Ann. Zool. Fennici 45: 248–254 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 27 August 2008

Interaction between populations of the bank vole and the yellow-necked mouse

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Received 1 Mar. 2007, revised version received 4 Jan. 2008, accepted 4 Jan. 2008

Bujalska, G. & Grüm, L. 2008: Interaction between populations of the bank vole and the yellow-necked mouse. — *Ann. Zool. Fennici* 45: 248–254.

Crabapple Island (located in Bełdany Lake, NE Poland) was the site of concurrent study on the reproduction and survival of bank voles (*Myodes glareolus*) and yellow-necked mice (*Apodemus flavicollis*) in 1994–2002. We evaluated the importance of reproduction and survival for seasonal population dynamics as well as the formation of a summer peak in population numbers. Yellow-necked mice started breeding earlier in the spring than did bank voles. However, early breeding and rapid increase in numbers of both species resulted in a particular seasonal distribution of pregnant female numbers indicative for delayed (even up to 40 days) maximum reproduction of yellow-necked mice as compared with that of bank voles. A high survival rate of mature females of the yellow-necked mouse preceeds the July peak in population numbers, and a low survival rate of immature individuals of this species contributes to a rapid decline of numbers following this peak. The survival rate of mature females of the bank vole does not affect the summer peak in population numbers of this species. A relatively high survival rate of immature individuals of bank voles following the summer peak results in a slow decrease of its population size.

Introduction

Rodent sampling on Crabapple Island was conducted from April 1966 to April 2004. During this period bank voles were constantly present while yellow-necked mice appeared and instantly vanished a few times. However, in April 1994 ten mice appeared, bred and formed a peak in July, and their descendants lived there until April 2003. High peaks in population numbers of both species appeared in the same years: yellow-necked mice always in July and bank voles in July or September (Bujalska 2000, Grüm & Bujalska 2000).

Reproduction of both species studied seems to be governed by different behaviours: the number of sexually mature females of the bank vole is limited by their tendency toward territoriality (Bujalska 1970, 1973), while the yellow-necked mouse does not exhibit limitation in the number of sexually mature females (Bujalska and Grüm 2005). The yellow-necked mouse is known to start breeding in late winter or early spring, e.g., in February or March (Adamczewska 1961). On the contrary, bank voles usually begin to reproduce in late March (Bujalska 1973).

A full evaluation of demographic differences between the species in question and their importance in producing peak populations necessitates the estimation of their reproduction and survival rates, which is the task of the present paper.

Study area and methods

The studies were conducted in 1994–2003. Crabapple Island, in Bełdany Lake, was the study site. The island, 4 ha in size, was covered by a mixed deciduous forest with predominant *Tilio–Carpinetum* association (nearly 80% of the area). During each year, five trapping sessions — each lasting seven days — were performed in even six-week intervals from the end of April to end of October. Rodents were captured in live traps that were inspected twice a day (at 7 a.m. and 7 p.m.), and arranged in a grid of 159 trap sites (three traps per site) covering the entire area. Animals caught for the first time were marked individually. Trapped animals were weighed, sexed and their reproductive status was noted. Immature (abdominal testes) and mature (scrotal testes) males were distinguished. Females were divided into three categories: immature (closed vaginal orifice), mature (perforate vaginal orifice) and pregnant (distinguished using both body mass and vaginal smears).

Apart from standard statistical tests the following index characterizing seasonal distribution (early or late) of the number of observed pregnancies, called weighed mean pregnancy day, was used:

$$\mathrm{WMPD} = \frac{\sum_{i=1}^{4} \mathrm{PF}_i d_i}{\sum_{i=1}^{4} \mathrm{PF}_i}$$

where i = trapping session, PF_i = number of pregnant females during a trapping session i, d_i = the number of the last day of the trapping session i (value between 1 and 365). Pregnant females of both species studied were never found in October.

Survival rate from one trapping session to the next was calculated as the percentage of animals recaptured in session $t + 1$ with respect to those captured in session t (i.e., after a six-week period). It happened that some individuals (mainly the mice) captured in session t were recaptured for the first time later than in $t + 1$; in such cases they were also considered to be present in $t + 1$. To estimate differences between the two percentages of recaptures a χ^2-test (d.f. = 1) was used (based on numbers captured and recaptured). Differences at $p < 0.05$ were considered significant.

Results

The percentages of unmarked individuals present in April — i.e., those absent in the year preceding the April series of captures — indicated early onset of reproduction in the current year, or winter breeding: among 67 of the unmarked yellow-necked mice caught in all April months, there were 41 individuals of body mass ranging from 9 to 20 g, and seven heavier than 30 g (pregnant females excluded). The percentages varied between species and year: mean for the yellow-necked mice was 34.6% (ranged = 0%–66.6%) (there was no data for April 1994). Bank voles showed a lower mean (3.3%), and range (0%–11.7%). Differences between the above mean values were highly significant: $\chi^2 = 115.77$, $p < 0.001$. This indicates that yellow-necked mice reproduce earlier than bank voles.

Taking into account that both species have similar litter sizes — 5–6 young per bank vole female (Zejda 1966), and 3–8 per yellow-necked mouse female (Adamczewska 1961) — and that the pregnancy periods are of similar lenghts — e.g., 22 days (Adamczewska 1961, Bujalska 1973) — it is expect that the seasonal maximum of population size of the yellow-necked mouse should precede that of the bank vole.

The yearly maximum population numbers of the two species correlated significantly (linear correlation coefficient: $r = 0.821$, $p < 0.01$). However, the maximum numbers of yellow-necked mice and bank voles occurred in the same trapping session in six years, and the yellow-necked mice exhibited maximum population numbers earlier than the bank voles in three years (Fig. 1). Early or late maximum densities may depend on the seasonal distribution of pregnant females and on the survival rate of their progeny.

In some years (e.g., 1994, 1996 and 2000) with high summer maximum (called peak) num-

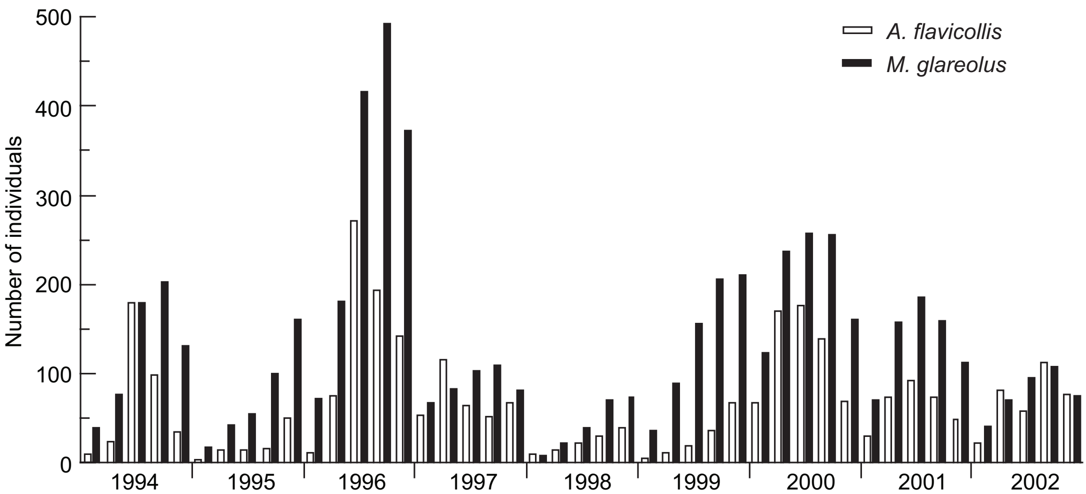

Fig. 1. Changes in population numbers from April 1994 to October 2002 (five estimates per year in April, June, July, September and October).

Table 1. Differences between numbers of pregnant females of *M. glareolus* and *A. flavicollis* in the 1st (April–June) and the 2nd parts (July–September) of the breeding season.

Years	Breeding season	*M. glareolus*	*A. flavicollis*	*p* (two-sided χ^2-test)
Peak years (1994, 1996, 2000)	1st part	196	92	< 0.0001
	2nd part	88	186	
Non-peak years	1st part	182	103	> 0.05
	2nd part	155	107	

bers (Fig. 1), there were more pregnant females of the bank vole during the first part of the breeding season (April and June), and more pregnant females of the yellow-necked mouse during the second part of the season (Table 1). On the contrary, in the years with low September–October maximum numbers of both species, similar numbers of pregnant females occurred in the first and second parts of the season, i.e. in July and September (Table 1).

Table 2. Weighed mean pregnancy day (95% confidence limits).

Year	*M. glareolus*	*A. flavicollis*
1994	171.5 (168.4–174.6)	205.0 (202.7–207.2)
1995	209.3 (205.3–213.3)	198.9 (185.0–212.9)
1996	164.9 (162.6–167.2)	205.2 (203.2–207.3)
1997	185.0 (181.1–188.8)	167.3 (162.8–171.7)
1998	203.1 (197.7–208.6)	208.8 (200.6–217.0)
1999	185.2 (181.6–188.8)	209.3 (203.7–214.9)
2000	145.8 (143.0–148.7)	164.1 (160.9–167.4)
2001	159.2 (155.6–162.9)	172.1 (167.3–176.9)
2002	155.0 (150.7–159.3)	179.4 (173.6–185.1)

A more detailed insight into the seasonal distribution of pregnant females was provided by the WMPD. There are years when WMPD indicates a 40-day reproduction delay for yellow-necked mice as compared with that for bank voles (Table 2). It is noteworthy that the highest delays in reproduction of the yellow-necked mice occurred in years with a high summer population peak of this species (Fig. 2), and in years with a relatively low October maximum the delays were substantially smaller (Fig. 2). A second-order polynominal regression describe the efect of maximum numbers of the yellow-necked mice on its delay in breeding (Fig. 2). Neither linear nor exponential models were significant. The polynomial formula indicates that a substantial delay in reproduction of yellow-necked mice creates a high seasonal peak in the population size, and that a lack of delay in reproduction results in a low September–October maximum. Moreover, the polynomial formula suggests that when WMPD for the yellow-necked mouse is smaller than that for the bank vole, the former species can attain a rather high seasonal maxima in population numbers. Bank voles did not show any significant correlation between their seasonal maxima and this delay, sugesting that they were unsusceptible to the presence of the yellow-necked mouse.

The delay in breeding of the yellow-necked mice breeding (as evidenced by a greater WMPD) did not seem to result from low breeding rate of sexually mature females: in April the mean percentage of pregnancies among mature females of this species was higher (82.3%) than in the population of the bank vole (71.2%): $\chi^2 = 5.06, p < 0.05$.

In general, bank voles survived better than yellow-necked mice: in each of the categories of individuals the percentages of survivors among bank voles were higher than those found among mice (Table 3).

Seasonal changes in survival rate were analysed for mature females (the pool of individuals directly responsible for the number of born and weaned), mature males, and for immature individuals of both sexes together. *Apodemus flavicollis* exhibited the following seasonal survival differences between the peak years (1994, 1996 and 2000) and the remaining non-peak years:

1. Mature females in the peak years survived much better from April to June than in the non-peak years (84% and 51.5%, respectively). On the other hand, in the period from July to October they survived better in the non-peak years (Table 4). Therefore, high survival rate of mature females from April to June seems to be favourable in producing peaks.
2. Mature males did not exhibit survival differences between peak and non-peak years (Table 4).
3. Immature individuals in peak years survived worse from July to October than during the same period in non-peak years, while there was no difference between those years in the period from June to July (Table 4). Thus, immature individuals contribute to the decline in numbers following the July peak.

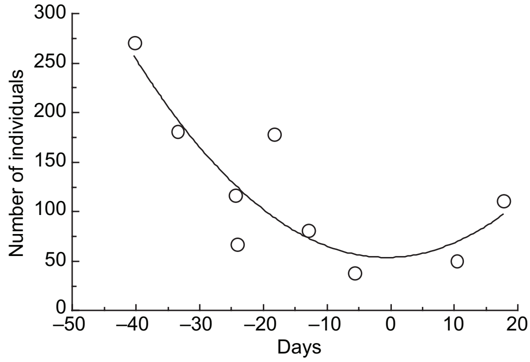

Fig. 2. Regression of the yearly maximum population numbers of *A. flavicollis* on its delay of WPMD relative to the WMPD of *M. glareolus.* Negative values on the horizontal axis denote the delay in days. Regression: $y = 55.16 - 0.089x + 0.127x^2$, $R = 0.863$, $p < 0.05$.

Seasonal differences in survival rates of *M. glareolus* between peak and non-peak years were as follows:

1. Mature females in peak and non-peak years survived equally well from April to July (Table 5), and from July to October they sur-

Table 3. Differences between percentages of recaptured individuals of *A. flavicollis* and *M. glareolus* in all trapping sessions.

Category	Captured/recaptured (%)		χ^2	p (χ^2-test)
	A. flavicollis	*M. glareolus*		
Mature females	984/64.9	1510/71.7	12.82	< 0.001
Immature females	238/54.4	831/71.6	25.71	< 0.0001
Mature males	615/58.0	728/63.9	4.76	< 0.05
Immature males	506/54.7	1500/74.7	73.28	< 0.0001

vived better in non-peak years (Table 5). One can conclude that their survival rates do not affect the formation of peaks.
2. Mature males in April–July survived equally well in peak and non-peak years (Table 5), and in July–October they survived better in non-peak years (Table 5).
3. Immature individuals showed significant difference in survival rates from July to September: 84.9% in peak years *vs*. 75.7% in non-peak years (Table 5). This points to their share in the creation of the peak (in September). Relatively high survival rate of immature individuals, as compared with that of *A. flavicollis*, from September to October contributed to less rapid decline in numbers following the peak (Table 5).

Discussion

The present study confirmed the notion (Adamczewska 1961) that yellow-necked mice are early breeders. On the other hand, early reproduction

Table 4. Differences in survival of *A. flavicollis* in peak years (1994, 1996 and 2000) *vs*. non-peak years (1995, 1997, 1998, 1999, 2001 and 2002).

		Peak years		Non-peak years		
Months	Category	Present at *t*	% survived to *t* + 1	Present at *t*	% survived to *t* + 1	*p* χ^2_1-test
April to June	Mature females	25	84.0	66	51.5	< 0.005
	Mature males	23	43.5	31	32.2	> 0.05
	Immature individuals	14	28.6	23	39.1	> 0.05
June to July	Mature females	96	66.7	107	63.6	> 0.05
	Mature males	68	57.3	63	50.8	> 0.05
	Immature individuals	101	69.3	107	65.4	> 0.05
July to September	Mature females	249	65.5	114	79.8	< 0.01
	Mature males	158	64.6	90	67.8	> 0.05
	Immature individuals	222	56.7	49	75.5	< 0.05
September to October	Mature females	211	61.6	116	72.4	< 0.05
	Mature males	106	59.4	76	60.5	> 0.05
	Immature individuals	106	34.9	122	50.0	< 0.05

Table 5. Differences in survival of *M. glareolus* in peak years (1994, 1996 and 2000) *vs*. non-peak years (1995, 1997, 1998, 1999, 2001 and 2002).

		Peak years		Non-peak years		
Months	Category	Present at *t*	% survived to *t* + 1	Present at *t*	% survived to *t* + 1	*p* χ^2_1-test
April to June	Mature females	123	70.7	121	72.7	> 0.05
	Mature males	105	53.3	111	60.9	> 0.05
	Immature individuals	1	–	2	–	–
June to July	Mature females	173	70.5	198	68.7	> 0.05
	Mature males	78	66.7	94	63.8	> 0.05
	Immature individuals	242	61.6	170	72.9	< 0.05
July to September	Mature females	182	73.1	260	84.2	< 0.01
	Mature males	64	59.4	110	77.3	< 0.025
	Immature individuals	598	84.9	259	75.7	< 0.01
September to October	Mature females	160	56.9	293	70.3	< 0.01
	Mature males	40	47.5	126	69.8	< 0.025
	Immature individuals	724	70.7	335	67.8	> 0.05

and rapid growth of numbers of yellow-necked mice and bank voles resulted in a delay of the former species' reproductive activity, although the delay did not seem to be a serious obstacle in the creation of summer peaks of the yellow-necked mouse, but rather an enhancement of peak formation.

In the present paper we showed that a high survival rate of mature females enhances rapid population growth of the yellow-necked mouse. Another factor favourable for growth is that female maturation rate is unlimited by territoriality (Bujalska & Grüm 2005). Bank voles present a reciprocal picture: an abundant population of overwintering females, rather than their high survival rate, favours the formation of a peak (Bujalska 2000). Besides, the maturation rate of newly weaned females is limited by mature female territoriality in the bank vole (Bujalska 1970). The above mentioned differences may explain why high seasonal peaks in numbers of the yellow-necked mice can occur in July, which is earlier than that of the bank vole, i.e., usually in September (Bujalska 2000).

The delay in breeding in the yellow-necked mouse is a possible reason for considering inter-specific competition between these species. The yellow-necked mouse is much heavier and physically stronger than the bank vole, and when individuals of those species encounter each other, the bank vole retreats (Andrzejewski & Olszewski 1963). On the other hand, the yellow-necked mouse is strictly nocturnal (Alcheikh 2001). Thus, the bank vole being both dusk, night and dawn active (Alcheikh 2001), is able to forage for longer during the spring and summer than the yellow-necked mouse. This may explain superiority of the bank vole in scramble competition for food, and consequently may explain restricted food availability for the yellow-necked mouse. However, another explanation of the delay is also possible (supported by a lower survival rate of the yellow-necked mouse compared with that of the bank vole): social stress due to excessive encounters with individuals of the other species, leading to suppression of the breeding rate at high population densities. We were unable to evaluate these hypotheses.

We also speculate on the importance of restricted female maturation rate due to mature female territoriality (Bujalska 1970, 1973). Its effect can be seen in the bank vole: there is a pool of immature females ready to replace died mature ones. Contrary to this, almost all females of the yellow-necked mouse attained sexual maturity, except during the last part of the breeding season (Bujalska & Grüm 2005). Therefore, there was almost no immature female pool. As a consequence, yellow-necked mice seem to be more vulnerable than bank voles in experiencing a rapid population decline, especially in that immature individuals of this species exhibited a low survival rate in the autumn and, according to Bujalska and Grüm (2006), also in the winter.

Conclusions

Bank voles appear to the affect breeding of yellow-necked mice when both populations rapidly increase from April to July.

Time separation of intensive breeding periods of bank voles and yellow-necked mice favour the formation of high population sizes of the latter species.

Both species seem to interact only in the years when their populations increase rapidly. However, only the yellow-necked mice show vulnerability to the presence of an abundant bank vole population.

Bank voles always survive better than yellow-necked mice.

Attainment of a high peak in population numbers by yellow-necked mice depend on good mature female survival at the beginning of the breeding season, while reaching the same target by bank voles does not depend on this factor.

A rapid decrease in population size following peak numbers of yellow-necked mice resulted from particularly low survival rate of immature individuals, while a higher survival rate of immature bank voles resulted in a rather slow decrease in numbers following the population peak.

Acknowledgement

Rodent sampling used in this paper was supported by the Institute of Ecology, PAS, and the State Commitee for Scientific Research grants 6P04F 015 13 and 6P04F 024 20.

References

Adamczewska, K. A. 1961: Intensity of reproduction of the *Apodemus flavicollis* (Melchior, 1834) during the period 1954–1959. — *Acta Theriologica* 5: 1–21.

Alcheikh, B. 2001: Trappability of *Clethrionomys glareolus* and *Apodemus flavicollis* inhabiting Crabapple Island, Masurian Lakeland, Poland. — *Polish Journal of Ecology* 49: 409–427.

Andrzejewski, R. & Olszewski, L. 1963: Social behaviour and interspecific relations in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber, 1780). — *Acta Theriologica* 7: 155–168.

Bujalska, G. 1970: Reproduction stabilizing elements in an island population of *Clethrionomys glareolus* (Schreber, 1780). — *Acta Theriologica* 15: 381–412.

Bujalska, G. 1973: The role of spacing behaviour among females in the regulation of reproduction in the bank vole — *Journal of Reproduction and Fertility*, Suppl. 19: 463–472.

Bujalska, G. 2000: The bank vole population in Crabapple Island. — *Polish Journal of Ecology* 48 Suppl.: 97–106.

Bujalska, G. & Grüm, L. 2005: Reproduction strategy in an island population of yellow-necked mice. — *Population Ecology* 47: 151–154.

Bujalska, G. & Grüm, L. 2006: Winter survival of *Apodemus flavicollis* in Crabapple Island (NE Poland). — *Hystrix Italian Journal of Mammalogy* 17: 173–177.

Grüm, L. & Bujalska, G. 2000: Bank voles and yellow-necked mice: what are interrelations between them? — *Polish Journal of Ecology* 48 Suppl.: 141–145.

Zejda, J. 1966: Litter size in *Clethrionomys glareolus* (Schreber, 1780). — *Zoologicke Listy* 15: 193–204.