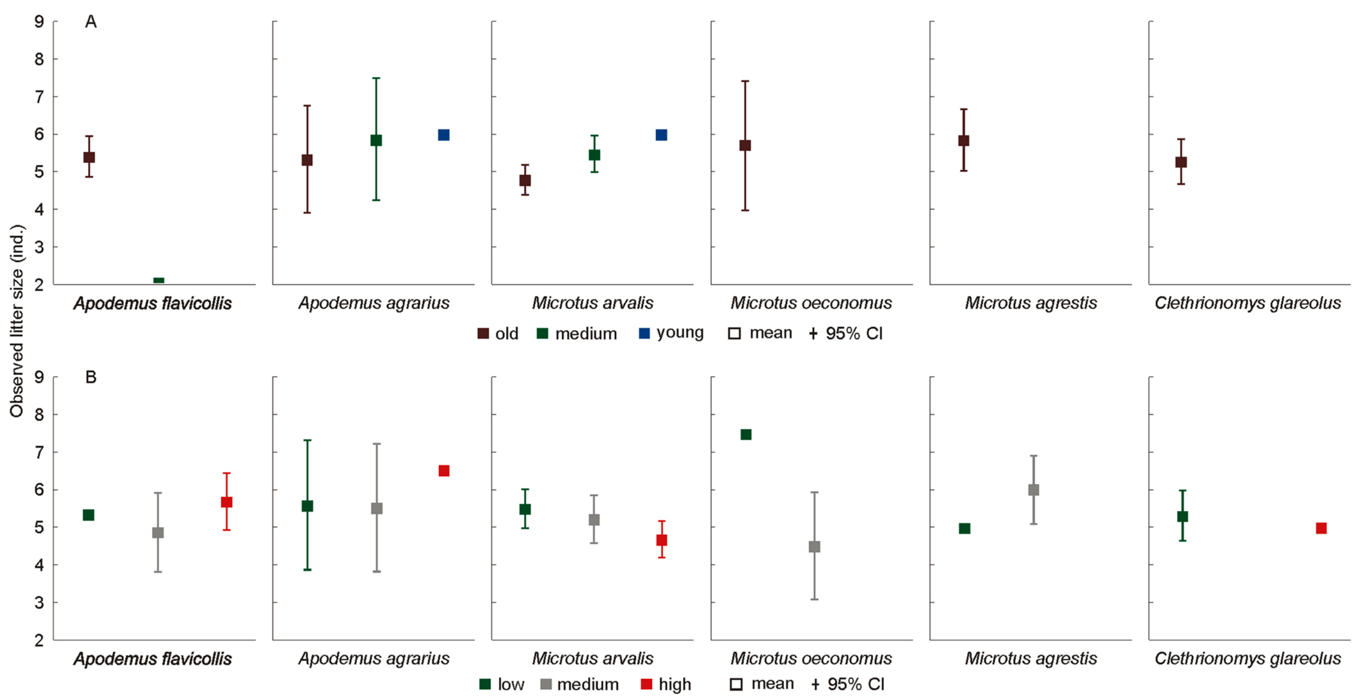

Fig. 3. Distribution of observed litter sizes in rodents in commercial orchards depending on habitat age (A) and intensity of agricultural practices (B).

13.9 g, with individuals under 20 g accounting for 4.9% of all adults. In females, the respective numbers were 10.7 g (embryos of 8 days) and 11.4%. In *M. oeconomus*, all reproducing males and 5.9% of females were over 20 g (minimum body mass 21.9 g). In *M. agrestis*, all reproducing males were over 30 g, while females below 25 g accounted for 28.6 g (minimum body mass 20.3 g).

In *C. glareolus*, the minimum body mass of reproducing males was 16.9 g, with individuals under 18 g accounting for 27.3% of all adult animals. In females of this species, all reproducing individuals were over 18 g.

Our trappings were seasonally-based; therefore information on the timing of reproduction is limited. In the first ten days of June, all trapped adult individuals of *A. flavicollis* and *M. oeconomus* were reproducing (males active, females had 10–21 day and 6–21 day embryos). Thus, both species started reproducing in May in commercial orchards. In *C. glareolus*, all males were active and females impregnated. However, three *C. glareolus* females were already after breeding and one pregnant with a second litter. Thus, this species started reproduction in April and May.

In the first ten days of October, 12.5% of adult males of *A. flavicollis* were still active and there were still impregnated females; thus reproduction continued to at least November. Only a few reproductively active males were trapped in *A. agrarius*, but no pregnant females. In *M. arvalis*, males were not active, and out of adult females only 20% were pregnant. Similarly, in *C. glareolus*, only 20% of adult females were pregnant. Thus, we may suppose that the last three species were at the end of their reproductive seasons. Neither *M. oeconomus* and *M. agrestis* were reproducing in October.

4. Discussion

Small mammals in commercial orchards contribute towards animal diversity within agrolandscapes, they are part of the food web (being preyed upon by carnivore mammals and myophagous birds) and provide ecosystem functions (Heroldová et al., 2007; Fischer et al., 2011; Janova and Heroldova, 2016). As shown in Balčiauskas et al. (2019), the diversity of small mammal communities in commercial orchards and berry plantations in Lithuania is higher than in crop fields and exceeds that in forests.

Reproduction is an important aspect of rodent biology, securing the survival and sustainability of their populations in the unfriendly agricultural habitats or leading to the restoration of populations after negative events and poisoning (Shilova and Tchabovsky, 2009; Werner and Griebeler, 2011; Bonnet et al., 2013; Golet et al., 2013; Jacob and Buckle, 2018; Lund, 2018). Better body mass and body condition in rodents may result in larger litters and better survival (Fokidis et al.,

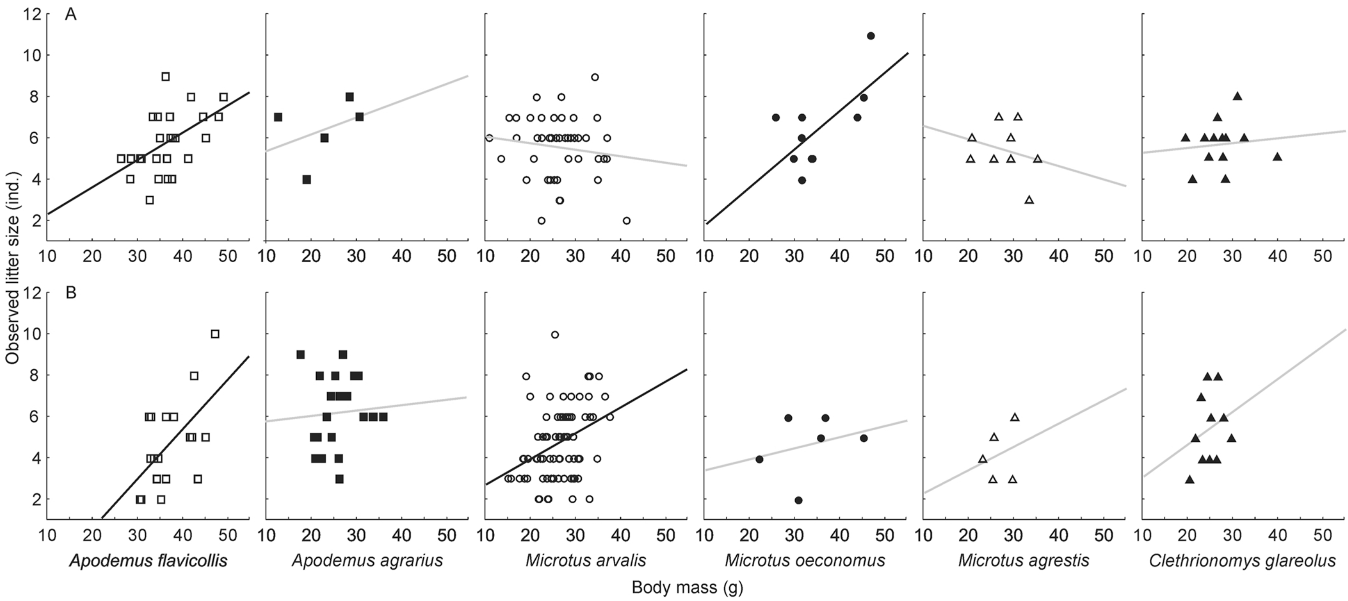

Fig. 4. Correlation of observed litter size and female body mass in rodents in commercial orchards in summer (A) and autumn (B). For non-significant correlations, regression line is in light grey.

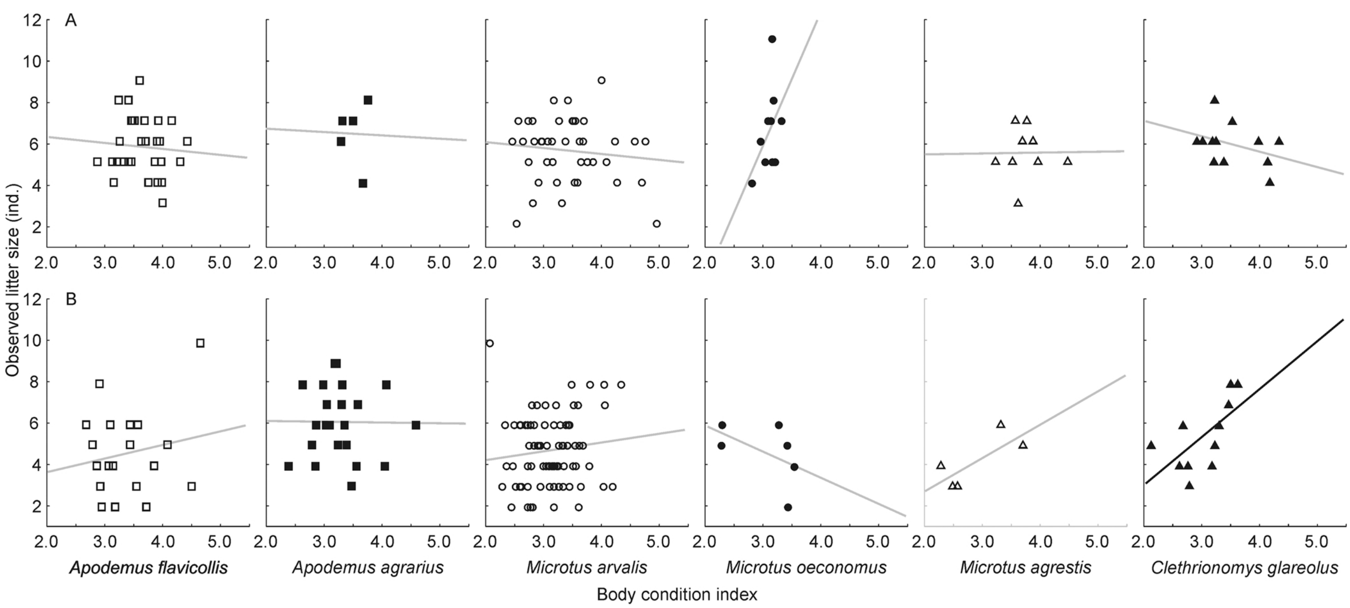

Fig. 5. Correlation of observed litter size and female body condition index of rodents in the commercial orchards in summer (A) and autumn (B). For non-significant correlations, regression line is in light grey.

2007; Somoano et al., 2016; Bonnet et al., 2017).

During a three-year study into rodent reproduction and its relationship with female body mass and condition in commercial orchards in Lithuania, we found that breeding failures were characteristic to all of the most numerous rodent species, with highest percentage observed in *M. oeconomus, C. glareolus* and *M. arvalis*. Potential litter size exceeded the observed sizes in all species, most significantly in *M. arvalis*. Comparing to 50-year old data (Prūsaitė, 1988), the current breeding season continued later in the autumn season. Compared to summer, litter size decreased in autumn in all rodents, most significantly in *M. arvalis* and *A. flavicollis*. Additionally, in *M. arvalis, M. oeconomus* and *C. glareolus*, litter size was smaller in habitats with a higher intensity of agricultural practices. In summer, female body mass was positively correlated with litter size in *M. oeconomus* and *A. flavicollis*, while in autumn the same was true in all rodent species. Correlations of litter size and female body condition index were weak.

Comparing litter size and breeding season data obtained in our study with average values in the species range (Ernest, 2016; Wilson et al., 2017) and neighboring Belarus (Savickyj et al., 2005), as well as with earlier data representing Europe (Niethammer and Krapp, 1978, 1982) and Lithuania (Prūsaitė, 1988), we found some general patterns (Table 5). Namely, litter size of *A. flavicollis, A, agrarius* and *M. arvalis* in commercial gardens was smaller, while that in *M. agrestis* and *C. glareolus* was larger (see Table 4). Likewise, the litter sizes of the former three species were smaller than the average values of the species across their distribution ranges, while they were larger for the last two species. There is a possibility that the above-mentioned differences are due to differences in data collection methods (e.g. trapping period and time of the year, data pooling for different habitats), but we are not able to check this from cited publications.

Table 5
Reproduction parameters of the analysed rodent species, geographic and time scale. Data sources: Ernest (2016) (1), Niethammer and Krapp (1978) (2), Wilson et al. (2017) (3), Savickyj et al. (2005) (4), Prūsaitė (1988) (5), Niethammer and Krapp (1982) (6), Balčiauskas et al. (2012) (7).

Species	Scale[1]		Litter size		LBR[2]	BM, g[3]		Source
	G	T	Average	Range		Male	Female	
Apodemus flavicollis	DR		5.54					(1)
	E	Pre 1978	5.5	4–9	III–XI			(2)
	F		5.7	3–8				(3)
	BY	1970–2000	6.0					(4)
	LT	1960–1985	6.4	2–12	IV–IX	17.8	16.2	(5)
Apodemus	DR		5.72					(1)
agrarius	DR		5.5	1–10				(3)
	E	Pre 1978	6–6.7		IV–IX			(2)
	BY	1970–2000		5–7	III–IX			(4)
	LT	1960–1985	7.6	2–12	IV–X			(5)
Microtus	DR		5.11					(1)
arvalis	DR		5.8–6.3[4]	1–13	III–XI			(3)
	E	Pre 1978	5.5	1–13	III–XI			(6)
	BY	1970–2000	4.6–5.4		IV–X			(4)
	LT	1960–1985	6.1	1–11	III–X			(5)
Microtus	DR		5.76					(1)
oeconomus	DR		4.5–8.6[5]	2–14	II–IX[6]			(3)
	E	Pre 1978	5.6–7.8[7]	2–12	IV–IX			(6)
	LT	1960–1985		4–6			20.2	(5)
	LT	2001–2009	5.93	2–14	IV–XI	17.9	16.5	(7)
Microtus	DR		4.42					(1)
agrestis	DR		4.7–5[8]	3–11	III–X[9]			(3)
	E	Pre 1978	4.7	2–10	II–XI[9]			(6)
	BY	1970–2000	6.1	3–6	IV–XI			(4)
	LT	1960–1985		3–7	IV–IX		10.2	(5)
Clethrionomys	DR		4.29					(1)
glareolus	DR		4.8		III–X			(3)
	E	Pre 1978	3.9–5.2[10]	10	III–X[9]			(6)
	BY	1970–2000	5.4					(4)
	LT	1960–1985	5.0	3–11	IV–IX			(5)

[1] G – geographic range of the dataset, T – time of the dataset, DR – distribution range of the species, E – Europe, F – France, BY - Belarus LT – Lithuania; [2] length of breeding season, months, from–to; [3] minimum registered body mass of breeding individuals; [4] 5.8 in the Czech Republic, 6.3 in Germany; [5] 4.5–5.4 in the south to 5.9–8.6 in the north of the range; [6] V–VIII in the north, II–IX in the south of the species range; [7] 5.7 in the south to 7.1 in the north of the range; [8] 2.3–5 in the Czech Republic, 3.8–7.4 in Finland; [9] year round reproduction possible; [10] excluding most northern populations,

How could this pattern be explained? First of all, Lithuania is in the northern part of the distribution ranges of *A. flavicollis, A, agrarius* and *M. arvalis* (Amori et al., 2016; Kaneko et al., 2016; Yigit et al., 2016), but around mid-range in *M. oeconomus, M. agrestis* and *C. glareolus* (Hutterer etal, 2016; Kryštufek et al., 2016; Linzey et al., 2016). Therefore, latitude related litter size increase is involved – northern litters are bigger in *M. agrestis* and *C. glareolus* (Niethammer and Krapp, 1982; Wilson et al., 2017) and in *M. oeconomus* (Tast, 1966; Balčiauskas et al., 2012).

Differences which show a decrease in litter size when comparing with data of previous decades (Table 5) could be related to climate change. A negative correlation of fertility and reproduction with increased temperature in mammals was explained by Takahashi (2011), and a long-term decrease in litter size in the North American deer mouse (*Peromyscus maniculatus*) was shown by McLean et al. (2019) to be associated with short- and long-term climate variables, whereas maternal body size itself was poorly predictive.

The hypothesis of optimal investment says that "a female will produce a particular litter size which gives the best reproductive success in the particular environment where offspring are nursed" (Mappes et al., 1995). Reproduction in a season when the young have poor chances of survival implies a risk for the offspring and for the reproducing females, as reproduction has high energy costs; therefore, energy is allocated to thermoregulation in harsh seasons, not breeding (Steinlechner and Puchalski, 2003). This is one of the reasons for the observed decrease in litter size in autumn in all of the analysed rodent species in the commercial orchards. Seasonal changes of litter size were also found in meadow voles (*Microtus pennsylvanicus*), with a sharp decline in autumn, a similar pattern to that reported widely for all species of the genus *Microtus* (Dobson and Myers, 1989). The second reason may be seasonal differences in the age structure of populations (Rajska-Jurgiel, 1992). Most of the young females enter breeding in autumn (e.g., Avenant and Smith, 2004). Due to smaller fecundity in the early stage of life (Tkadlec and Krejčová, 2001), they have smaller litters, influencing the decrease of average litter size.

However, in the seasonal litter size decline, changes in female body mass or body condition cannot be ignored. In *M. pennsylvanicus*, the seasonal litter size decline reflects also a decrease in the body mass of females (Dobson and Myers, 1989). In the spring, a negative correlation between female body mass and their litter size results from the better survival of small individuals during winter in some species (Bonnet et al., 2017). In Lithuania, winter growth depression and decline in body mass have been observed in *M. arvalis* (Balčiauskienė et al., 2009a), *C. glareolus* (Balčiauskienė et al., 2009b) and *A. flavicollis* (Balčiauskienė et al., 2009c). Correlation between litter size in summer and female body condition in all three species was negative and not significant (see Fig. 5), and the correlation between litter size and female body mass in *M. arvalis* was also negative and not significant (see Fig. 4).

In general, mammal litter size is often positively correlated with maternal body mass (Sikes and Ylönen, 1998). Significant correlations were found in 11 species of the genus *Microtus* (Innes, Millar, 1994), being strong (Tast, 1966) or moderate (recalculated from Balčiauskas et al., 2012) in *M. oeconomus* and the postpartum mass of the mother being a decisive factor during reproduction in *M. pennsylvanicus* (Dobson and Myers, 1989). Body mass and body condition were also positively correlated with litter size in *A. amphibius* (Evsikov et al., 2008; Somoano et al., 2016). Precocious reproduction, observed in *M. oeconomus* (Tast, 1966) and *M. arvalis* (Tkadlec and Krejčová, 2001), does not fit to this pattern, as very young and small females have unexpectedly large litters in this case. We did not find change of the minimum body mass of reproducing individuals of *A. flavicollis, M. agrestis* and *M. arvalis* in

Lithuania during the last 40–50 years (see Table 5). Therefore revealed changes in litter size should not be related to changes of life history of these species.

Breeding failures (in the form of embryo resorption or non-implantation) are characteristic to many rodent species (Rolan and Gier, 1967). While the proportion of pregnancies with resorbing embryos in different rodent species may be moderate (2.3–9.4% in *Calomys, Bolomys, Oligoryzomys* and *Akodon* species) even in cultivated habitats (Mills et al., 1992), it may be significantly higher at sites with industrial contamination. For example, in a mining-contaminated area, embryonic resorptions were observed in 10–40% of pregnancies in *C. glareolus*, being 3–4 times higher than those in a control zone (Ivanter and Medvedev, 2015).

In Lithuania, breeding failures were registered in up to 47.2% of pregnancies of *M. arvalis* in cultivated pastures, non-implantations constituting 1.9–15.4% and resorptions 1.4–31.8% of pregnancies (Mažeikytė, 1993). In the zone of a nuclear power plant, breeding failures were characteristic to 22.7–68.4% of pregnancies in *C. glareolus* in 1984–1989 (Balčiauskas, 2005). In the flooded meadows and other natural habitats breeding failures in *M. oeconomus* constituted 30%, most of these being resorptions (Balčiauskas et al., 2012, recalculated). The proportion of breeding failures registered in commercial orchards (see Table 4) is comparable with these numbers. In addition to intensive agricultural practices, the application of rodenticides may have been a cause of the increased breeding failures, as shown by Chetot et al. (2020). Commercial herbicides may have similar teratogenic influence (Cavieres et al., 2002). It was shown that resorptions also depend on the gestation term, number of viable embryos declining in advanced gestation (Loeb and Schwab, 1987). For the other mammals, infectious causes may be involved in embryo mortality (Givens and Marley, 2008). In other *Microtus* species, namely prairie voles (*M. ochrogaster*) pregnancy may be disrupted by presence of unfamiliar males (Fraser-Smith, 1975). In some rodent species (*P. maniculatus, Clethrionomys gapperi* and *M. pennsylvanicus*) age of the female was reported as a possible factor: resorption rates being greater in the young females (Beer et al., 1957). Litter size and body mass positively correlated to the resorption rates also in *M. arvalis*, this being 5.75% on average (Pelikan, 1970).

Our pilot study revealed that commercial orchards support substantial small mammal diversity which is higher than in crops and in most types of forest (Balčiauskas et al., 2019) Here we show that the litter size of the six most numerous rodent species in orchards did not differ from that in the adjacent control meadows or forest. As reproduction in rodents is positively affected by resources and their availability (Ylönen et al., 2003, 2004), we may suppose orchards sustain sufficient amounts of food to maintain diverse rodent communities and to secure the year-round reproduction of some species at the lower latitudes (Somoano et al., 2017).

5. Conclusions

Recognizing latitude and climate change effects on rodent breeding patterns, we confirm that despite disturbances in form of agricultural activities and application of rodenticides, commercial orchards sustain substantial rodent diversity and litter sizes equal to those in adjacent non-agriculture habitats (meadows and forests). However, in three of the six most numerous rodent species inhabiting commercial orchards in Lithuania (northern Europe), the potential litter sizes exceeded the observed sizes and breeding failures were observed, the most affected species in autumn being *M. arvalis*, *A. flavicollis* and *M. oeconomus*, while in spring the first two species. The observed litter size in *M. arvalis* showed an increase in young-aged habitats, while the litter size in *A. flavicollis* was significantly larger in old aged habitats. *M. oeconomus*, *M. agrestis* and *C. glareolus* did not reproduce in any commercial habitats other than old ones. In summer, litter size was significantly correlated with female body mass in *M. oeconomus* and *A. flavicollis*, the body mass explaining 45% and 27% of the variation in the litter size respectively. In autumn, the strongest correlations of litter size and female body mass were found in *A. flavicollis* and *M. arvalis*, the body mass explaining 34% and 13% of the variation in the litter size. Female body condition index and litter size correlations were weak. Knowledge of reproduction patterns may help in planning sustainable rodent control strategies in orchards and similar habitats.

Funding

In 2018 and 2019, this research was funded by the Ministry of Agriculture of the Republic of Lithuania [contract No. MT-18–3].

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

After publication, research data will be available from the corresponding author upon request.

Acknowledgments

We thank Jos Stratford for checking and editing the language. Dr. Gintautas Vaitonis helped in the preparation of the figures.

References

Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Palomo, L.J., 2016. *Apodemus flavicollis* (errata version published in 2017) (Available online). IUCN Red. List Threat. Species 2016, e. T1892A115058023. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T1892A22423256.en. accessed 17 November 2020.

Avenant, N.L., Smith, V.R., 2004. Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). Polar Biol. 27, 99–111. https://doi.org/10.1007/s00300-003-0569-x.

Balčiauskas, L., 2005. Results of the long-term monitoring of small mammal communities in the ignalina nuclear power plant region (Drūkšiai LTER site). Acta Zool. Litu. 15, 79–84. https://doi.org/10.1080/13921657.2005.10512378.

Balčiauskas, L., Balčiauskienė, L., Janonytė, A., 2012. Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. Turk. J. Zool. 36, 668–675. https://doi.org/10.3906/zoo-1111-20.

Balčiauskas, L., Balčiauskienė, L., Stirkė, V., 2019. Mow the grass at the mouse's peril: diversity of small mammals in commercial fruit farms. Animals 9, 334. https://doi.org/10.3390/ani9060334.

Balčiauskienė, L., Balčiauskas, L., Čepukienė, A., 2009a. Winter growth depression of common vole (*Microtus arvalis*). Acta Zool. Litu. 19, 85–92. https://doi.org/10.2478/v10043-009-0019-2.

Balčiauskienė, L., Balčiauskas, L., Čepukienė, A., 2009b. Growth of the bank vole *Myodes glareolus* in the non-vegetative period in NE Lithuania. Est. J. Ecol. 58, 86–93. https://doi.org/10.3176/eco.2009.2.02.

Balčiauskienė, L., Balčiauskas, L., Čepukienė, A., 2009c. Demographic and morphometric parameters of the yellow-necked mouse (*Apodemus flavicollis*) in late autumn-early spring in Lithuania. Acta Biol. Univ. Daugavp. 9, 25–34.

Beer, J.R., MacLeod, C.F., Frenzel, L.D., 1957. Prenatal survival and loss in some cricetid rodents. J. Mammal. 38, 392–402. https://doi.org/10.2307/1376237.

Bertolino, S., Asteggiano, L., Saladini, M.A., Giordani, L., Vittone, G., Alma, A., 2015. Environmental factors and agronomic practices associated with Savi's pine vole abundance in Italian apple orchards. J. Pest. Sci. 88, 135–142. https://doi.org/10.1007/s10340-014-0581-7.

Bonnet, T., Crespin, L., Pinot, A., Bruneteau, L., Bretagnolle, V., Gauffre, B., 2013. How the common vole copes with modern farming: Insights from a capture-mark-recapture experiment. Agric. Ecosyst. Environ. 177, 21–27. https://doi.org/10.1016/j.agee.2013.05.005.

Bonnet, T., Wandeler, P., Camenisch, G., Postma, E., 2017. Bigger is fitter? Quantitative genetic decomposition of selection reveals an adaptive evolutionary decline of body mass in a wild rodent population. PLoS Biol. 15, e1002592 https://doi.org/10.1371/journal.pbio.1002592.

Brakes, C.R., Smith, R.H., 2005. Exposure of non-target small mammals to rodenticides: short-term effects, recovery and implications for secondary poisoning. J. Appl. Ecol. 42, 118–128. https://doi.org/10.1111/j.1365-2664.2005.00997.x.

Cavieres, M.F., Jaeger, J., Porter, W., 2002. Developmental toxicity of a commercial herbicide mixture in mice: I. Effects on embryo implantation and litter size. Environ. Health Persp. 110, 1081–1085. https://doi.org/10.1289/ehp.021101081.

Chetot, T., Taufana, S., Benoit, E., Lattard, V., 2020. Vitamin K antagonist rodenticides display different teratogenic activity. Reprod. Toxicol. 93, 131–136. https://doi.org/10.1016/j.reprotox.2020.02.003.
Daniel Givens, M., Marley, M.S.D., 2008. Infectious causes of embryonic and fetal mortality. Theriogenology 70, 270–285. https://doi.org/10.1016/j.theriogenology.2008.04.018.
Dobson, F.S., Myers, P., 1989. The seasonal decline in the litter size of meadow voles. J. Mammal. 70, 142–152. https://doi.org/10.2307/1381677.
Eccard, J.A., Rödel, H.G., 2011. Optimizing temperament through litter size in short-lived, iteroparous mammals in seasonal environments. Dev. Psychobiol. 53, 585–591. https://doi.org/10.1002/dev.20547.
Ernest, S.K.M., 2003. Life history characteristics of placental nonvolant mammals, 3402–3402 Ecology 84, 3402. https://doi.org/10.1890/02-9002.
Ernest, S.K.M., 2016. Data Paper. Dataset. Wiley. https://doi.org/10.6084/m9.figshare.3523109.v1 accessed on 17 November 2020.
Evsikov, V.I., Nazarova, G.G., Muzyka, V.Y., 2008. Body condition and reproductive characteristics of female water voles (*Arvicola terrestris* L.). Russ. J. Ecol. 39 (6), 414–417. https://doi.org/10.1134/s1067413608060052.
Fischer, C., Thies, C., Tscharntke, T., 2011. Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. Biol. Conserv. 144, 1130–1136. https://doi.org/10.1016/j.biocon.2010.12.032.
Fischer, C., Schröder, B., 2014. Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area. Agric. Ecosyst. Environ. 189, 145–153. https://doi.org/10.1016/j.agee.2014.03.039.
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, 479–488. https://doi.org/10.1016/j.anbehav.2006.08.010.
Fraser-Smith, A., 1975. Male-induced pregnancy termination in the prairie vole, *Microtus ochrogaster*. Science 187, 1211–1213. https://doi.org/10.1126/science.1114340.
Glazier, D.S., 1985. Energetics of litter size in five species of *Peromyscus* with generalizations for other mammals. J. Mammal. 66, 629–642. https://doi.org/10.2307/1380789.
Golet, G.H., Hunt, J.W., Koenig, D., 2013. Decline and recovery of small mammals after flooding: implications for pest management and floodplain community dynamics. River Res. Appl. 29, 183–194. https://doi.org/10.1002/rra.1588.
Heroldová, M., Bryja, J., Zejda, J., Tkadlec, E., 2007. Structure and diversity of small mammal communities in agriculture landscape. Agr. Ecosyst. Environ. 120, 206–210. https://doi.org/10.1016/j.agee.2006.09.007.
Heroldová, M., Tkadlec, E., 2011. Harvesting behaviour of three central European rodents: Identifying the rodent pest in cereals. Crop Prot. 30, 82–84. https://doi.org/10.1016/j.cropro.2010.09.002.
Holmberg, M. 2000. Uncertainty of Critical Loads in the Baltic Countries: Report from a Project Funded by the Nordic Council of Ministers, TemaNord: Environment. Nordic Council of Ministers.
Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Palomo, L.J., Henttonen, H., Vohralík, V., Zagorodnyuk, I., Juškaitis, R., Meinig, H., Bertolino, S., 2016. Myodes glareolus (errata version published in 2017). The IUCN Red List of Threatened Species 2016, e.T4973A115070929. Available online: https://dx.doi.org/10.2305/IUCN.UK.2016–3.RLTS.T4973A22372716.en. (accessed 17 November 2020).
Innes, D.G.L., Millar, J.S., 1994. Life histories of Clethrionomys and *Microtus* (Microtinae). Mammal Rev. 24, 179–207. https://doi.org/10.1111/j.1365-2907.1994.tb00142.x.
Ivanter, E.V., Medvedev, N.V., 2015. Impact of industrial contamination on the populations of small forest rodents. Dokl. Biol. Sci. 464, 254–256. https://doi.org/10.1134/s0012496615050130.
Jacob, J., Buckle, A., 2018. Use of Anticoagulant Rodenticides in Different Applications Around the World. In: Van den Brink, N., Elliott, J., Shore, R., Rattner, B. (Eds.), Anticoagulant Rodenticides and Wildlife. Emerging Topics in Ecotoxicology (Principles, Approaches and Perspectives). Springer International Publishing, Cham, pp. 11–44.
Janova, E., Heroldova, M., 2016. Response of small mammals to variable agricultural landscapes in central Europe. In: Mamm. Biol, 81, pp. 488–493. https://doi.org/10.1016/j.mambio.2016.06.004.
Kaneko, Y., Kryštufek, B., Zagorodnyuk, I., Vohralík, V., Batsaikhan, N., Avirmed, D., Sukhchuluun, G., 2016. *Apodemus agrarius* (errata version published in 2017). The IUCN Red List of Threatened Species 2016, e.T1888A115057408. Available online: https://dx.doi.org/10.2305/IUCN.UK.2016–3.RLTS.T1888A22422191.en (accessed 17 November 2020).
Kryštufek, B., Vohralík, V., Zima, J., Zagorodnyuk, I., 2016. *Microtus agrestis* (errata version published in 2017). The IUCN Red List of Threatened Species 2016, e.T13426A115112050. Available online: https://dx.doi.org/10.2305/IUCN.UK.2016–3.RLTS.T13426A22349665.en. (accessed 17 November 2020).
LHMT, Lithuanian Meteorological Service, 2021. Climate regions of Lithuania. Available online: ⟨http://www.meteo.lt/en/climate-regions-of-lithuania⟩ (accessed 9 September, 2021).
Linzey, A.V., Shar, S., Lkhagvasuren, D., Juškaitis, R., Sheftel, B., Meinig, H. Amori, G., Henttonen, H., 2016. *Microtus oeconomus* (errata version published in 2017). The IUCN Red List of Threatened Species 2016, e.T13451A115113894. Available online: https://dx.doi.org/10.2305/IUCN.UK.2016–3.RLTS.T13451A22347188.en (accessed 17 November 2020).
Loeb, S.C., Schwab, R.G., 1987. Estimation of litter size in small mammals: bias due to chronology of embryo resorption. J. Mammal. 68, 671–675. https://doi.org/10.2307/1381601.
Lund, M., 2018. Rodent problems in Europe. In: Prakash, I. (Ed.), Rodent Pest Management. Taylor and Francis, Boca Raton, pp. 39–44. ⟨https://dx.doi.org/10.1201/9781351076456⟩.
Mappes, T., Koskela, E., Ylönen, H., 1995. Reproductive costs and litter size in the bank vole. P. Roy. Soc. Lond. B. Biol. 261, 19–24. https://doi.org/10.1098/rspb.1995.0111.
Mažeikytė, R., 1993. Fertility and embryonal losses of females in Microtus arvalis Pall. population on cultivated pastures of the lowland of Middle Lithuania depending on changes of their numbers. Proceedings of the 31th meeting of the international working group on the project "Species and its productivity in the distribution area" for the UNESCO programme "Man and the biosphere"; Institute of Ecology, Vilnius, pp. 24–28.
McLean, B.S., Barve, N., Flenniken, J., Guralnick, R.P., 2019. Evolution of litter size in North America's most common small mammal: an informatics-based approach. J. Mammal. 100, 365–381. https://doi.org/10.1093/jmammal/gyz057.
Millar, J.S., 1977. Adaptive features of mammalian reproduction (doi.org/). Evolution 31, 370–386. https://doi.org/10.1111/j.1558-5646.1977.tb01019.x.
Mills, J.N., Ellis, B.A., McKee, K.T., Maiztegui, J.I., Childs, J.E., 1992. Reproductive characteristics of rodent assemblages in cultivated regions of central Argentina. J. Mammal. 73, 515–526. https://doi.org/10.2307/1382017.
Moors, P.J., 1985. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao islands, Hauraki Gulf, New Zealand. N. Z. J. Ecol. 8, 37–54.
Handbuch der Säugetiere Europas – Band 1. In: Niethammer, J., Krapp, F. (Eds.), 1978, Nagetiere 1, 377. AULA–Verlag, Wiesbaden, p. 334.
Handbuch der Säugetiere Europas – Band 2/1. In: Niethammer, J., Krapp, F. (Eds.), 1982. Nagetiere 2. AULA–Verlag, Wiesbaden, pp. 131–133, 304–305, 365–366, 388–389.
Pelikan, J., 1970. Embryonic resorption in Microtus arvalis (Pall). Zool. Listy 19, 93–101.
Prūsaitė, J. (comp.), 1988. Fauna of Lithuania. Mammals. Mokslas, Vilnius, pp. 123, 125, 137, 142, 144, 146.
Rajska-Jurgiel, E., 1992. Demography of woodland rodents in fragmented habitat. Acta Theriol. 37, 73–90.
Riojas-López, M.E., Mellink, E., Luévano, J., 2018. A semiarid fruit agroecosystem as a conservation-friendly option for small mammals in an anthropized landscape in Mexico. Ecol. Appl. 28, 495–507. https://doi.org/10.1002/eap.1663.
Rolan, R.G., Gier, H.T., 1967. Correlation of embryo and placental scar counts of peromyscus maniculatus and microtus ochro*gaster*. J. Mammal. 48, 317–319. https://doi.org/10.2307/1378040.
Savickyj, B.P., Kučmel, S.V., Burko, L.D., 2005. Mammals of Belarus. BGU, Minsk, pp. 183, 192, 196, 199, 202, 208.
Sibly, R.M., Brown, J.H., 2007. Effects of body size and lifestyle on evolution of mammal life histories. P. Natl. Acad. Sci. USA 104, 17707–17712 https://dx.doi.org/10.1073_pnas.0707725104.
Shilova, S.A., Tchabovsky, A.V., 2009. Population response of rodents to control with rodenticides. Curr. Zool. 55, 81–91. https://doi.org/10.1093/czoolo/55.2.81.
Sikes, R.S., Ylönen, H., 1998. Considerations of optimal litter size in mammals. Oikos 83, 452–465. https://doi.org/10.2307/3546673.
Somoano, A., Ventura, J., Miñarro, M., 2016. Reproductive potential of a vole pest (Arvicola scherman) in Spanish apple orchards. Spanish. J. Agric. Res 14, e1008. https://doi.org/10.5424/sjar/2016144-9870.
Somoano, A., Ventura, J., Miñarro, M., 2017. Continuous breeding of fossorial water voles in northwestern Spain: potential impact on apple orchards. Folia Zool. 66, 29–36. https://doi.org/10.25225/fozo.v66.i1.a6.2017.
Steinlechner, S., Puchalski, W., 2003. Mechanisms for seasonal control of reproduction in small mammals. In: Heldmaier, G., Werner, D. (Eds.), Environmental signal processing and adaptation. Springer, Berlin, Heidelberg, pp. 233–250. https://doi.org/10.1007/978-3-642-56096-5_11.
Stenseth, N.C., Gustafsson, T.O., Hansson, L., Ugland, K.I., 1985. On the evolution of reproductive rates in microtine rodents. Ecology 66, 1795–1808. https://doi.org/10.2307/2937375.
Stenseth, N.C., Leirs, H., Skonhoft, A., Davis, S.A., Pech, R.P., Andreassen, H.P., Singleton, G.R., Lima, M., Machang'u, R.S., Makundi, R.H., Zhang, Z., Brown, P.R., Shi, D., Wan, X., 2003. Mice, rats, and people: The bio-economics of agricultural rodent pests. Front. Ecol. Environ. 1, 367–375. https://doi.org/10.1890/1540-9295(2003)001%5b0367:mraptb%5d2.0.co;2.
Suchomel, J., Šipoš, J., Čepelka, L., Heroldová, M., 2019. Impact of *Microtus arvalis* and *Lepus europaeus* on apple trees by trunk bark gnawing. Plant Prot. Sci. 55, 142–147. https://doi.org/10.17221/64/2018-pps.
Sullivan, T.P., Sullivan, D.S., Hogue, E.J., Lautenschlager, R.A., Wagner, R.G., 1998. Population dynamics of small mammals in relation to vegetation management in orchard agroecosystems: compensatory responses in abundance and biomass. Crop Prot. 17, 1–11. https://doi.org/10.1016/s0261-2194(98)80006-9.
Sustainable Plant Protection Transition: A global health approach (SPRINT), 2020. ⟨https://www.ecologic.eu/17478⟩ (accessed on 11 November 2020).
Takahashi, M., 2011. Heat stress on reproductive function and fertility in mammals. Reprod. Med. Biol. 11, 37–47. https://doi.org/10.1007/s12522-011-0105-6.
Tast, J., 1966. The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. Zool. Fenn. 3, 127–171. https://doi.org/10.2307/23731273.
Tkadlec, E., Krejčová, P., 2001. Age-specific effect of parity on litter size in the common vole (*Microtus arvalis*). J. Mammal. 82, 545–550. https://doi.org/10.1644/1545-1542(2001)082<0545:aseopo>2.0.co;2.
Tobin, M.E., Fall, M.W., 2004. Pest control: rodents. In Encyclopedia of Life Support Systems. Eolss. Publishers, Oxford.
Werner, J., Griebeler, E.M., 2011. Reproductive biology and its impact on body size: comparative analysis of mammalian, avian and dinosaurian reproduction (. oi:). PLoS One 6, e28442. https://doi.org/10.1371/journal.pone.0028442.
Western, D., 1979. Size, life history and ecology in mammals. Afr. J. Ecol. 17, 185–204 https://dx.doi.org/10.1111/j.1365-2028.1979.tb00256.x.
Wilson, D.E., Lacher, T.E., Mittermeier, R.A. (Eds.), 2017. Handbook of the Mammals of the World. Rodents II. Lynx Edicions, Barcelona.

Yigit, N., Hutterer, R., Kryštufek, B., Amori, G., 2016. *Microtus arvalis*. The IUCN Red List of Threatened Species 2016, e.T13488A22351133. Available online: https://dx.doi.org/10.2305/IUCN.UK.2016–2.RLTS.T13488A22351133.en (accessed 17 November 2020).

Ylönen, H., Jacob, J., Runcie, M.J., Singleton, G.R., 2003. Is reproduction of the Australian house mouse (Mus domesticus) constrained by food? A large-scale field experiment. Oecologia 135, 372–377. https://doi.org/10.2307/4223598.

Ylönen, H., Horne, T.J., Luukkonen, M., 2004. Effect of birth and weaning mass on growth. Evol. Ecol. Res. 6, 433–442.

Yoccoz, N.G., Ims, R.A., 1999. Demography of small mammals in cold regions: the importance of environmental variability. Ecol. Bull. 47, 137–144.