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Research Article

Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range

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Abstract: Data on the reproduction of the root vole (*Microtus oeconomus*) in Lithuania, the margin of its geographic range, are presented in the context of litter size analysis. In Lithuania, the breeding season lasts from April until the end of October. The average litter size was 5.93 ± 0.11 (2-14), decreasing from a mean of 8.0 embryos in June to 4.3 in October, with 2-3 litters per year. The average body mass of breeding females was 40.4 ± 0.6 (16.5-77.0) g. However, 6.25% of females start breeding with a body mass of under 25 g. Litter size was found to increase from south to north in the geographical distribution range of the species and is described by the regression *Litter size = 0.11147 × latitude – 0.2646* (R^2 = 0.79). The small litter size and the comparatively small number of litters in the Lithuanian population indicate that reproduction is similar to that of other populations in the southern part of the geographical range of the species.

Key words: *Microtus oeconomus*, reproduction, litter size, Lithuania

Introduction

The geographical range of the root vole (*Microtus oeconomus*) extends from northwestern Europe in the west to Alaska and northwestern Canada in the east. In the Palaearctic, the range is fragmented (Wilson and Reeder, 2005). The continuous range extends from Germany and northern Fennoscandia to Poland, Belarus, and Russia. Isolated populations are found from the Netherlands to Hungary (Linzey et al., 2008). The Lithuanian population of *M. oeconomus* is at the edge of the range (Mitchell-Jones et al., 1999). To the immediate north, the species is not found in Latvia or Estonia, with Lithuania itself only being colonized in the last 50 years (Balčiauskas et al., 2010).

Information on the reproductive parameters (litter size, number of litters, and seasonal and geographical variations) of *M. oeconomus* is not very extensive. Generally, the species is known to breed 2-3 times per year. With typically 4 to 8 young per litter, and an average of 6.4 ± 0.2 (Innes and Millar, 1994) to 6.9 (Bieberich and Olson, 2007), the litter size of *M. oeconomus* is reported as being relative large for the genus *Microtus*. Sexual maturation occurs at 1-2 months (Bieberich and Olson, 2007). According to Ims (1997), in Norway, litter size tends to be larger in southern populations of *M. oeconomus*. Such a finding did not match the general pattern, whereby the litter size of small mammals increases from the south to the north (Fleming and Rauscher, 1978; Innes and Millar, 1994), but there are no more

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publications of litter size related to latitude for this species. In general, the northern breeding pattern is characterized by a short breeding period, a bigger litter size, and a high number of litters (Fleming and Rauscher, 1978; Tamarin, 1985; Innes and Millar, 1994; Ims, 1997).

The aim of this paper was to present data on the reproduction (timing and litter size) of *M. oeconomus* in Lithuania. This seems of interest, as the population of *M. oeconomus* is spreading from the southwest to the northeast, populating the country in the last 50 years, but still not reaching Latvia and Estonia. Our data will contribute to the knowledge on reproduction of *M. oeconomus* in an expanding population at the margin of its range. The rationale of the study was to assess litter size across the geographical range of the species, and to find where Lithuanian voles may fit into the latitudinal gradient. It is generally accepted that climate change influences the biological adaptations of the species (Walther et al., 2002) and it could be expected that litter size in northern populations will decrease in size. However, this aspect in *M. oeconomus* was not analyzed because of data deficiency; there are no new data published on the breeding of this species. Presenting not only litter size and timing, but also body mass dimensions of the breeding females, we thereby expand the database for the species, facilitating a reevaluation of the commonly known theories of bigger litters in the northern environment, at a peripheries of the distribution range and in mixed landscapes (Ims, 1997; Réale et al., 2003).

Materials and methods

Information on reproduction was collected from trapped animals in 8 localities in Lithuania during 2001-2009 (Table). Snap traps were set at a distance of 5 m apart, in lines of 25 traps placed along transects. The traps were baited with bread and sunflower oil and checked once per day for 3 consecutive days (Balčiauskas, 2004).

After weighing to the nearest 0.1 g, captured voles were dissected and the sex and age were recorded. The determination of maturity and age category was based on the expert judgment of the status of sex organs and atrophy of the thymus, as this decreases with the animal's age (Terman, 1969). The voles were categorized as juvenile, subadult, or adult (Terman, 1969; Myllymäki, 1977; Gliwicz, 1996; Prévot-Julliard et al., 1999; Crespin et al., 2002). We defined all of the overwintered and breeding individuals with an atrophied thymus as adults (females pregnant, with developed nipples, perforated vagina, having fresh/old placental scars and/or corpora lutea; males with scrotal, developed testes, full epididymis,

Table. Sampling localities and number of *M. oeconomus* trapped between 2001 and 2009 (NP: national park, SNR: strict nature reserve, RP: regional park, and n/a: data not available). Locality numbers correspond to Figure 1.

Locality (center)	Dates of trapping (number of trap/days)	Total, N	Breeding, n	
			♂♂	♀♀
1. Kuršių Nerija NP (55°25′12″N, 21°04′33″E)	13-23.08.2001 (1875)	123	16	39
2. Žemaitija NP (56°01′07″N, 21°53′09″E)	7-10.10.2001 (450); 1-4.10.2002 (450)	8	1	3
3. Kamanos SNR (56°16′43″N, 22°43′20″E)	28-30.08.2008 (477)	29		8
4. Žagarė RP (56°15′31″N, 23°18′34″E)	11.08-24.09.2008 (1950)	48		8
5. Čepkeliai SNR (54°04′29″N, 24°18′38″E)	1-5.09.2001 (n/a)	39	8	10
6. Gelgaudiškis environs (55°02′23″N, 23°01′09″E)	25-27.09.2001 (450); 14-17.08.2002 (450)	25	3	15
7. Viešvilė SNR (55°07′58″N, 22°25′07″E)	17-19.08.2001 (n/a)	9		1
8. Rusnė environs (55°20′10″N, 21°18′54″E)	28-30.06, 24-26.08.2004 (2485); 1-5.09.2005 (460); 30.06-02.07, 13-15.08, 8-9.10.2006 (2710); 8-10.10, 27-29.10.2008 (1025); 8-10.07, 12-14.09, 14-16.10.2009 (4200)	513	55	172
Total		794	83	256

and additional glands). Those voles that remained nonbreeders during the year of birth, having developed, but inactive reproductive organs and partially involuted thymus, fell into the category of subadults. All of the individuals without expressed sex attributes (reproductive organs still developing, e.g., nonscrotal testes, thread-like uterus, closed vagina) and fully developed thymus were treated as juveniles (Balčiauskienė and Balčiauskas, 2009).

To show how many voles start breeding at an early age, we used body mass as a proxy of age; this certainly is true for young voles (Balčiauskienė, 2007). The body mass of voles was grouped in 5 g intervals (according to Sokal and Rohlf, 1995).

The number of embryos, the number of corpora lutea, and the number of fresh placental scars were counted (macroscopically) without dissection. Fresh placental scars, according to Innes and Millar (1994), were also used to estimate litter size. The macroscopic count of fresh placental scars (old scars take the form of dark oblong 1-2 mm long grains) and visible corpora lutea may impose limitations on the detection of earlier litters, especially those of overwintered females**.** With respect to this fact, we did not present statistical data relating to the number of litters produced by a female during her lifetime. The maximum number of litters registered was 3; in this case old placental scars were of different sizes and positioned in groups, some very close to each other. We considered that both the embryo number and fresh placental scar number could count as observed litter size.

The number of corpora lutea was considered as potential litter size. The difference between the number of placental scars and the number of corpora lutea was related to the nonimplantation of the embryo. The difference between the number of embryos and the corpora lutea was treated as embryo resorption. We also counted resorbed embryos directly (they are smaller than the rest of the embryos in the uterus, dark in color, and have partially disappeared).

The absolute magnitude of breeding disorders was defined as the number of resorbed or nonimplanted embryos; the relative magnitude of breeding disorders was calculated as the percentage of resorbed or nonimplanted embryos from the number of corpora lutea.

The reproductive status of male voles was judged from the appearance and size of the genitals (Jameson, 1950); full epididymis show active spermatogenesis (McCravy and Rose, 1992). After breeding, the testes and related glands become slumped, slate-colored, and diminish in size.

The breeding season was defined as the period of the year (months) when voles were reproductively active (males with full epididymis, females from perforation till the end of pregnancy).

The majority of voles were trapped in the Rusnė flood meadows in the western part of Lithuania. The Rusnė trapping site is characterized by low lying flood meadows, overgrown with various plants belonging to the families Poaceae and Cyperaceae. A polder system has been created with artificially raised embankments with meadows or agricultural areas between them. Some of these areas are flooded in spring; thus the voles recolonize them every year. All of the polders are surrounded by ditches. On the margins of the ditches, reeds (*Phragmites australis*) grow in belts 2-5 m wide, parts of which are beginning to overgrow with shrubs. At other sites, located in north, west, southwest, and south Lithuania (Figure 1), traps were set in bogs, reed beds and meadows. According to Balčiauskas et al. (2010), these habitats in the country are optimal for *M. oeconomus*. The trapping time (June to October) corresponded to the vegetative season, positive weather temperatures, and abundant vegetation. Earlier trapping in the spring-flooded areas is meaningless, as *M. oeconomus* only starts to recolonize the formerly flooded meadows in Rusnė at the beginning of June (Janonytė, unpubl.)

Litter size variation (interannual, interpopulational, or depending on season/month and number of litters) was analyzed with ANOVA/MANOVA and independent Student's t-test. The difference between the observed and potential litter size was assessed with depended sample Student's t-test. All of the differences with $P > 0.05$ were considered nonsignificant. Calculations were done with Statistica for Windows, ver. 6.0 software (StatSoft, 2004).

Results

The total number of trapped individuals was 794, and the number of adult voles that were reproductively

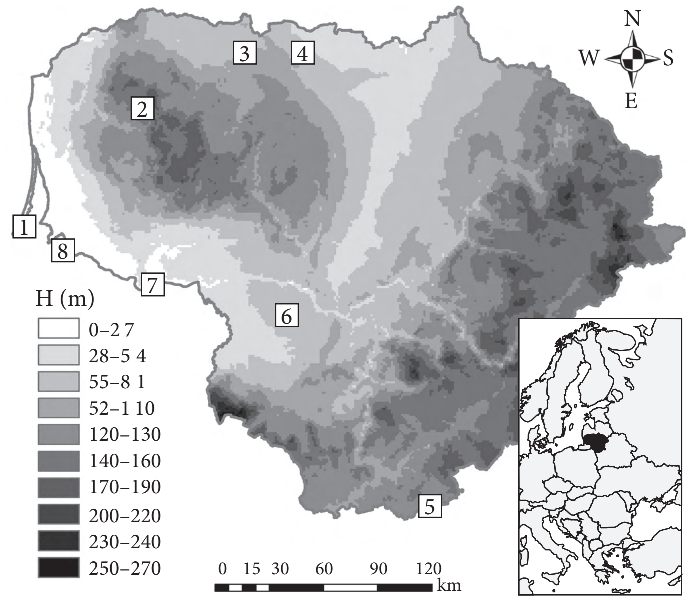

Figure 1. *M. oeconomus* trapping sites in Lithuania, 2001-2009. For altitudes (DTEM, coordinate system LKS94), data from the National Land Service under the Ministry of Agriculture of the Republic of Lithuania were used.

active was 339 (Table). The distribution of the numbers of breeding voles (♂♂:♀♀) was as follows: June, 0:2; July, 25:43; August, 30:100; September, 20:47; and October, 8:64. The number of registered embryos in June was 8; July, 220; August, 304; September, 129; and October, 43.

Female reproduction

Of 256 breeding females, we counted the embryos, number of fresh placental scars, or number of corpora lutea in 249 individuals. The litter size ranged from 2 to 14, with the most frequent embryo/fresh placental scar number being 5-7. Small (2-3) and large (10-14) embryo/scar numbers were not frequent, comprising 8.03% and 2.0%, respectively.

The observed litter size averaged 5.93 ± 0.11 (embryo and fresh placental scar count, n = 249), whereas the potential litter size was 6.11 ± 0.14 corpora lutea (n = 141). When both embryos and corpora lutea were present in the same individual, the difference on average was equal to 0.44 lost embryo per female (Student's test for dependent samples, t = 5.93, df = 105, P < 0.0001). One case of twins (a total of 8 embryos, but 7 corpora lutea) was recorded. The average magnitude of disorder was 6.77 ± 0.97% of the potential litter size.

Interannual (between years) and interpopulational (between localities) differences of the observed (ANOVA, $F_{(4,110)}$ = 1.33 and $F_{(5,110)}$ = 0.65, both NS) and potential ($F_{(4,110)}$ = 0.75 and $F_{(5,110)}$ = 0.54, respectively, both NS) litter sizes of *M. oeconomus* were not significant. However, we found the number of litters and the season (month) had a significant influence on the litter size (MANOVA, Wilks lambda = 0.218, $F_{(6, 196)}$ = 37.324, P < 0.0001).

Both the observed and potential litter sizes decreased from June to October (ANOVA, $F_{(4,117)}$ = 98.7, P < 0.0001 and $F_{(4,117)}$ = 131.9, P < 0.0001). Most significant was the decrease in embryo number (Figure 2a): from 7.1 in July to 5.4 in August (Student's t = 5.2, df = 85, P < 0.0001), and from 5.6 in September to 4.3 embryo in October (t = 2.5, df = 31, P < 0.02). The decrease in potential fecundity (Figure 2b) was most obvious between July and August, declining from 7.6 to 5.7 (t = 5.5, df = 93, P < 0.0001). Changes in the number of resorbed or nonimplanted embryos were not significant between months

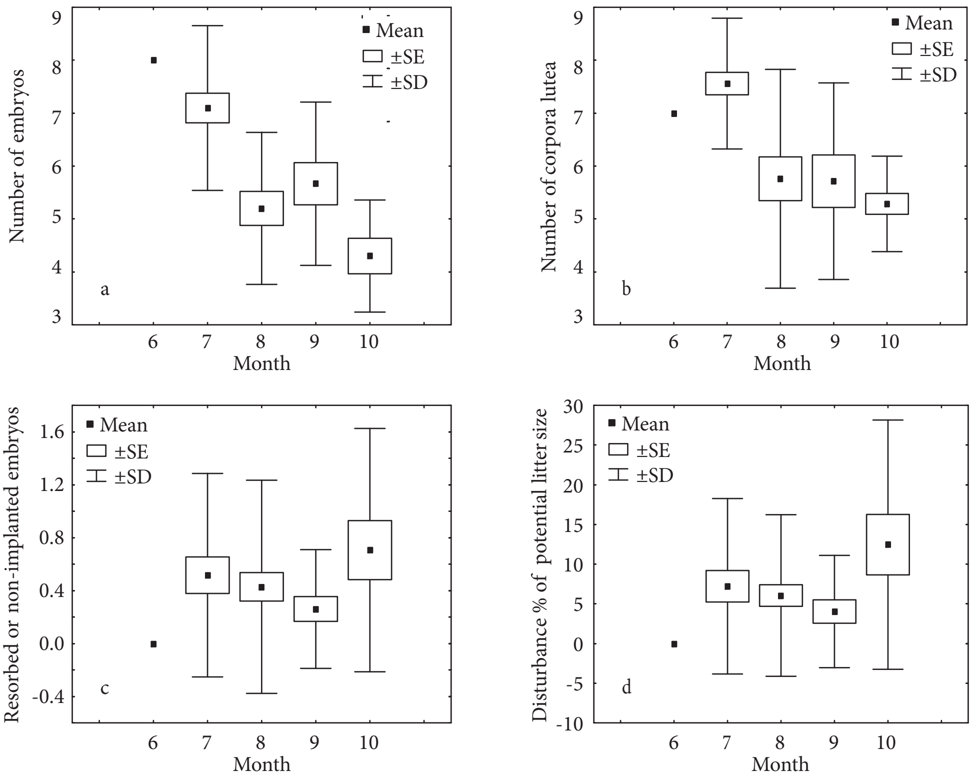

Figure 2. Dynamics of breeding data of *M. oeconomus* in Lithuania: a) observed litter size (number of embryos), b) potential litter size (number of corpora lutea), c) absolute magnitude of breeding disorders (number of resorbed or nonimplanted embryos), and d) relative magnitude of breeding disorders (in percentage of potential litter size).

(Figure 2c). There were no significant changes in the relative magnitude of breeding disorders between July and September (Figure 2d), but from September to October this percentage rose from 4.0 to 12.5 ($t = 2.3$, $df = 38$, $P < 0.03$).

Our data show 2-3 litters per year. We registered 2 litters in 23 out of 256 (8.98%) reproductive adult *M. oeconomus* females. The observed fecundity (5.70 ± 0.12 embryos in the first litter vs. 6.04 ± 0.39 embryos in the second, Student's $t = 0.89$, $df = 240$, $P = 0.37$) and potential fecundity (6.07 ± 0.15 vs. 6.44 ± 0.41 corpora lutea, respectively, $t = 0.87$, $df = 139$, $P = 0.38$) was not significantly greater in the second litter.

In 2006, at the end of June and in the first days of July, out of 16 adult females of *M. oeconomus* trapped at the Rusnė site, 9 had had second litters. One female (with a body weight of only 27 g) with old placental scars was trapped in the second half of June 2004. In June and July 2004, 2006, and 2009, a number of nonbreeding individuals, young and subadult specimens presumably born in May were trapped. In the second half of October, only a few cases of pregnancy were recorded, suggesting the end of the breeding season. We have no data to show whether breeding may occur in November. Thus, the length of the breeding season of *M. oeconomus* is about 7 months in Lithuania, from April to October.

The average body mass of adult breeding females was 40.4 ± 0.6 (16.5-77.0) g, including the mass of the embryos. Among the breeders, the body mass of 2 individual females was ≤20 g (0.78% of the total number), while 16 individuals (6.25%) were less than 25 g and 42 individuals (16.41%) were less than 30 g. The average body mass of the females remained fairly constant through the whole breeding season: 43.5 ± 16.5 g in June, 40.16 ± 1.49 g in July, 41.14 ± 1.02 g in August, 38.86 ± 1.60 g in September, and 40.39 ± 1.11 g in October (ANOVA, $F_{(4,250)} = 0.47$, NS).

Male reproduction

From July through to the end of September, more than 80% of males had scrotal testes, full epididymis, and additional glands, i.e. were breeding. At the beginning of October, the sexual activity of the males decreased considerably and, by the end of October, the males were not active; two-thirds of trapped adult individuals were without any signs of reproduction activity, while one third were shortly after breeding (testes and related glands were slumped and diminishing).

The average body weight of adult males, being in or after reproduction, was 50.4 ± 1.0 (31.0-67.0) g. It changed little through the whole breeding season: 47.11 ± 2.12 g in July, 52.94 ± 1.42 g in August, 49.72 ±2.13 g in September, and 49.40 ± 2.30 g in October (ANOVA, $F_{(3,79)} = 1.94$, NS). Of the breeding males, 4 individuals (4.81%) were ≤35 g, 13 individuals (15.66%) less than 40 g, and 26 individuals (31.33%) less than 45 g. Thus, in comparison to females, males enter the reproduction process older and with a much higher body mass.

Changes in the litter size in the geographical range of species

According to the data published by other authors (Ognev, 1950; Bauer, 1953; Hoyte, 1955; Hoffmann, 1958; Tast, 1966; Novikov et al., 1970; Popov, 1977; Cherniavskij, 1984; Ims, 1997; Batzli and Henttonen,1990; Spitzenberger et al., 2001; Savickij et al., 2005; Borkowska et al., 2009) and our data, covering 48° to 70° N in Europe, 52° to 70° N in Siberia, and up to 72° N in Alaska, the average litter size is larger in the northern parts of the range. Correlation of the litter size with latitude is obvious (Pearson's r = 0.90, n = 15, P < 0.001), and the dependence is linear (Figure 3).

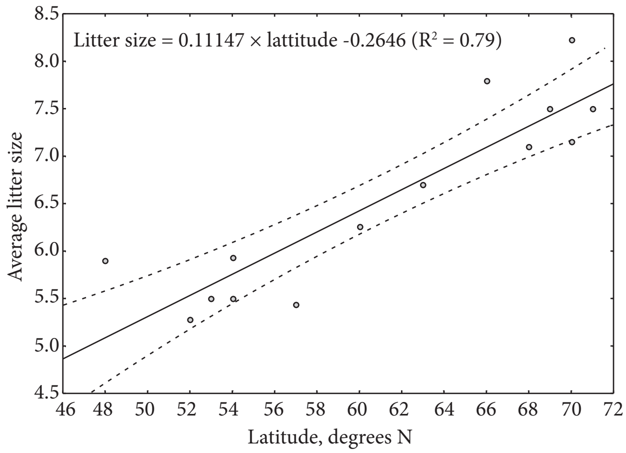

Figure 3. Change in average litter size of *M. oeconomus* in the south-north direction. The dashed line indicates 95% confidence limits.

Discussion

According to Ims (1997), litter size tends to be larger in southern populations of *M. oeconomus*, although this conclusion was obtained only by comparing populations from Norway, 60° to 69° N. Our results of the regression analysis revealed a linear dependence of litter size and latitudes, and it is in concordance with Innes and Millar (1994). These authors suggested that, in short season (northern) environments, small mammals should have large litters; vice versa, smaller litters should be expected in southern, long season environments. Fleming and Rauscher (1978) explain bigger litters by the age structure of small mammals; in the higher latitudes it is shifted towards more fecund, older females.

We had no possibility to evaluate the influence of season on the litter size of *M. oeconomus* from most of the sources listed in the caption of Figure 3. In the northern part of the geographic range, a decrease in litter size towards the end of the season was noted by Hoffmann (1958), Tast (1966), and Popov (1977): from 7.18 ± 0.11 young in June-July to 6.42 ± 0.16 in August in Yakutia, and from 7.8 in June to only 5.0 towards September in Alaska. Litter size reduction in the autumn is also characteristic of other *Microtus* species, i.e. *M. californicus* (Hoffmann, 1958; Tamarin, 1985). In Lithuania, we also found that the litter size of *M. oeconomus* decreased significantly in October, at the end of the breeding period.

The relative breeding disturbance in Lithuanian *M. oeconomus* females (6.77 ± 0.97% of potential litter size) was comparable with data from Norway (9.25%) (Hoyte, 1955). However, as mentioned by Tast (1966), additional corpora lutea in *M. oeconomus* may be produced. Hoffmann (1958) called this phenomenon "polyovulation" and mentioned it in relation to several *Microtus* species.

Hence, the difference between the number of embryo or placental scars with that of corpora lutea does not necessarily mean a breeding disturbance. In Finland, nonimplantations were not registered, and resorption of embryos was in the range of 0%-2.4% of the total embryo number (Tast, 1966).

The low body mass of some breeding female *M. oeconomus* individuals is related to the delayed maturation of males. Females may start to reproduce at the age of 3 weeks, while for males it is at 2 months of age. This sex-based delay in maturation serves as a defense against inbreeding, i.e. females are almost always fertilized before their male siblings are able to mate (Bieberich and Olson, 2007). In northern Finland, a female of just 12 g, with a perforated vagina and sperm in the cornua uteri, was trapped in July (Tast, 1966). Regarding breeding at a young age, in Lithuania we found a female with a plugged vagina and body mass of only 16.5 g in July and another with a body mass of 20 g in August that had already bred (6 placental scars from the first litter).

After registering a juvenile animal in June, Krebs et al. (1995) suggested that *M. oeconomus* may start breeding under snow cover in April or May. We found exceptionally that breeding may start even earlier. As for nonoverwintered females that have signs of 2 litters in June/beginning of July, the breeding season of her mother had to have started in March (2 pregnancies of 3 weeks each, reaching puberty before the first pregnancy: 2 weeks, time before second pregnancy 1 week, pregnancy of the mother of such female: 3 weeks; and total: ca. 3 months).

In the northern part of the distribution range, not only litter size, but also the average number of litters was higher, although the breeding season was shorter (Popov, 1977; Siivonen, 1979; Cherniavskij, 1984; Krivosheev, 1984; Tamarin, 1985; Innes and Millar, 1987; Savickij et al., 2005). The high number of litters in the northern environment is only limited by the length of interbirth intervals, which may be just 20 days in cases of 5-litter breeding (Ims, 1997). In the south of the geographic range, the breeding season lasts longer, but with smaller litter sizes (Ognev, 1950; Spitzenberger et al., 2001; Borkowska et al., 2009; our data).

In regions neighboring Lithuania, published data on the breeding of the species are very limited and are based on insufficient sample size. In northeastern Poland, the average litter size is 5.28 ± 0.27 embryos (n = 21, Borkowska et al., 2009), while in Belarus a range of only 5-6 young is reported (Savickij et al., 2005). Earlier published data from Lithuania show a litter size of 4-6 (n < 10, Prūsaitė, 1988), or 4.9 (3-7) embryos (n < 10, Mažeikytė, 2004), with 2-3 litters per year, and a breeding season lasting from April to October. Thus, our data strongly contribute to the regional knowledge of the species biology. As snap trapping is not usual anymore, our data may be one of the last opportunities for sampling a free-living population of the species in Europe. The small litter size and the number of litters in the long breeding season show that the breeding pattern of Lithuanian *M. oeconomus* should be considered a southern one. This is in accordance with the recent shift of species distribution northwards (Balčiauskas et al., 2010) in the Baltic.

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