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Bank vole biology: Recent advances in the population biology of a model species				

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BANK VOLES AND YELLOW-NECKED MICE: WHAT ARE INTERRELATIONS BETWEEN THEM?

ABSTRACT: Literature survey has revealed similarity of ecological niches of bank voles and yellow-necked mice. Behavioral observations that show subordination of bank voles to yellow-necked mice suggest that the latter is a superior competitor. Nevertheless, neither spatial nor time separation of those species can be evidenced. Competition between these species seems to be occasional (or rare). Perhaps, their microhabitat niches are sufficiently separated to allow for coexistence.

KEY-WORDS: ecological niche, behavioral interactions, spatial distribution, multi-annual dynamics, competition

1. INTRODUCTION

This article evaluates interactions between bank voles (*Clethrionomys glareolus* Schreber) and yellow-necked mice (*Apodemus flavicollis* Melchior) after examination of numerical data found in the literature, and with special reference to the populations inhabiting Crabapple Island. It must be recognized, however, that the data available for yellow-necked mice are relatively scarce in comparison to those for bank voles. Therefore, in many instances generalised arguments characterising *Apodemus* are considered instead of the specific for *A. flavicollis*.

2. ECOLOGICAL NICHE

Bank voles are widely distributed in Western, Central and Eastern Europe (Raczyński 1983). The same is true for yellow-necked mice (Holišová 1969, Kovalenskij and Korenberg 1980, Angerman 1972, Flowerdew 1985, Karaseva and Telitsyna 1996). In Poland they occur in many places (Pucek and Raczyński 1983). Both species prefer mature deciduous and mixed forests (Holišová 1969, Pucek 1983, Döhle *et al.* 1984, Geuse 1985). They are also partly arboreal (Holišová 1969, Montgomery and Gurnell 1985, Abe 1986), though the yellow-necked mouse seems to penetrate into higher strata of the forest than the bank vole does (Holišová 1969). Yellow-necked mice seem predominantly nocturnal (Montgomery and Gurnell 1985) whereas bank voles are also active during the day (Bashenina 1981).

Hansson (1985) who summarised their food preferences described *A. flavicollis* as typical granivorous species and *C. glareolus* as an intermediate between granivorous and folivorous. Obrtel (1974) provided evidence that both species prey on small arthropods, though this component seems to be more fre-

quent in the diet of the yellow-necked mouse. Jensen (1985) found equal preferences for seeds of deciduous trees in the bank vole and the yellow-necked mouse. Bujalska (unpubl.) observed grazing on the foliage of the same herb layer plants by bank voles and yellow-necked mice in Crabapple Island.

3. SOCIAL ORGANIZATION

Social organization of the bank vole, and particularly of the population inhabiting Crabapple Island, is well recognised. Mature females are territorial (Bujalska 1970) and holding a territory is the prerequisite for attainment of sexual maturity. Also mature males exhibit group territoriality, that is they seem to form clans consisting of mutually tolerant individuals, though each of the clan members seem to possess an exclusive territory (Bujalska and Grüm 1989). The territory size of a mature male and of a mature female seems equal to about 150 m², whereas the mean home range size in mature males, according to Bujalska and Grüm (1989) 1753 m², is on the average twice of that of mature females (Bujalska 1994). An important consequence of territoriality of mature individuals is suppression of maturation rate resulting in accumulation of a reserve pool of immature males and females allowing for some replacement of dying mature voles. Immature bank voles exhibit the "sit and wait" strategy (Bujalska 1990) that reduces mortality rate and increases the probability of replacing a dead mature individual (Bujalska and Grüm 1994, Grüm and Bujalska 1994).

Numerous indices allow one to suggest similarity of spatial organization in populations of *Clethrionomys* and *Apodemus*. Kikkawa (1964) found similar size of home ranges for *C. glareolus* and *A. sylvaticus*, with higher estimates for males than for females. Also Zejda and Pelikán (1969) obtained higher estimates of home range size for males (3208 m²) than for females (1308 m²) of *A. flavicollis*. According to Golikova (1968), pregnant and lactating females of *A. flavicollis* hold individual territories. Gurnell (1978) states that *Apodemus* males are tolerant of familiar or kin ones but intolerant of strangers. According to Montgomery (1980) home ranges of *Apodemus* males overlap, similar to the overlapping of home ranges of mature males of bank voles. Bujalska (1981) showed similarity in *C. glareolus* and *A. agrarius* in the curves relating the

numbers of mature females to the total population numbers, and concluded that in the latter species maturation rate of females could be suppressed, too. Wolton and Flowerdew (1985) conclude that there is a remarkable similarity of spatial organization of *A. sylvaticus*, *A. flavicollis* and *C. glareolus*, consistent with earlier results.

One can expect that both in *Apodemus* and *Clethrionomys* the basic unit of spatial organization is a cohesive group of mutually tolerant mature males and females, with male home ranges overlapping (at least partly) and covering the home ranges of mature females. Such a group of bank voles was named "breeding colony" (Bujalska 1990). One can also speculate that in mice, as in voles, territoriality suppresses maturation rate of newly recruited individuals.

4. INTERSPECIFIC RELATIONS

Direct, visual observation of encounters between bank voles and yellow-necked mice (Andrzejewski and Olszewski 1963) showed that yellow-necked mice were aggressive toward the other species, and bank voles withdrew or were chased off by the stronger and heavier species. Also Bergstedt (1965) and Greenwood (1978) conclude that surface activity of bank voles can be affected by *Apodemus*. Bujalska and Janion (1981) reported an increase of home range size of bank voles following removal of co-occurring population of *A. agrarius*. Gliwicz (1981) removed *C. glareolus* and *A. flavicollis* and observed that in the remaining population of *A. agrarius* reproduction decreased and the offspring survival increased.

One could therefore expect that yellow-necked mice, being a stronger contest competitor than bank voles, affect either population dynamics or spatial distribution and/or demographic variables of bank vole populations.

5. POPULATION DYNAMICS

The literature data on population dynamics of co-occurring bank voles and yellow-necked mice, especially multi-annual, are really scarce. Djuzhaeva *et al.* (1983) found increased bank vole participation in the rodent community was accompanied by increased numbers of yellow-necked mice and a decrease of numbers of wood mice. Döhle *et al.* (1984) presented data on population numbers sampled in two woodland areas (Bit-

terfeld and Bernburg) from April through October in consecutive 4 years. Their samples reveal rather parallel than reciprocal changes in mean yearly numbers of bank voles and yellow-necked mice caught during the study years. Gurnell (1985) concludes that there is substantial similarity between changes of numbers of bank voles and wood mice and yellow-necked ones. Stubbe and Stubbe (1991) presented data on numbers of bank voles and yellow-necked mice caught during an 8-year period, and similarity between changes in numbers of those species is remarkable (Fig. 1). Zejda (1996) compared changes in percent dominance of bank voles and yellow-necked mice in the same area in two periods, 1956–1961 and 1983–1989, and discovered that their share in the rodent community increased: from 3.1 to 9.6 and from 1.3 to 11.3%, respectively. In his opinion, the increased share was due to favorable changes of food base for both species in question. Grüm (in press) estimated mean yearly numbers of bank voles and yellow-necked mice in Crabapple Island in years 1994–1998, and came to the conclusion that their population sizes change in parallel. The changes in numbers were uncorrelated with biomass production of the herb layer. Neither was he able to demonstrate that demographic parameters (reproduction rate, mortality rate) in the bank vole population differed between the years with presence of yellow-necked mice (1994–1998) and the years without yellow-necked mice (1966–1993).

There is further evidence that population numbers of bank voles and wood mice change in concert (Kikkawa 1964, Geuse *et al.* 1985).

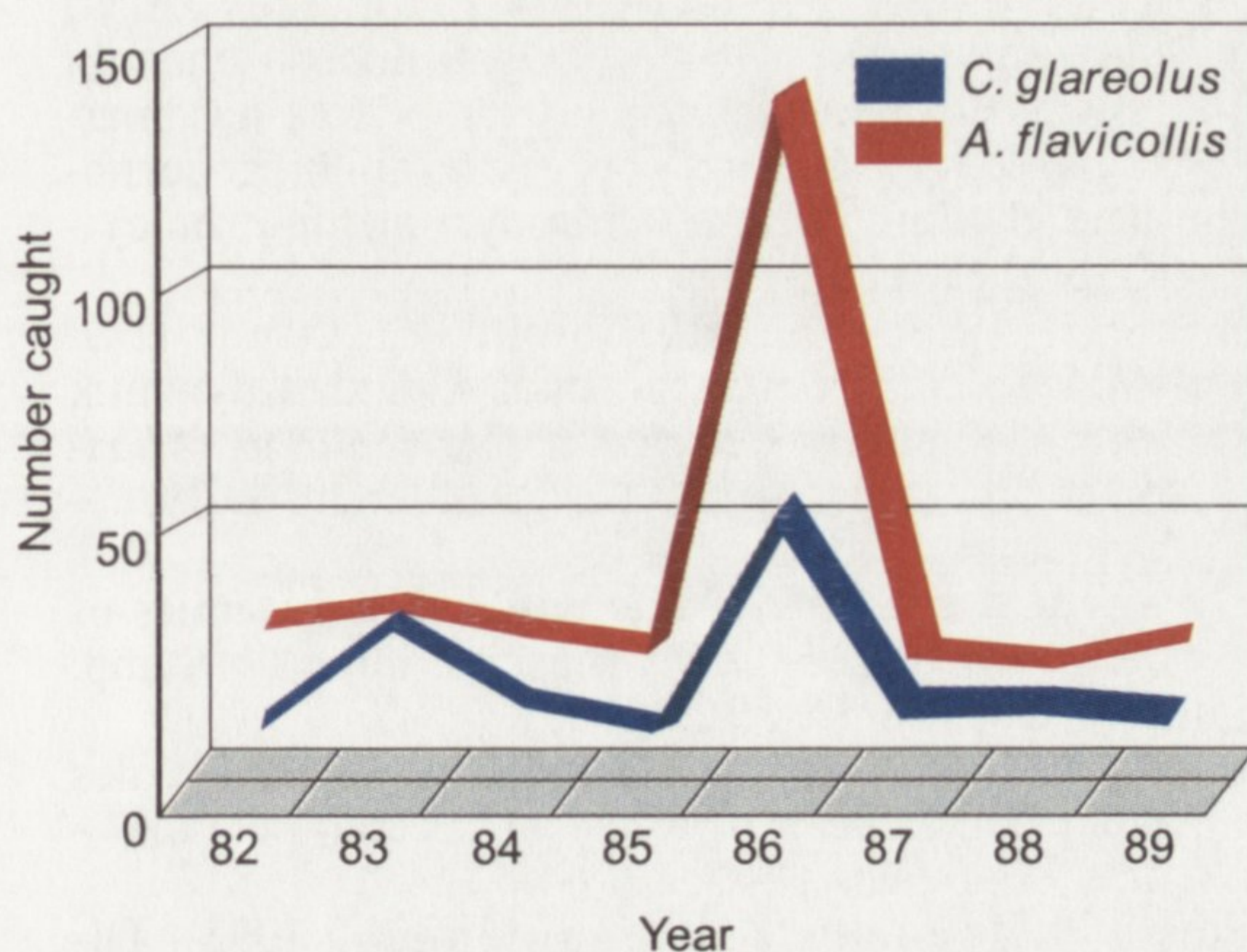


Fig. 1. Multi-annual changes in population numbers of bank voles and yellow-necked mice. Mean values of the yearly samples from April to October, recalculated from Stubbe and Stubbe (1991), are shown

6. SPATIAL DISTRIBUTION

It is evident that there can be differences between *Apodemus* and *Clethrionomys* as far as their microhabitat preferences are concerned. Kikkawa (1964) concludes that spatial distribution of bank voles is strongly affected by ground cover, and that of wood mice is not. Healing *et al.* (1983) showed, for instance, that bank voles preferred sites covered with bracken, whereas wood mice avoided these sites. Such microhabitat preferences do not seem to result in spatial separation of co-occurring *Apodemus* and *Clethrionomys*, but they rather affect frequency of visits to certain sections of individual home ranges, which for the latter are extensive and may contain diversified ground cover. A review of estimates of home range size of wood mice (Wolton and Flowerdew 1985) reveals values (varying also in relation to the method applied) ranging from about 1000 m² to over 2 hectares. The home range of individual bank voles seems to vary within smaller ranges, from a few hundred sq. m. to a few thousand square meters (Zejda and Pelikán 1969, Bujalska 1970, Wolton and Flowerdew 1985).

Bujalska (in press) attempted to evaluate spatial distribution of bank voles and yellow-necked mice inhabiting Crabapple Island by comparing the observed and expected number of trap sites visited by both of the species in question. The expected number of trap sites was proportional to the numbers of trap sites visited by each of the species, and was calculated on the assumption of random distribution of them. She was unable to provide statistical evidence that the numbers of trap sites observed and expected differ for mature females or mature males. It appeared, however, that sexually immature bank voles and yellow-necked mice co-occur more often than expected (Bujalska, in press).

7. DISCUSSION AND CONCLUSIONS

Quantitative data on changes of population sizes of bank voles and yellow-necked mice of Crabapple Island conform to earlier data presented by various authors cited above, and also to the earlier interpretations (e.g. Gurnell 1985): the populations of these two species seem to coexist rather than compete. The spatial distribution of these species over Crabapple Island area remains in

accord with such interpretation (Bujalska, in press). On the other hand, the direct observations of individual encounters between bank voles and yellow-necked mice (e.g. Andrzejewski and Olszewski 1963) indicate limitation of use of habitat resources by bank voles due to aggressive behavior of the mice. The latter species seems a stronger contest competitor than the bank vole.

The question thus arises whether the bank vole can counterbalance the impact of aggressive yellow-necked mice because it is superior in scramble type of competition? Or, as stressed by Gurnell (1985) is competition between these species rather occasional (or rare) because their microhabitat niches are sufficiently separated? The latter question could be answered provided one could estimate both the actual (and multidimensional) niche overlap and the amount (upper limit) of overlap allowable for coexistence.

The most serious problem, however, is that severity of interspecific competition cannot be measured directly. In fact, to infer about competition one has to assess variables influenced by other factors, too. In accordance with the competitive exclusion idea, reciprocal changes in distribution of numbers in space or time can be considered as resulting from competition (Grant 1966, Gilpin and Diamond 1982, Hansson 1983, Henttonen and Hansson 1984, Higgs and Fox 1993). And, consequently, absence of reciprocal changes forces one to interpret the results as mutual tolerance or coexistence (based on presumed niche separation), or to seek balance between contest *versus* scramble competition. Moreover, accepting the logic of inference presented above, one has to forget both habitat variability as well as intrapopulation processes. Therefore, it is rather doubtful that data on co-occurrence are satisfactory to decide about competitive relations (Hastings 1987).

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