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AGE- AND DENSITY DEPENDENT SURVIVAL IN A YELLOW-NECKED WOOD MOUSE *APODEMUS FLAVICOLLIS* (MELCH.) POPULATION OF A FOREST HABITAT

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Horváth, Gy. and Wagner, Z. (2003): Age- and density dependent survival in a yellow-necked wood mouse *Apodemus flavicollis* (Melch.) population of a forest habitat. — *Tiscia 34, 33-39.*

Abstract. A 10-month live trapping investigation was carried out in a *Querco robori-Carpinetum* habitat in south-Hungary in 1997. During a total of 6050 trap-nights with 5-night sessions, 306 *A. flavicollis* individuals were captured and marked, and for their demographic parameters, age-dependent survival models were tested using the JOLLYAGE program. The estimators in the program recorded a September population maximum for *A. flavicollis*. Adults had significantly higher survival rates which decreased as the population grew. Survival probability and capture probability were significantly correlated with age. Based on goodness-of-fit tests our data fitted all three models of JOLLYAGE; the group of age-dependent models proved to be appropriate for our *A. flavicollis* capture data. A comparison of the models revealed that the general model A2 rejected B2 which is reduced in its calculation of survival rate, but it did not reject model D2 which uses constant capture and survival probability. Accordingly, based on our model selection results we consider the simplest D2 model with reduced parameters to be the most appropriate.

Keywords: Apodemus flavicollis, survival analyses, age-dependence, JOLLYAGE

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Introduction

The "life-history" analysis of the subject species of the present study (e.g. Gliwicz *et al.* 1968, Bujalska *et al.* 1968, Bujalska 1975), as well as several case studies published in this field and presenting results primarily about *Peromyscus* species (Wolf 1986, Millar 1989, Duquette and Millar 1995) and New-World *Microtus* species (Mihok 1984, Boonstra 1989) showed that variations in the fitness in a population is basically determined by variations in fecundity, survival, or both (Lebreton *et al.* 1992). The probability of survival is influenced, on the one hand, by characteristics of the individual such as age, sex, weight, genotype and phenotype, and, on the other hand, by abiotic environmental variables together with inter- and intraspecific competition and predation. It is, thus, important in testing an ecological hypothesis to use estimates of survival so as to better understand the dynamics of a studied population (Lebreton *et al.* 1992). It is essential to test for possible variation in survival and capture rates among different age groups (Pollock 1981).

Regarding small mammals, in Europe it was Paradis *et al.* (1993), using the program SURGE, to analyse sex- and age-dependent survival of the Mediterranean pine vole (*Microtus duodecimcostatus*). Also, Paradis and Croset (1995) looked at to what degree the demographic changes in a habitat were determined by "source-sink" dynamics. Different survival rates have been shown to exist in habitats differing in food availability (Paradis 1995).

In a population of *A. flavicollis* Bobek (1973) analysed the effect of density on survival, based on data from trapping in a *Tilio-Carpinetum* forest habitat. He demonstrated a decrease in survival rates at high population density. He also found that mortality rates decreased with increasing age. Earlier investigations proved that reproductivity, abundance and, through these, population dynamics are determined by habitat structure and concordant food availability. Gosálbez and Castién (1995) investigated the above parameters of *A. flavicollis,* during two years differing in forest seed production and showed that the amount of available food had an effect on the number of reproductive periods in females and on the level of testicular activity in males.

Our sample area was a *Querco robori-Carpinetum* forest habitat situated in South-Hungary, with *A. flavicollis* being a dominant component of the resident rodent community. Based on capture results in 1997, our aims have been to demographically analyse the *A. flavicollis* population found there and to test for a possible effect of age on survival.

Material and methods

Our study area is located between the villages Vajszló and Páprád (N 45° 51', E 18° 00') in county Baranya, on the Dráva Lowlands. The 1-ha sampling quadrat was set up in a hornbeam-oak (*Querco robori-Carpinetum*) forest section, where the height of the upper canopy was around 25 m, with the characteristic species being *Quercus robur, Fraxinus angustifolia* and *Robinia pseudoacacia*. The lower canopy layer was 4-10 m high where *Carpinus betulus, Ulmus minor, Fraxinus angustifolia* were characteristic. The shrub layer of 1-4 m height consisted of *Cornus sanguinea, Ligustrum vulgare, Crategus monogyna, Sambucus nigra* and young specimens of *Robinia pseudoacacia*. Patches of the area with high undergrowth of 90-100 % cover were characterised by species indicating nitrogen-rich habitats.

The sampling quadrat was oriented approximately along the northeast-southwest geographic axis. The grid covered one hectare with 11 by 11 box-type live traps at an equal distance of 10 m from each other. Bacon and whole cereals were used as bait. Data from 10 months in 1997 were processed. Five-night sampling sessions were repeated monthly from February to November 1997, yielding 6050 trap nights. Traps were checked twice daily (8^{00} CET and 20^{00} CET). For individual identification of the animals the removal of the first knuckle of toes (O'Farell 1980, Nichols and Conley 1982) was used, and the following data were recorded: species, sex (in females gravidity or lactation too), age and weight. Age was determined based on external features and weight, with the help of the study by Haferkorn and Stubbe (1994). The computer program JOLLYAGE (Hines 1988) was used for testing age-dependent survival models and to estimate survival and population size.

For age dependent modelling the following conditions are required: all individuals of a particular age group (v) have equal capture probability ($p_i^{(v)}$), if the individual is present alive in the population at the time of the i^{th} sampling (i=1, 2,...,k) (1); all marked individuals of a particular age group (v) have equal survival probability ($\Phi_i^{(v)}$) during the trapping period between i and (i+1), if the individual is present alive in the population at the time of the i^{th} sampling (i=1, 2,...,k) (2); no markings are lost during the study and all are correctly identified upon capture (3); emigration is constant (4); the age of each individual is identified correctly (5).

Before the estimations are done, it is essential that possible ratios of survival and capture rates of the various age groups can be tested for. This can be done, as Pollock (1981) indicated, by using a series of chi-tests relying on proper statistical data. The program JOLLYAGE uses a model assuming three constant survival and capture probabilities. These models use a limited number of parameters which results in a high accuracy of estimated values, because the number of estimations is smaller. They simplest reduced-parameter, age-dependent models apply two age-groups (0 and 1, or juvenile and adult), and assume that the time necessary for individuals to enter adult category from the juvenile one equals the time between the samplings (usually 1 year). Brownie *et al.* (1986) developed two such models, which are the generalized versions of Models B and D calculated by the JOLLY program (Hines 1988) applying the Jolly-Seber estimator for open populations, where juvenile and adult animals are marked in each period. Following the terminology of the JOLLY program, we refer to these as Models B2 and D2. These models, with Pollock's (1981) age-dependent model added, are the following:

In model A2, or the generalized Pollock Jolly-Seber model l = 1; and the model assumes a time-dependent survival rate for both juveniles and adults ($\phi_i(0)$), and ($\phi_i(1)$), and a time-dependent adult capture probability (p_i (1)).

Model B2 assumes constant survival rate for both juveniles and adults (ϕ_i (0) = ϕ (0) , ϕ_i (1) = ϕ (1) , i = 1,..., k-1), and time-dependent capture probability (p_i (1)).

Model D2 assumes constant survival rate for both juveniles and adults (ϕ_i (0) = ϕ (0) , ϕ_i (1) = ϕ (1) , i=1,..., k-1) and constant capture probability (p_i (1) = p (1) , i = 2, ..., k).

The detailed description of estimations and tests applied in model selection is presented by Brownie *et al.* (1986), and its supplemented version, for developing computer algorythms, appears in Brownie (1985). These algorythms were combined and were incorporated in the JOLLAGE program, which (in addition to analyses described above) also provides estimation for B2 and D2 models, "goodness of fit-tests", and homogeneity tests among models (χ^2-test).

All three models of the program were applied and tested with capture data of *A. flavicollis* (Pollock *et al.* 1990).

From the standard error of estimated population size (N_i), the relative accurateness of the estimation, i.e. the variation coefficient of N ($cv(N)$) was calculated (White *et al.* 1982).

Results

During the 6050 trap nights, 306 *A. flavicollis* individuals were marked. Both our capture results and the JOLLYAGE output parameters showed that the number of adult specimens was higher than that of juveniles (Table 1). The appearance of a relatively large number of juvenile specimens occurred in June, since the reproductive period reached its peak around the end of spring. There were no young individuals in the last two (autumn) study months.

Table 1. Capture parameters under the output of JOLLYAGE for *A. flavicollis*

Sampling period	m_i	n_i		R_i		r_i		z_i
	Adult	Adult	Juv.	Adult	Juv.	Adult	Juv.	
February	0	18	0	18	0	15	0	0
March	11	21	0	21	0	13	0	4
April	11	19	3	19	3	11	0	6
May	12	35	9	35	8	22	0	5
June	20	35	25	35	24	19	4	7
July	19	32	1	32	1	14	0	11
August	18	53	8	53	8	26	1	7
September	27	68	8	65	8	37	0	7
October	41	56	0	51	0	27	0	3
November	30	39	0	38	0	0	0	0

m_i : is the number of marked individuals caught in sample i
n_i : is the total number caught in sample i
R_i : is the number in the ith release
r_i: is the the number of the R_i that are subsequently recaptured
z_i: is the number of marked individuals present at the time of sample i, not caught in sample i, but subsequently recaptured

The age-dependence of survival probability and capture probability was proved by the significant χ^2 values of the 2×2 contingency tables, in four sampling occasions. The test on the entire sampling period also supports the age-dependence of the two probability parameters (Table 2).

JOLLYAGE tests the capture parameters of the two age-groups with a series of goodness-of-fit ('GOF' that is) tests, in two steps (in accordance with capture histories): with a 2×3 and a 2×4 contingency table, using which it compares the capture rates of each age group. Our data of the 2×3 contingency table were homogenous with the theoretical values in all of the periods and, of course, in the total χ^2 value as well (χ^2 = 9.17, P = 0.327). In the case of the 2×4 table the test did not work in all of the periods, but eventually it showed homogeneity between our data and the theoretical values (χ^2 = 9.17, P = 0.327). The results of the goodness-of-fit test comparing the three models are shown in Table 3.

Table 2. Contingency chi-square test for age-dependent survival and capture probabilities

Sampling periods (i)	Contingency table		Test statistics		
	$r_i^{(0)}$	$R_i^{(0)} - r_i^{(0)}$			
	$r_i^{(1)}$	$R_i^{(1)} - r_i^{(1)}$	χ^2	df	P
5. (June)	22	0	10.29	1	0.0013
	13	8			
6. (July)	19	4	8.47	1	0.0036
	16	20			
8. (September)	26	1	3.76	1	0.0523
	27	7			
9. (October)	37	0	9.23	1	0.0024
	28	8			
Overall test statistics			31.77	4	< 0.001

$R_i^{(0)}$: the number of juvenile individuals released after the ith sample
$R_i^{(1)}$: the number of adult individuals released after the ith sample
$r_i^{(0)}$: the number of the $R_i^{(0)}$ that are captured again at least once after the ith sample
$r_i^{(1)}$: the number of the $R_i^{(1)}$ that are captured again at least once after the ith sample

The goodness-of-fit test of model A2 shows that the age-dependent A2 model fit the data, implying that the group of age-dependent models is appropriate for the data of *A. flavicollis*. The test did not reject models B2 and D2 either, therefore it is concluded that all three models fit the data. When the models were compared, model A2 did not reject the simpler model D2, while in the pair B2 vs. A2 a difference with 10% error was found between the two, suggesting that at this low level of significance A2 rejected model B2 which is simplified in its survival estimation. Accordingly, both A2 and D2, the latter using constant capture and survival probability, were appropriate for the analysis of the sample *A. flavicollis* population.

The age-specific survival estimates of models B2 and D2 were more accurate than the age- and time-dependent estimates of A2. The survival values of model D2, especially those calculated for adults, are close to the mean values of A2. The test between models B2 and D2 is not valid, and it was shown that model A2 rejected B2, whereas it did not reject D2. Consequently, among the age-dependent reduced-parameter models, it is the simpler D2 model fitting our data that appeared more applicable in analysing the population of *A. flavicollis*.

Table 3. Results of goodness-of-fit tests and tests comparing models for *A. flavicollis*

	Goodness-of-fit test				Test between models		
Model	χ^2	df	*P*	Models	χ^2	df	*P*
A2	13.26	11	0.2764	B2 vs. A2	12.33	7	0.0899
B2	25.6	18	0.1092	D2 vs. B2	8.89	8	0.3516
D2	33.23	26	0.1556	D2 vs. A2	19.96	15	0.1734

Based on the above findings of model selection, results of model D are shown: the numbers of marked individuals in the trapping periods appear in Fig. 1. There are two maxima in the demographic trend of *A. flavicollis* in 1997, based on the estimated number of marked animals. The first peak in July drops back by August, and the second maximum in the proportion of marked individuals occurs in autumn.

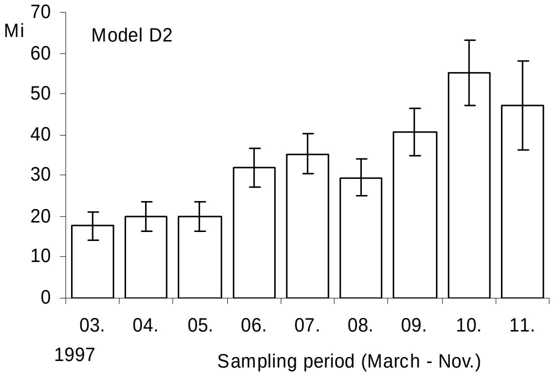

Fig. 1. Estimated numbers of marked individuals in the sampling periods for *A. flavicollis* (with 95% confidence intervals also indicated).

The population size estimates calculated using model D do not show the bimodality in the number of marked individuals, which is a consequence of the higher number of recaptures (Fig. 2). The peak of *A. flavicollis* numbers occurred in September (ND2 = 105.07).

The relative accurateness of population size was tested by calculating the coefficient of variance (Fig. 3). Values of model D2 are well below 20 %, which means that the estimated values of population size are acceptable.

Model A2 of the program JOLLYAGE calculates survival rates of both adults and juveniles, and the capture rates of adult animals for each period. Model B2 operates with a constant survival rate in both age groups, while it calculates adult capture rates for each period. Model D2 gives a constant survival rate for both age groups and a constant value for capture probability of adults. Survival rates are given for all models (Table 4). Adult and juvenile survival rates were compared using t-test, which revealed that model A2 produced significantly higher survival rates of adult individuals (t = 11.41, $P < 0.001$). Similarly, the combined results of models B2 and D2 showed that adult survival rate was the higher.

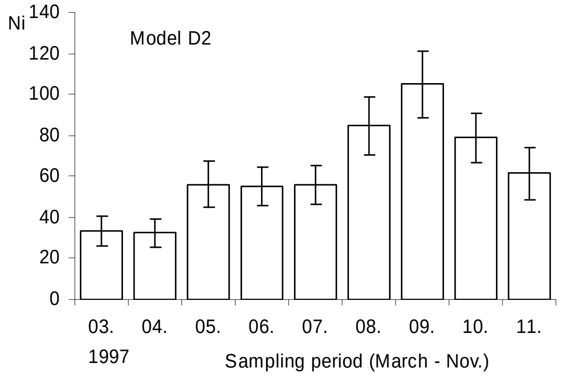

Fig. 2. Estimated population size under the Model D2 of JOLLYAGE for *A. flavicollis* (with 95% confidence intervals also indicated)

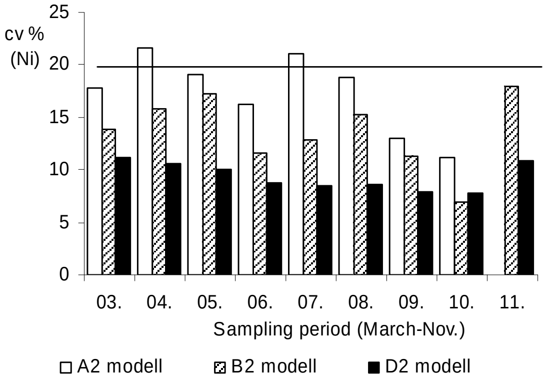

Fig. 3. Coefficient of variation of the population size estimators (A2, B2 and D2 model)

Survival rates calculated by model A2 decreased as numbers of *A. flavicollis* grew (Fig. 4). However, the number of sampling months was not sufficient to prove the negative correlation between the number of marked individuals and survival rates, therefore this relationship cannot be considered significant. The effect of density, despite the lack of significance in the correlation, should be viewed as an important factor, in addition to age.

Table 4. The survival and capture rates of *A. flavicollis* under the models of JOLLYAGE

Model	Sampling period	Adult survival rates $\phi_i^{(1)}$ (S.E.)	Juvenile survival rates $\phi_i^{(0)}$ (S.E.)	Adult capture rates $p_i^{(1)}$ (S.E.)
A2	1. (February)	0.96 (0.13)	* (*)	
	2. (March)	0.76 (0.16)	* (*)	0.64 (0.14)
	3. (April)	0.68 (0.14)	-	0.52 (0.14)
	4. (May)	0.76 (0.12)	-	0.61 (0.13)
	5. (June)	0.78 (0.16)	0.24 (0.11)	0.61 (0.11)
	6. (July)	0.56 (0.12)	-	0.44 (0.11)
	7. (August)	0.57 (0.09)	0.14 (0.13)	0.56 (0.11)
	8. (September)	0.60 (0.07)	-	0.69 (0.09)
	9. (October)			0.88 (0.06)
	Mean	0.71 (0.03)	0.06 (-)	0.62 (0.04)
B2	2. (March)			0.70 (0.12)
	3. (April)			0.57 (0.12)
	4. (May)			0.61 (0.12)
	5. (June)			0.64 (0.10)
	6. (July)			0.52 (0.09)
	7. (August)			0.57 (0.10)
	8. (September)			0.65 (0.09)
	9. (October)			0.83 (0.08)
	10. (November)			0.76 (0.11)
	Overall	0.67 (0.03)	0.12 (0.05)	0.65 (0.11)
D2	Overall	0.69 (0.03)	0.11 (0.05)	0.64 (0.04)

* Mathematically unvalid

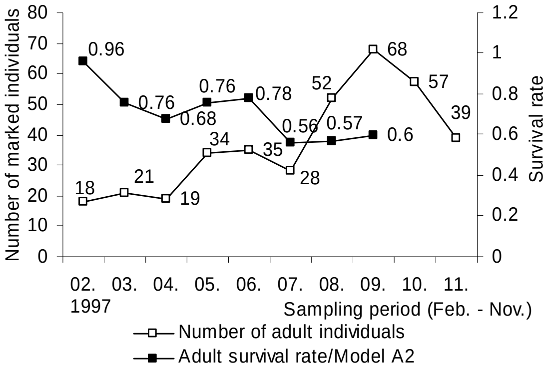

Fig. 4. Number of adult individuals and survival rate in different sampling periods

Discussion

The GOF-analysis of *A. flavicollis* capture data showed that the application of age-dependent model-groups of the programme JOLLYAGE was reasonable, since we proved the age-dependence of survival- and capture probability, the testing of which was thought to be important also by Pollock *et al.* (1990). The capture parameters of *A. flavicollis* were adequate for the condition system of the model, with the GOF-tests yielding homogeneity for all three models. Following Lebreton *et al.* (1992) we first analysed the application of the global model in our model selection, then, based on the homogeneity tests between the models, we chose the simplest, reduced-parameter model. Besides the reduced-parameter D2 model, the global A2 model also appeared appropriate, yet based on the above finding we decided to rely on the estimated values of the simpler D2 model. In the case studies cited by Pollock *et al.* (1990) the probability of the loss of a certain proportion of the individual markers was mentioned as a factor likely to distort JOLLYAGE results. In our case when *A. flavicollis* individuals were toe-clipped, marking was permanent, thus the possibility of the loss of the marker could be exluded.

In the annual cycle of *A. flavicollis* population dynamics, abundance maxima usually occur between August and October (Flowedew 1985). Jensen (1975), however, recorded that peak density in a beech forest occurred later, in November. The results of this study confirm the former period, since the maximum value of estimated population size was obtained for September. The subsequent drop in numbers is remarkably influenced by the amount of available food. In cases when food is abundant in the habitat and there is winter reproduction, population size can grew even through the winter (Bobek 1973). Although in our study we analysed only one period, there is evidence from earlier studies for big differences between annual peaks, which, again, is related with food availability and the length of the breeding period (Adamczewska 1961, Hoffmeyer and Hansson 1974, Montgomery 1980).

Our estimated survival rates, obtained within a one-year period, decreased as population density grew. This negative correlation was not significant but was in accordance with similar findings by Bobek (1973) for the same species. The growth of density raises the question of how the spatial organisation and the age-structure of the population, and the dynamics of immigration and emigration change. There is relatively little information about the spatial organisation and movement patterns of *A. flavicollis* (Wolton and Flowerdew 1985). We can assume that as density grows, space utilisation also increases, which will, beyond a certain degree of food source decrease, lead to increasing emigration. At the same time, appropriate food availability for individuals within the habitat, together with intraspecific relations within the population and territoriality in home ranges will restrict the number of recruitment individuals. Accordingly, survival as estimated from capture-recapture will also decrease, thus is density-dependent. When studying mainly the spatial relations and behaviour, Mazurkiewicz and Rajszka-Jurgiel (1988) attributed primary role to food source in the forming of density. Their analysis of emigration and immigration showed that considerable dispersion in search for food occurred at low levels of density, which finding appears to contradict the above assumption. Their case study, however did not include estimations and comparisons of survival which has prime importance in the density-dependent explanation of spatial and temporal patterns of populations.

Obviously, a longer trapping period would have provided more data for proving the density-dependence of survival. However, within the same habitat, enormous differences between population sizes of the years could have resulted from variations in the amount of available food and changes in intra- and interspecific relations, which can greatly influence values of survival estimated from capture-mark-recapture data, and can thus considerably distort statistics that could prove the density dependence of survival.

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