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Estimating and modelling parameters of small mammal populations

Ph.D. theses

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1. Introduction

The expression "small mammals" is an umbrella term denoting non-flying terrestial mammals weighing less than 1 kg – a category whose members have proved to be practical subjects at the levels of individuals, populations, communities and ecosystems for the investigation of issues of theoretical ecology, and for testing hypotheses raised in practical nature conservation. Because small mammals can reach high abundance values, they allow their various sampling data to be analysed statistically with robust methods and in a wide range of ways. There are altogether 27 species of small mammals living in Hungary, belonging taxonomically to the order of insectivorous mammals (*Insectivora*) and that of rodents (*Rodentia*). They occur abundantly, and some of their species are characterised with periodic gradation, thus carrying the potential of causing serious damage in agricultural lands. It is important for agriculture to be able to foresee the population fluctuations of species prone to overpopulate. Some other species are important insect eaters or rare elements of the native fauna.

Hungary's protected broad-leaved forests and wetland habitats are ecologically optimal areas with high productivity and lush as well as highly varied macrophytic assemblages, which allow high biodiversity with a number of different small mammal species. In these forests with dense undergrowth and in the wetland habitats there are several small mammal species living together, this co-existence making them highly suitable for the study of their ecological demand, habitat selection and habitat use, as well as for the investigation of interspecific relationships such as microhabitat division, competition or predator-prey interrelations. From a nature conservation aspect, small mammal fauna, population and community analyses can provide important information

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for the conservation evaluation, qualification of particular habitats, or for producing adequate management plans. Being key elements of trophic relationships as food items for a wide range of protected raptors and carnivorous mammals, small mammals play an important role in the communities of the aforementioned habitat types. To learn more about their habitat choice and to provide faunistic descriptions of their habitats can yield important contributions of fundamental research knowledge to the better understanding of the ecological requirements of the various species, which, in turn, serves also the protection and proper conservation management of valuable habitats.

Regarding protected areas along river Drava, small mammals are a highly suitable group of indicator organisms for monitoring the status of remaining forest habitats with various vegetation structure (softwood and hardwood gallery forests), thus they are important monitoring objects. One disturbing phenomenon in habitats along the Drava is the fluctuation of water levels (in riverside gallery forests), and the high variation of groundwater levels farther off from the river, these dynamics considerably influencing the colonisation and re-colonisation activities of small mammals, and their resulting spatial patterns. The other highly important disturbing effect is forestry activities in the remaining forests. The population and community level monitoring of small mammals was performed as a sub-project of the distinguished biodiversity monitoring programme along the upper Hungarian Drava section between 2000-2006. As part of a Croatian-Hungarian cross-border interregional programme, this monitoring was continued in 2007, with an additional, Croatian forest fragment also being included in addition to samplings done in Hungary. Thus, the population and community level monitoring of small mammals was performed in three distinct habitats that differed in vegetation structure, forestry activities and conservation management. Small mammal research in the Drava Lowlands had been started well before co-ordinated biodiversity monitoring was launched or Duna-Drava National Park was established: small mammals have been trapped in a variety of habitats since 1994. Our research history thus covers more than a decade, including data series spanning several years as well as samplings with data form shorter periods in habitats of the upper Drava reach.

The present dissertation summarises the results of our small mammal investigations on the basis of two synbiological aspects (population biological and demographic changes, survival estimation and modelling). In the first subject we dealt with the population dynamics of common species, demographic changes and the estimation of population size. Secondly, in addition to analysing and estimating abundance and its changes over time, the dissertation deals also with survival estimation and modelling, which comprise one of the most speedily developing subjects of population biology. Part of this research can be regarded, most of all, as syn-phenobiological investigation, as we have revealed synbiological phenomena, and analysed the temporal-spatial changes of certain population biological characteristics. In several cases, however, we evaluated our data in respect of various background variables (e.g. weather factors, physiognomy of the vegetation in the analysed habitats), thus the revealed phenomena could be scrutinised in a causal interrelation.

2. Introducing the subject; Objectives; Raising the hypothesis

2.1 Population dynamics and demographic changes

As part of our research looking at small mammal populations the dissertation touches two basic issues in the field of a population dynamics and

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demographic changes. We have dealt with the long-term analysis of population dynamics in common small mammal species, providing an evaluation of differences between yearly patterns, fluctuation of abundance and the density dependence of demographic changes. Based on samplings with sufficient trapping investment we have tested the use of the combined (robust) method that works simultaneously with estimators designed for closed and open populations respectively.

The importance of external, density-independent factors and the cyclic nature of populations are long-debated topics in ecological studies produced about the temporal changes of animal populations. Long-term temporal patterns of population dynamics were analysed in the case of yellow-necked wood mouse (*A. flavicollis*), striped field mouse (*A. agrarius*) and bank vole (*C. glareolus*) populations, all being frequent species in the Bükkhát-forest. Our trapping survey between 1994-2003 was suitable for the analysis of demographic fluctuations of these frequent species.

The objectives of the 10-year study looking at population dynamics in the sampling site of Bükkhát forest were as follows:

1. Evaluate the temporal changes of capture parameters – total number of captures, number of recaptures, "minimum number alive" (MNA) – of the three character species of the studied lowland oak-hornbeam forests (*A. flavicollis*, *C. glareolus* and *A. agrarius*).

2. Investigate on the basis of the monthly data of 10 years, using an auto-correlation method, the temporal pattern of demographic changes of the three populations. No regular cyclicity has been demonstrated by Central-European studies of these species in this respect so far.

3. Analyse the assumed correlation between autumn and spring abundance values i.e. the density dependence of demographic changes.

In respect of the latter, the following null hypothesis and alternative hypothesis were put forward:

H_0: Autumn population sizes fundamentally determine spring densities, i.e. the degree of winter population decline.

H_A: Because of the high variability of small mammal demography within any year, the assumed linear correlation between autumn and spring abundance does not exist in the long run.

The use of capture-recapture models relying on random *k*-samples meant a departure point in the analysis of open populations. In the estimation of various parameters – especially in small mammal studies – stochastic models have become more widely used, besides direct census methods. In the improvement of the statistical evaluation of capture-recapture data an important line is the development of the combination of sampling methods. The first of such intentions leading to this direction produced a scheme that combined open and closed population models within a single analysis. How to schedule sampling while carrying out the programmes of the National Biodiversity Monitoring System and while working out its monitoring protocols seemed to be a problematic issue in planning the population-level monitoring of small mammals using live trapping. Accordingly, we tested for the suitability of Pollock's robust method, for which we used data of the three frequent species occurring in the Bükkhát-forest habitats (*A. flavicollis*, *A. agrarius*, *C. glareolus*).

In accordance with the principle of Pollock's robust method, primary samplings are done on a monthly basis, and between these intervals, the

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heterogeneity. The patch-level multistate modelling of microhabitats further supported our conclusions specified above, in that the pine vole highly prefers patches with closed vegetation type whose quality is an important ecological constraint in forming the spatial distribution patterns of the population, which is an important precondition for the strategically adequate utilisation of resources (food, shelter, home range), and thus for successful survival.

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populations were considered to be open. On the other hand, the short time between the five-day sampling sessions i.e. secondary periods allowed that populations were considered to be closed. In this respect, the following objectives were formulated in the combined estimation study:

1. To estimate the size of the studied populations from data of the secondary periods, using closed models both with the open and the robust method.
2. To statistically evaluate the fit of the open Cormack-Jolly-Seber (CJS) model and the closed models to our data, with regard to heterogeneity factors that may be considered in the case of closed models.
3. To statistically compare population size and population growth values estimated using the two methods, for all three studied populations.

2.2 Survival estimation and modelling

Survival is one of the major determining factors of the size and perspective of animal populations, therefore the estimation and modelling of survival has been widely discussed in population and conservation biological research studies looking at abundance changes of various ecological systems. In the recent 15-20 years it has become increasingly obvious from studies performing survival estimation and modelling that the quality of consequences drawn in these studies highly depends on the objective choice of the statistically adequate model required for data analysis. As the discipline developed, model selection became the central issue in the analysis of capture-recapture data. With a view to the known biology of a particular animal population, one needs to select from within a category of suitable models on which data analysis can be based.

In survival estimation and modelling, we first dealt with the long-term analysis of winter survival and its estimation with various methods. Two methods were used for estimating the survival of bank voles from capture data obtained in the Bükkhát forest habitat. First, the 28-day survival calculated on the basis of the exponential winter decrease of abundance, then we used life-history matrices produced from capture data from an eight-year period (1994-2001), to estimate survival using the MARK computer program. When calculating 28-day survival rates we looked at how the values depended on weather factors (average winter temperature, average winter precipitation, average snow depth), and on the biotic factors of the population (bodily condition of adult individuals, proportion of reproductive females in the autumn period). In addition to these we also looked at what effect did the autumn abundance of the population have on winter survival rates. Based on conventional winter survival estimation, bank vole capture data from a series of years were processed in line with the following objectives:

1. The winter survival of the trapped dominant bank vole population is analysed with the conventional method (calculating the 28-day survival rate), and it is investigated how winter survival rate was influenced by autumn population size.

2. It is investigated how much the calculated values of winter survival depend on abiotic (weather) factors.

3. The assumed effects of a number of biotic factors characterising the population are dealt with, including the physical status of adult individuals and the proportion of reproductive (gravid or lactating) females in the autumn periods.

immigration and colonisation. This rate of population growth and the resulting dispersion and spatial translocation in the case of bank vole is specially notable with a view to the fact that striped the field mouse that was competed out in our case is known in small mammal ecology as an expansive species with rapid population growth capacities.

From modelling survival and movement probabilities between the grids representing habitat islands in the metapopulation analysis of the European pine vole in the mosaic habitat beside Matty lake it could be concluded that one of the most important factor throughout the four sampling periods was the time dependence of estimated parameters (survival probability, movement probability between sampling sites or habitats). Among the constraint factors and effective factors incorporated in this global model it was distance that played a more important role rather than the quality of habitats representing the most suitable patch mosaic for the species.

At a microhabitat scale we could indicate that the most suitable microhabitat for pine voles was the patch dominated by Galium, as supported by data from all three grids. Among the three patches, the one with Solidago coverage was the microhabitat with the tallest vegetation, with the dominating goldenrod stand not thinning up even in the dry summer periods, unlike in the case of microhabitat patches characterised with monocotyledon plants or with the dominance of Galium. Pine voles are active mostly on the soil surface, moving about on their own paths, thus it is essential, for being able to avoid the risks of predation, that there is high plant coverage in the microhabitats used by them. From the results of patch preference calculations we concluded that the pine vole reacts to the alteration of microhabitat quality by the spatial rearrangement of individuals, i.e. it shifts to the use of optimal patches at the finer spatial scale, thus presenting a coarse grained response to habitat positive linear correlation was found between the size of autumn population and abundance in spring. The 28-day winter survival values calculated on the basis of exponential winter population loss was found to be in correlation with average winter temperature and average snow depth. The result of modelling performed using the MARK program was the same as what was revealed by performing the traditional way of winter survival calculation. Data matrices generated from yearly capture-recapture values were suitable for modelling the effects of the assumed limiting co-variables on winter survival. Model selection was done on the basis of AIC-values. Statistical results of model selection showed that the winter survival of bank voles was positively influenced by higher winter temperatures and by the presence of snow cover. Among the biotic variables, it was the mean body mass of adult individuals i.e. the physical condition of adults in the autumn, and the proportion of reproductive females at that time in the population that determined the estimated value of survival. Thus, our results from estimating and modelling winter survival proved our hypothesis we had raised in respect of the bank vole population.

When estimating survival, reproduction and population growth rate, our results showed that it was population growth resulting from the survival of adults that had the greatest importance in forming the growth tendencies in dominant rodent species of various forest habitats. In respect of the studied reforested habitat we emphasised that the decline of striped field mouse population, a species preferring highly dense vegetation, was positively influenced by bank voles intensively spreading in the area. This finding on expansion dynamics was supported by our calculations of population growth rate: expansion was proved mostly by the high values obtained for new individuals appearing in the population. Accordingly, the considerable rate of bank vole population growth in the reforested habitat was mostly due to

As regards the dependence of survival rate on biotic and abiotic factors, the following hypotheses are raised:

H_1: 28-day survival rates change in relation with autumn abundance values.

H_2: 28-day survival rates change in relation with weather parameters.

H_3: Winter survival depends on the physical condition of adult males and females.

H_4: Because the social structure of bank vole populations is fundamentally determined by female individuals, survival rates will follow the proportion of gravid and lactating females.

As part of further analyses of bank vole populations, winter survival was estimated and modelled based on life-history matrices of yearly capture data within the studied period (1994-2001), in line with the following objectives:

1. Survival is estimated for winter periods, based on open Cormack-Jolly-Seber (CJS) models, and the suitability of capture- or life-history matrices interpreted for years is tested.
2. The effect of abiotic (weather) and biotic (physical condition, proportion of reproductive females) variables acting as constraint factors on winter survival is modelled.
3. The 28-day winter survival values calculated from standardised MNA-values are compared to results obtained by estimations with MARK.

Looking at the latter objective we tested how much the results from modelling with MARK are in line with results obtained for calculations of 28-day winter survival and with the correlation analysis between these values and the studied co-variables (biotic and abiotic variables).

A turning-point in capture-recapture data evaluation was the retrospective analysis of capture history; based on this approach it became possible to estimate true population growth between study periods. Furthermore, this method allows the researcher to see at what degree the various demographic parameters actually contributed to the growth of population size. This method was used for the population dynamic analysis of the dominant rodents (yellow-necked wood mouse, striped field mouse and bank vole) in the three different forest habitats selected along the Hungarian upper Drava section, with view to the objectives specified below:

1. Performing the simultaneous estimation of survival, population increment and, together with these, population growth rate, for populations of dominant species in the various sampling sites.
2. As part of the comparison of areas, investigate and perform the modelling of the time dependence of survival and population increment, as well as statistically evaluate the estimated parameters.
3. As part of the comparison of co-existing populations in a particular area, draw conclusions based on the estimations about the temporal patterns of population growth or decline.

For survival estimations, we finally applied metapopulation approaches of multistate models. We studied the space use of the European pine vole (*M. subterraneus*) in two landscape scales in a mosaic habitat complex besides the Matty lake, on the basis of a five-year trapping period. First we considered larger the sample areas as habitat islands, then looked at the habitat selection of the same species on a finer, microhabitat scale. As well as for patch preference calculations, we considered the mapped microhabitat patches for survival estimations, too.

density values late into the autumn was partly due to the favourable weather conditions in autumn 1996 (higher average temperature, rainfall, no frost in November). The significance of this irregular year was reflected also in the regression analysis of abundance values from the autumn and the successive spring. The hypothesis that autumn abundance values are crucial in forming abundance relations in the spring i.e. at the onset of the reproductive season had to be rejected in all sampling years. This is due to the atypical years with favourable autumn and mild winter weather, allowing reproduction late in the autumn or into the winter. Only when these atypical years were left out from our calculations, did we receive the expected linear correlation in the case of the yellow-necked wood mouse, i.e. that autumn population size determined spring densities.

Our results obtained with Pollock's robust method proved to be in line with Pollock's simulation which indicated a greater difference of Jolly-Seber estimators. Based on our monitoring experience, it seems reasonable to select more than three primary periods. As to secondary periods, our experience have showed that five sampling nights per one period are essential for the analysis of small mammal capture-recapture data with robust statistical methods.

4.2 Survival estimation and modelling

As part of survival estimation and modelling, first we dealt with the winter survival of the bank vole. A hypothesis was first raised in respect of the 28-day survival calculated on the basis of winter exponential population decline, namely that the survival of the autumn population has determining effect on winter survival, but we could not prove this assumption from data of the study periods. However, apart from the years with exceptional condition,

4. Results and evaluation

4.1 Population dynamics and demographic changes

The long-term population dynamic analysis of the common rodent species of the Bükkhát-forest (yellow-necked wood mouse *A. flavicollis*, striped field mouse *A. agrarius* and bank vole *C. glareolus*) revealed that the fluctuation recorded in the case of the bank vole showed a 3-year repetition of waves with large amplitude, suggesting quasi-cyclic population dynamics. Similar result was obtained for the yellow-necked wood mouse: three higher abundance peaks were recorded, forming after three and four years, respectively. However, in the case of the striped field mouse population, unlike in the two other species, regular oscillation was revealed in the majority of the analysed 10 year period, and this oscillation was continuously fading out. Thus, peculiar annual population dynamics were recorded with the abundance peak occurring in August-September. The auto-correlation analysis greatly supported what had been found out already about the striped field mouse population in that this species has yearly cycles with autumn peaks followed by a spring population collapse and than another cycle starting over with the peak setting in autumn.

As regards winter population decline, considerable reductions of abundance were recorded in each of the winter periods for the yellow-necked wood mouse and the striped field mouse. In bank voles, four winter seasons yielded significant drop in numbers, mostly coinciding with severe winters, but there was one winter period when abundance was increasing instead of declining. The reason for population growth in the winter of 1996-1997 was that the climbing of small mammal density values started quite late in the season in the preceding year (1996). Accordingly, autumn maxima, too, formed later in the season, and remained lower than in the former years. The growth of

Accordingly, the spatial organisation of the European pine vole was investigated on the basis of two problem areas. One of them was how survival, estimated for particular subpopulations, was determined in this species preferring closed vegetation by the mosaic pattern of habitats or their smaller-scale vegetation patches i.e. microhabitats. For this issue, multi-state models make it possible to investigate the role of movements between habitats or between patches within the same habitats in survival modelling. In this field, the following null hypothesis and alternative hypothesis were formulated:

H_0: In the case of the European pine vole, the quality of habitats and microhabitats or vegetation patches (i.e. their plant composition and physiognomic structure) have greater importance in the survival of particular subpopulations than the movement probabilities of individuals between habitats or patches and the distance factor determining such probabilities.

H_A: The assumed constraint factors (habitat quality and distance factor) do not have an influence on survival.

The other problem area was the analysis of microhabitat-scale patch preference, during which we analysed the microhabitat use of the pine vole on the basis of available patch areas and actual patch use. In this issue, the primary question was whether the response of the pine vole population to habitat heterogeneity in the studied mosaic-pattern land is coarse-grained or fine-grained.

Based on the two question areas and the hypotheses we looked at European pine vole capture data with the following objectives in view:

1. Statistically evaluate capture results of pine voles trapped in the mosaic-pattern habitat besides the Matty lake.

2. Provide estimations of survival and movement probability between habitat complexes and among microhabitats, using multistate models.

3. Perform a modelling for the constraint factors of multistate models (such as the effects of habitat quality and distance), and for the effects of quality and size of microhabitat patches.

3. Material and methods

3.1. Study areas

The synbiological analysis and monitoring of small mammals was performed between 1994-2007 in habitats of Baranya and Somogy counties, along river Drava. The first sample area was selected in 1994 in Baranya, in a lowland oak-hornbeam forest habitat where small mammal studies were then continued for 10 years. In 1997 we performed the small mammal fauna survey of a mosaic habitat beside the Matty lake in the lower Drava section, which was followed by the analysis of the spatial and temporal pattern of small mammals in this lakeside habitat with heterogeneous vegetation for another six years. As a separate programme beside regional and national level projects of the Hungarian National Biodiversity Monitoring System, the biological monitoring of the upper Drava reach was launched, as part of which we started the monitoring of small mammal populations in 2000, in additional habitats. Two sampling sites were selected in Lankóci-forest near Gyékényes, differing from each other in their vegetation structures (a strictly protected, closed alder gallery forest, and a neighbouring reforested area). Furthermore, trappings were performed in 2007 along the upper Drava reach in Croatia, where small mammals were studied in Repas forest, a lowland oak-ash-elm gallery forest

"survival and recruitment" model was applied for estimating survival and recruitment together.

Population changes of the pine vole beside the Matty lake was followed between 1998-2003, with the help of three sampling grids (A, B, C) representing three different patch compositions. Based on data from 5 years, Wilcoxon's paired test was used for comparing capture parameters of the pine vole in the three sampling sites. The occurrence of this species in the quadrates was tested using independence tests, whereas microhabitat preference was analysed with the help of Ivlev's index.

Before looking at multistate models, we first analysed the usage of the sample areas by the rodents. For this purpose, we used individuals captured more than twice. It was our data from 2002 that proved to be the most suitable for an analysis with multistate models. As a first step, we considered the three sampling grids in the mosaic-pattern habitat beside the Matty lake to correspond with three "layers" or "isolatum areas". In the next part of multistate modelling, we performed the modelling of survival and movement probabilities between microhabitat patches within individual sampling sites. Based on capture parameters, here again we used our data from 2002, and generated the input matrix of multistate models from the recorded presence of the small mammals in the three patches of sample area C (E: Monocotyledons, G: Galium, S: Solidago). On the basis of the three most highly utilised patches, it was reasonable to perform modelling of the microhabitats too, within the habitat complex represented by our sampling grids, because if time dependence or constancy is assumed, there is less variation in movements with a minimum of three patches, which fact considerably reduces the number of model parameters.

respectively, in the autumn period, and the proportions of these two categories were treated separately.

For modelling the survival probability of the bank vole the most recent version of the program MARK was used. MARK provides multiple possibilities for erecting the models which we categorised into two different groups in our data processing. The first group of models was made up by the Cormack-Jolly-Seber (CJS) basic model and its derivatives. The CJS model is the basic one among open population models where survival and trappability change with time. If it is assumed that either survival or trappability or both of these parameters are constant in time, then three additional, reduced models can be differentiated. The other group of models is made up by constraint factor models operating with biotic and abiotic factors. The most economical model that could be interpreted biologically was derived based on AIC-statistics from the global model containing the highest number of parameters.

Estimations of survival, population increment and growth rate were performed for populations of the character species (*A. flavicollis*, *A. agrarius*, *C. glareolus*) of three different forest habitats along the Hungarian upper Drava reach studied in 2007. As part of the analysis, first we specified the seasonal number (i.e. cumulated for spring and autumn, respectively) of captures in the three studied species, and the monthly values of relative proportions of the species. The seasonal differences between capture data were analysed using χ^2-test, whereas for investigating the differences in the proportions of the various among different habitats variance analysis was applied (Kruskal-Wallis ANOVA). Parameters of population dynamics i.e. survival, growth rate and recruitment resulting from births and immigration were estimated using the Pradel models of the program MARK. Of the four Pradel models, the

located in a higher terrain than the floodplain, this habitat type representing at the same time areas under forestry management.

3.1. Trapping methodology

The method applied in each of the sampling areas was capture-mark-recapture, with the same box-type live-traps (75x95x180 mm). Just like the traps themselves, the trapping technique was also alike in all cases: bacon and cereals mixed with aniseed extract and vegetable oil were used as bait. The traps were checked twice daily in each of the forest habitats (Bükkhát-forest, Lankóci-forest, Repas-forest): from 7^{00} in the morning and from 19^{00} in the evening, with the traps being left triggered during the day, because they did not heat up considerably inside the forest. However, the traps were left open for the day hours in the summer period beside the Matty lake, thus we had data from the morning trap checking sessions that resulted from greater nocturnal small mammal activity. The same code table was used for marking in all the sample areas.

3.3. Data processing; statistical and modelling methods

A separate database system was developed under *Microsoft Access* for storing and processing multiple capture and recapture data. SQL filtering of capture-recapture data made it possible or us to organise and process our data in a versatile and effective way. Each record of the database corresponds with data of one captured individual (either marked or unmarked), and the structure of its attributes, fields and associations with other data tables can be continuously widened.

3.3.1 Population dynamics, demographic changes

The 10-year long (1994-2003) population dynamic analysis of the three character species of the studied Bükkhát-forest (*A. flavicollis*, *C. glareolus* and *A. agrarius*) was based on the "minimum number alive" (MNA) values (obtained from Manly-Parr' diary of captures) standardised for 100 trap nights. The comparison of MNA trends for the 10-year period was done for each of the species pairs, for which Spearman's rank-correlation was applied. The temporal changes of recapture rates and the relative proportions of the obtained values were analysed for the three populations. The long-term sampling performed on a monthly basis yielded a data set suitable for the investigation of cyclicity of the three populations. Auto-correlation tests were performed using the SPSS 7.5 program. The assumed correlation between spring and autumn mean MNA values was tested for using regression analysis.

Parameters of the aforementioned three populations were further investigated using Pollock's robust method. In this combined type of estimating method the populations were considered to be closed during the 5-day monthly trapping sessions, therefore the capture data recorded for the sampling days were evaluated with the closed estimation method of the program CAPTURE. Thus, population sizes were estimated based on capture probabilities that were in highest accordance with the empirical data series. As suggested also by natural conditions, the populations were considered to be open between the primary periods i.e. monthly samplings. Thus, the other parameters of the population – survival probability (ϕ_i) and birth rates (B_i) – were estimated from population sizes (N_i) calculated for the primary periods, using equations available in the Cormack-Jolly-Seber method. The standard errors (±SE) of estimated values were given in the case of both estimation methods, as well as the value of the coefficient of variation (cv%) expressing

the relative exactness of the estimation. Wilcoxon's paired tests were used for making comparisons between population sizes obtained from open and closed estimators, different closed models, and calculated birth rate values.

3.3.2 Survival estimation and modelling

During our monitoring activities in Bükkhát-forest, winter survival was analysed in the case of the bank vole population living there. Based on the 10-year long study of population dynamics, this species was found to be the most typical representative of rodents in the oak-hornbeam forest, its population going through a considerable drop only in the very last year of the studies. The winter survival of this species was thus evaluated with the last year being omitted, on the basis of a data matrix covering eight years (1994-2001). First, 28-day survival rates were estimated based on the assumption that winter abundance decreases along an exponential function. For this estimation, standardised MNA values, obtained for a given autumn month (September, October) and the first spring month (March) were used. So as to be able to look at the combined effect of biotic and abiotic constraints as well as the importance of individual factors, multiple regression analysis was used. Values of the abiotic (weather) variables for Baranya county (winter average temperature, winter average precipitation, average snow depth) were made available for us by the Hungarian Meteorological Service (Országos Meterológiai Szolgálat – OMSZ). Among biotic variables, physical status was characterised by providing values of mean body mass of adult individuals, calculated from body mass values of captured individuals as measured in the field. The proportion of reproductive females in the autumn population was separated as an important variable characterising the population; this was divided into two segments: the presence of gravid and lactating females,