

## EFFECT OF DENSITIES OF TWO COEXISTENT SMALL MAMMAL POPULATIONS ON THE SURVIVAL OF *APODEMUS FLAVICOLLIS* IN A FOREST HABITAT

Gy. Horváth and Z. Wagner

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**Abstract.** Small mammal populations were observed by live-trapping in a forest reserve area of *Quercus robori-Carpinetum* plant association on the Dráva Lowlands in southern Hungary in 1997. During the 6050 trap-nights resulting from the 5-night sampling periods, 306 individuals of *Apodemus flavicollis*, 269 of *A. agrarius* and 293 of *Clethrionomys glareolus* were captured and marked. The comparative analysis of population dynamics showed that synchronous changes in the number of individuals occurred only in the case of *C. glareolus* and *A. agrarius*, while in the other two pairings these changes advanced without any similarities. The interaction matrix which was constructed based on the calculated partial regression coefficient, indicated negative interaction relation among the three species. The present study investigates whether the densities of the two coexistent populations have an effect on the survival of *A. flavicollis*. The hypothesis was analysed with the program MARK. A constrained-parameter model was designed and our assumption was proved: according to the model selection procedure the survival of *A. flavicollis* is influenced by the two coexistent populations. In further analyses the values of estimated survival probabilities were compared and as a result no consistent difference could be indicated between the survival probabilities calculated by the derived CJS and the constrained parameter models. Thus, the influence of the two coexistent populations is not so notable that it could cause significant differences.

*Key words: Apodemus flavicollis, survival, constrain parameter, model selection*

**Gy. Horváth, Z. Wagner,** Department of Zootaxonomy and Synzoology, University of Pécs, 7624 Pécs, Ifjúság útja 6.

### Introduction

The typical generalist species in Central-European deciduous forest area are the yellow-necked wood mouse, *Apodemus flavicollis* (Melchior 1834), the bank vole, *Clethrionomys glareolus* (Schreber, 1780) and the striped field mouse, *Apodemus agrarius* (Pallas, 1771). Their habitat preferences differ only to a little extent. *A. flavicollis* and *C. glareolus* are characteristic forest dwellers (Flowerdew *et al.* 1985, Mazurkiewicz 1994), while *A. agrarius* can be found in fields, agricultural areas, yards and wet, bushy habitats, along rivers and in forest edges, forest stripes (Zejda 1967, Pucek 1983, Szacki and Liro 1991).

The trophic niches of the three species are very similar, the pattern of their spatial distributions are comparable, though the food resources in the different habitats and seasons can adequately be differentiated (Holisova 1967, Obrtel and Holisova 1974, Hansson 1985). If the three species are either temporarily or permanently present in a given habitat, competition relations can evolve. Several studies have been published on the analyses of the different interspecific interactions of these species. Andrzejewski and Olszewski (1963) investigated the direct competition of *A. flavicollis* and *C. glareolus*. They also observed the daily activity of the two species, on which the fluctuation of their densities is of great influence. At high density the activity of *C. glareolus* decreased, when the *A. flavicollis* was at

its activity peak (Wojczik and Wolk 1985). With respect to *A. flavicollis* and *C. glareolus* the selective removal of the former caused an increase in the number of *C. glareolus* adult females in the area (Bujalska and Janion 1981). It was proved that *C. glareolus* had a constraining effect on the density and spatial distribution of *A. agrarius*, although the relationship between the two species is highly influenced by the qualitative characteristics of the given habitat (Kozakiewicz *et al.* 1987). Based on the evaluation of density values, Gliwicz (1981) indicated negative associations between *A. flavicollis* - *A. agrarius* and *C. glareolus* - *A. agrarius*, and suggested significant overlap between the food resources as the cause for competition in the case of the two pairings but he also mentioned competition for hiding places as an alternative hypothesis. Kozakiewicz and Boniecki (1994) studied the inter- and intraspecific behaviour of *C. glareolus* and *A. agrarius*, and they reported that intolerant relations are likely to evolve between them, which are as strong as the agonistic relations within the species. However, these experiments did not prove the earlier statements that the *Apodemus* genus is dominant over *Clethrionomys* (Gurnell 1985).

Applying the density values of three earlier years in the present study area, an interaction matrix was constructed based on the calculated partial regression coefficient and in the case of all three pairings of the three populations strong negative interactions were pointed out (Horváth *et al.* 1996). 1997 was a very high-density year regarded all three populations. According to our assumption, the interactions among the three species have great influence on the density of each given population and the changes in it have effects on the survival of the individuals. The present study observes the hypothesis whether the densities of *C. glareolus* and *A. agrarius* higher than their average density in each period have constraining effect on the survival and recapture probabilities of *A. flavicollis* based on the data from 1997. The purpose of the analysis is to find out if the negative interaction shown by the interaction matrix could also be proved by modelling the survival, thus the densities of the two coexistent populations have justifiable constraining effect on the survival of *A. flavicollis*.

## Materials and methods

Our study area is located between the villages Vajszl6 and Páprád (N 45° 51', E 18° 00') in Baranya county, in the Dráva Lowlands of Southern Hungary. The trapping grid covering 1-ha area was laid out in a hornbeam-oak (*Quercus robor-*

*Carpinetum*) forest section where the height of the upper canopy is around 25 m, and the characteristic species are *Quercus robur*, *Fraxinus angustifolia* and *Robinia pseudoacacia*. The lower canopy layer is 4-10 m high, where *Carpinus betulus*, *Ulmus minor*, *Fraxinus angustifolia* are the typical representatives of plants. The shrub layer of 1-4 m height consists of young individuals of *Cornus sanguinea*, *Ligustrum vulgare*, *Crataegus monogyna*, *Sambucus nigra* and *Robinia pseudoacacia*. Sections of the sampling area with the densest plant cover of 90-100 % are characterised by high undergrowth comprising many weed species and ones indicating dampness and soil rich in nitrogen.

The area was oriented approximately to northeast-southwest with 11×11 live traps positioned 10 m apart from each other. Mixed cereals and bacon were used as bait. Data from 10 months of 1997 were used in the research. Sampling with five-day trapping sessions each month from February to November made up 6050 trap nights. Traps were checked twice daily (8<sup>00</sup> CET and 20<sup>00</sup> CET). We marked the individuals by removing the terminal knuckle of certain toes (O'Farell 1980, Nichols and Conley 1982). The temporal changes of population sizes in the three observed species were characterized by "minimum number alive" (MNA) (Krebs 1966, Boonstra and Krebs 1978). Based on the MNA-values the trends in the numbers of individuals were compared and evaluated with Spearman rank-correlation (Zar 1996). Interaction matrices were constructed using the demographic data and calculating the partial regression coefficient (Dueser and Hallett 1980).

The analysis of time-dependence in the survival and recapture rates of *A. flavicollis* was carried out with program MARK (Cooch and White 1998). The model chosen by the goodness-of-fit (GOF) tests was held as the basic model and it was compared to the constrained parameter model, where the effect of densities of *C. glareolus* and *A. agrarius* was built in the model-matrix using the applications of the program MARK. Constraining effects were considered in those periods where the densities of *C. glareolus* and *A. agrarius* were higher than that of the *A. flavicollis* population. The constrained parameter model-matrix also allows to take the conjugate effects of densities into account. The model selection between the basic and the constrained parameter models was based on the differences in the models' deviances and the values of AIC (Akaike Information Criterion) calculated by MARK (Anderson *et al.* 1994). The latter handles not only the model-bias from our data, but also the number of parameters (PAR) that influences the

accuracy of the estimates [AIC = Dev. + 2 × PAR]. The survival rates estimated by the models were compared using the one-sample *t*-test.

## Results

During the 6050 trap nights 306 specimens of yellow-necked wood mice (*Apodemus flavicollis*), 269 striped field mice (*A. agrarius*) and 293 bank voles (*Clethrionomys glareolus*) were captured and marked. The demographic trends of the rodent populations throughout the 10-month sampling period were evaluated based on the changes in the MNA values (Fig. 1). Two abundance maxima can be observed in both *A. flavicollis* and *C. glareolus* which do not coincide in the two species. The former had its maximum in May-June and later in September, while the latter was the most abundant in July and October. *A. agrarius* was captured in low numbers in February-March, suggesting low overwintering survival in the high-density autumn population, according to the numbers of captures. Thereafter, similarly to earlier years, the density of *A. agrarius* decreased over the summer period but in autumn it showed intensive increase again and by September its MNA value outnumbered those of the other two species. The intensive increase in the density of this species raises the question how this high density evolving in such short a period would effect the actual number of the two coexistent populations. The decline in the population sizes after the autumn period in the case of all three species indicates the reduction in resources and the beginning of the lower-density winter period.

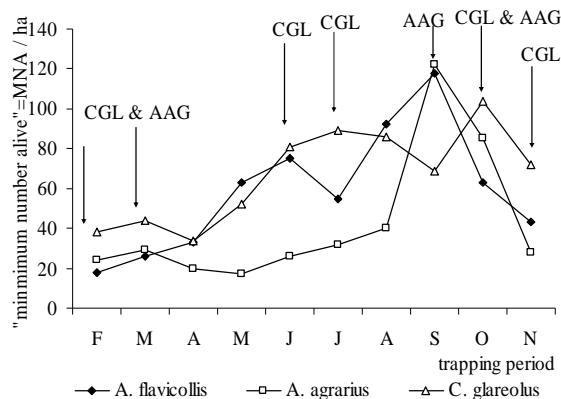


Fig. 1. Demographic changes in the three rodent populations. Sampling occasions where the density of *C. glareolus* or *A. agrarius* or of both was higher than that of *A. flavicollis* were indicated with arrows.

As revealed by the comparative analysis of population dynamics during the sampling year, the

demographic trends of *C. glareolus* and *A. agrarius* showed significant synchronous changes ( $R_S = 0.636$ ,  $p < 0.05$ ), while no rank-correlation values were obtained in the population shifts in the other two pairings ( $R_S = 0.516 - 0.565$ , NS). The interaction matrix based on the calculation of partial regression coefficient from the demographic data indicated negative relation among the three species (Table 1).

Table 1. Interaction matrix for captured rodent species based on the partial regression coefficients

Species	<i>A. flavicollis</i>	<i>A. agrarius</i>	<i>C. glareolus</i>
<i>A. flavicollis</i>	-		
<i>A. agrarius</i>	$r = -0.9929 *$	-	
<i>C. glareolus</i>	$r = -0.9916 *$	$r = -0.9919 *$	-

\*:  $p < 0.001$

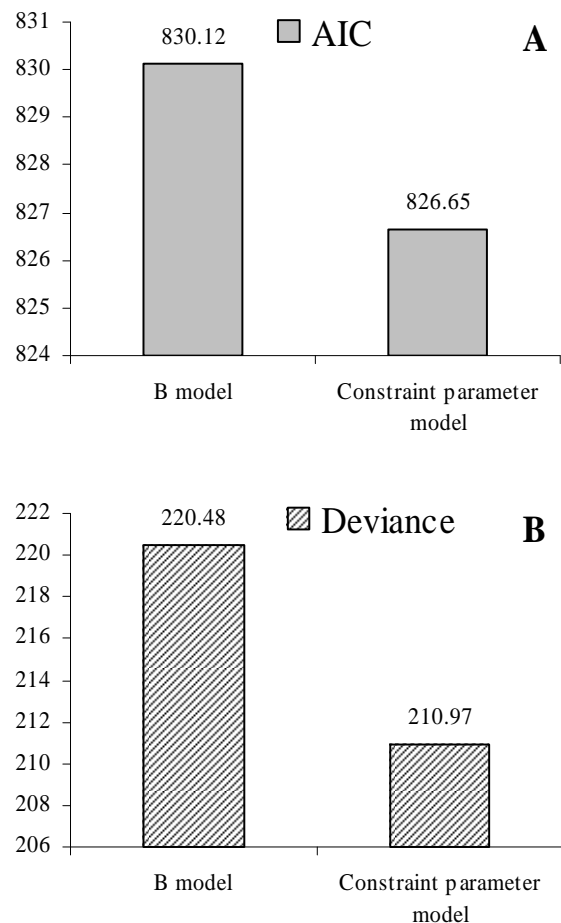


Fig. 2. The values of AIC (A) and deviances (B) by fitting the data of *A. flavicollis* on the B and the constraint parameter model.

The two statistical analyses above suggest a competition relation among the three coexistent populations, therefore our assumption was that on

any of the three populations the density of the other two had a constraining effect, which has influence on the survival probability of the given population. Thus, survival models were carried out further on.

First, the time-dependence of survival and recapture probabilities of *A. flavicollis* were tested based on the capture history of the individuals in the population. According to the GOF-test of MARK, the B model [ $\phi(t), p()$ ] assuming time-dependent survival through the sampling periods derived from the basic CJS model was accepted as the most parsimonious model ( $\chi^2 = 0.645, df = 6, p = 0.9956$ ). The constrained parameter model was compared to this one. The density of *A. flavicollis* was in six periods lower than that of *C. glareolus*, in four periods lower than *A. agrarius* and in three periods both of the two coexistent populations exceeded the density of the observed population (Fig. 1). The estimated deviance for the constrained parameter model that could handle, in addition to their individual effect, the conjugated effect of the two coexistent populations on *A. flavicollis*, was lower than the basic model, assuming survival to be time-dependent ( $\chi^2 = 9.52, df = 1, p < 0.01$ ). Besides, considering the AIC values it was again the constraint parameter model that fitted our data better (Fig. 2). The results of model-selection proved our hypothesis assuming the density of *A. agrarius* and *C. glareolus* to be a constraining factor, which therefore could have negative influence on the periodically estimated survival probabilities of *A. flavicollis*. The density of *A. agrarius* and *C. glareolus* plays a role in the survival of *A. flavicollis* as a biotic factor.

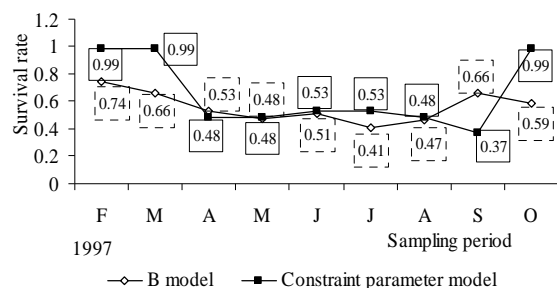


Fig. 3. The estimated survival rates of *A. flavicollis* population.

The survival probabilities estimated by the basic and the constrained parameter models are shown in Fig. 3. Based on the results of model-selection the survival values estimated by the constraint parameter model were expected to be lower in those periods when the two other populations were present as constraining factors. In several periods marked

differences occurred: in two months (April, September) the survival probabilities were lower than those estimated by the basic model, however in three other months (February, March, October) they were higher. Thus, Fig. 2 directly shows that the survival probabilities of *A. flavicollis* were not reduced significantly by the densities of the two coexistent populations. Despite of the result of the model selection these parameters did not change according to our expectance. As a further analysis, *t*-test was administered between the survival probabilities estimated by the two different models and there was no significant difference between them ( $t = 0.77, df = 8, NS$ ).

Based on the model-selection carried out by MARK, the constrained parameter model was accepted as the most adequate for simulating the population dynamics of *A. flavicollis*, according to which the two persistent populations have real effect on its survival probability. However, this effect was not so notable to cause statistically significant differences between the values. Of course the interaction among populations is one factor from the numerous background variables in charge of the changes in survival probability. As shown in the present experimental study the fluctuation in density and its effect was not as great as it was assumed by the interaction matrix constructed on the basis of demographic changes in the populations.

## Discussion

Research has been carried out in the forested study area since 1994. Regarding the changes in population dynamics, the sampling data of 1997 i.e. the fourth year of experiment proved earlier observations. This study year yielded much higher captures which was not only a result of the modification of sampling procedures but also an aftermath of favourable weather (mild winter and better spring conditions for the overwintered individuals as an initial generation). According to earlier studies if *A. flavicollis* reaches a demographic peak, it will show aggression against other species (Hoffmeyer 1973), though in grassland area it only passively effects the dispersion of the coexistent populations. The negative interaction could be a result of aggression evolving in the reproductive period (Sadleir 1965). Hansson (1971) claims that the negative relation between *A. flavicollis* and *C. glareolus* evolves because of their demand for similar food supply. In 1997, beside *A. flavicollis* the number of individuals of *C. glareolus* increased to a great extent. Ylönen and Viitala (1991) also observed the decrease in the densities of the two

species over the winter period as it was shown in the present study, and they declared that the two most important factors in population distribution are the availability of food supplies and the patchiness of the area. The growth in number of individuals justifies the statement of Grant (1974), where he claims that there is a 3-4-year periodicity in the demographic peaks of *C. glareolus*, which was also reflected in our earlier observations.

On having carried out researches on interactions between populations, Gliwicz (1988) investigated *A. flavicollis* and *C. glareolus* using the removal method, during which she reported two dispersion periods: in spring - early summer and in autumn. The rate of dispersion and the rate of population growth are in correlation, and their correlation is effected by the presence of reproductive periods. Social mechanisms depend highly on the habitat and its structure, on food supply and the animal's space of life, i.e. its residence resulting from its behavior and searching strategies. Each population showed two peaks during the one-year experiment, which is in accordance with the idea of more dispersion waves pointed out by Gliwicz (1988). The periods of peaks recorded in our sampling area are identical with those observed in Poland. The Spearman rank correlation indicated synchrony between the demographic trends of *A. agrarius* and *C. glareolus*. However, the interaction matrix based on the calculated partial correlation coefficient proved the existence of the assumed negative interaction between them. It has already been pointed out in our earlier studies that the negative partial regression value suggests competition relation (Horváth *et al.* 1996). Their interaction with respect to competition was discussed by Gliwicz (1981) in details, she indicated the negative relation between the two populations by calculating the Cole association coefficient. The interaction matrix based on her data is identical with the results of Polish researches. Flowerdew (1985) observed the demographic dynamics of *A. flavicollis* and he noted that its reproduction is effected by the density, the food supply and the climatic factors, but in the reproduction period (Feb/Mar - Oct), the population growth is not disturbed by the lack of recruits. The reproduction period of *A. flavicollis* begins in spring, peaks in autumn and decreases in winter, but its survival remains sufficient throughout the whole year. The over-reproduction in the autumn-winter period is suppressed by the density-dependent reproduction and dispersion of *A. flavicollis* females. In cases of abundant acorn yield and after probable winter mating the population number increases.

Considering the above mentioned competition relation, the survival of *A. flavicollis* was analysed assuming the constraining effect of the two coexistent populations. According to the model selection procedure we could prove the effect of the two coexistent populations but the survival probabilities estimated by the models did not differ significantly. The hypothesis that the constraining effect of density decreases the estimated values of survival could not be proved in every sampling period. A long-term observational period with extended data from several years could provide more precise results that would support our hypothesis more adequately. Among the background effects, the density of coexistent populations is only one factor that has influence on the survival rate. Several biotic and abiotic factors should also be examined when the changes in survival are to be appropriately interpreted.

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