



Quantifying whether different demographic models produce incongruent results on population dynamics of two long-term studied rodent species

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ABSTRACT

1. Population density (ind/ha) of long-term (>15 years) series of CMR populations, using distinct demographic models designed for both open and closed populations, were analysed for two sympatric species of rodents (*Myodes glareolus* and *Apodemus flavicollis*) from a mountain area in central Italy, in order to test the relative performance of various employed demographic models. In particular, the hypothesis that enumeration models systematically underestimate the population size of a given population was tested.

2. Overall, we compared the performance of 7 distinct demographic models, including both closed and open models, for each study species. Although the two species revealed remarkable intrinsic differences in demography traits (for instance, a lower propensity for being recaptured in *Apodemus flavicollis*), the Robust Design appeared to be the best fitting model, showing that it is the most suitable model for long-term studies.

3. Among the various analysed demographic models, Jolly-Seber returned the lower estimates of population density for both species. Thus, this demographic model could not be suggested for being applied for long-term studies of small mammal populations because it tends to remarkably underestimate the effective population size. Nonetheless, yearly estimates of population density by Jolly-Seber correlated positively with yearly estimates of population density by closed population models, thus showing that interannual trends in population dynamics were uncovered by both types of demographic models, although with different values in terms of true population size.

KEYWORDS

Rodent population dynamics, demographic models, long-term study, Italy

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INTRODUCTION

There are many reasons behind monitoring the surveys of wild populations (e.g., Caughley 1977), and there is a wide range of methods that allows the implementation of these monitoring surveys (Krebs 1989). The sampling design is important in order to reduce the variation and potential biases among observations or among categories of treatment (Garton et al. 2005). The choice of a specific sampling method depends on the objectives of the study and/or on the assumptions made, the sampled population and other extrinsic factors, such as climate, logistics, equipment, time available and the desired size of the sample (Garton et al. 2005). Lebreton et al. (1992) recommended a four-step procedure in order to select the best model for a given type of demographic dataset: (1) start from a global demographic model compatible with the biology of the studied species and with the design of the study, and assess its fit; (2) select a more parsimonious model using Akaike's Information Criterion to limit the number of formal tests; (3)

test for the most important biological questions by comparing this model with neighbouring ones using likelihood ratio tests; and (4) obtain maximum likelihood estimates of model parameters with estimates of precision. The purpose is to get the best estimate with the least confidence interval and at the lowest cost (Krebs 1989). With the above-mentioned criteria in mind, a suite of field studies has been published on the demography of animals during the last few decades (e.g., Hoyle et al. 2001).

As concerning the monitoring of wild rodent populations, the most readily used field methodology has been the Capture – Marking – Recapture (CMR; see Flowerdew 1976). This methodology has also been repeatedly used in recent years (e.g., Lambin et al. 2006; Amori et al. 2015). Based on the CMR data, and using appropriate demographic models, it is possible to evaluate distinct remarkable components such as survival, density, recruitment, dispersal, population size, and even movements of individuals that occur in the population (Pollock et al. 1990).

Several studies have been conducted to test for the effectiveness of different demographic models to estimate the density of animal populations (e.g., Chiari et al. 2013). However, to our knowledge, these studies were almost invariably short-termed (i.e., with less than 4 years of data; e.g., Lebreton et al. 1992), and in general, an abuse of the use of open population models (Jolly-Seber) was noted (Begon 1983).

The main aim of this paper is to try to compare the results on population size and density of long-term series of CMR populations, using distinct demographic models designed for both open and closed populations. For this aim, we utilize a long-term time series of data, spanning over 15 years, on two sympatric species of rodents (*Myodes glareolus* and *Apodemus flavicollis*) from a mountain area in central Italy (Amori et al. 2015). This dataset is noteworthy because it is characterized by (i) high inter-annual, non-cyclic density oscillations, (ii) almost absent long-term survival of individuals, and (iii) high short-term survival of individuals (Amori et al. 2015), thus allowing for comparative testing of the relative performance of various employed demographic models. In addition, we also compared the probabilistic demographic models for open and closed populations with the enumeration model MNA (Minimum Number Alive), that has been repeatedly used for demographic studies of rodents (e.g., Krebs 1966; Pollock et al. 1990). In particular, we test the hypothesis that enumeration models systematically underestimate the population size of a given population, despite being more intuitive and easy to interpret (e.g., see Canova 2003; Krebs 1999).

1. MATERIALS AND METHODS

1.1. Study area and trapping design

The study was conducted in a beech forest (*Fagus sylvatica*) area of central Italy, situated in the Natural Reserve Orfento Valley (PE) (42° 08' N, 14° 05' E, 1100 m above the sea level). Details of the field protocol are provided in Amori et al. (2015). Here, we give a summary of the main points. Individuals of *Myodes glareolus* and *Apodemus flavicollis* were captured with live traps (Locasciulli et al. 2015), arranged in a grid square of 1.44 ha. Each trap was identified by a code Txy, where x and y are a pair of coordinates on the plane (Fig. 1). Each trap was spaced 12 m apart from each other. Along the perimeter of the grid, a band of width equal to half the minimum distance between the traps was included, taking into consideration the margin effect. The data were obtained by the method of Marking - Capture - Recapture (CMR; Gurnell & Flowerdew 1982); using 'ear-tag' as in Le - Nguyen and Le Boulengé (1986). Each captured individual was sexed (as given in Gurnell & Flowerdew 1990) and its age (adult versus young; determined using the value of 16 g as a threshold value for *M. glareolus* (Amori et al. 2000), and 14 g in *A. flavicollis* (Pucek et al. 1993)) was recorded. Sampling sessions, lasting three nights, were conducted from May to November, once per month, since 1988 to 1995, and from 2000 to 2005.

1.2. Statistical analyses

To estimate the density of the two populations, several demographic models were applied. Each year of the study was counted separately, as there was not any single individual that survived from one year to the next one (Amori et al. 2015).

The models applicable to closed populations, chosen for this study, were:

(a) 'Equal Catchability (M_0)' (Pollock et al. 1990), or null model. This demographic model states that the probability of capture during the course of the study is the same for all individuals of the population.

(b) 'Schnabel-Petersen' (ML) (Krebs 1989). This demographic model provides that the probability of capture of individuals at each sampling event remains the same and different between one event and another sample.

(c) 'Chao temporal change in capture probabilities (M_t)' (Chao 1988). This demographic model assumes that the probability of capture of each individual is influenced by temporal parameters.

(d) 'Heterogeneity Model (M_h)' (Chao 1988). In this demographic model, every individual of the sampled population has a different chance of being captured constant for all capture sessions (Pollock et al. 1990), that is determined by parameters such as sex and age.

(e) 'Both individual and temporal differences in capture probability (M_{th})'. This demographic model assumes that the probability of capture varies depending on the temporal parameters and individual parameters (Chao et al. 1992).

We also applied Jolly-Seber (Seber 1965) as open demographic model (thus, subject to immigration/emigration, birth/death), and the 'Robust Design'; this provides the primary sampling periods (k), inside which are the secondary periods (l) (Pollock 1982). This latter demographic model assumes that in each sampling period k, the size of the population in the secondary periods is constant. As an example of the enumeration methodology, we used the Minimum Number Alive (MNA) (Krebs 1966, 1999).

To find out which of these competing models is more appropriate, we applied the Akaike information criterion (AIC; see Akaike 1973). This procedure can identify the model that best describes the structure of the dataset (best model) that provides the best balance between under-fitting and over-fitting (Burnham and Anderson 2003).

We correlated year-by-year population density estimates obtained with various models for *A. flavicollis* versus *M. glareolus* by Pearson's correlation coefficient. The same type of analysis was also performed to determine whether the population density estimates obtained with the model for open populations (Jolly-Seber) correlated with the population density estimates obtained with models for closed populations. A Generalized Linear Model (GLM) was used to evaluate the yearly effects on the population density estimates of Jolly-Seber and enumeration methods (MNA), with the two species entered separately in the analysis. The mean annual differences in population density estimates obtained with probabilistic

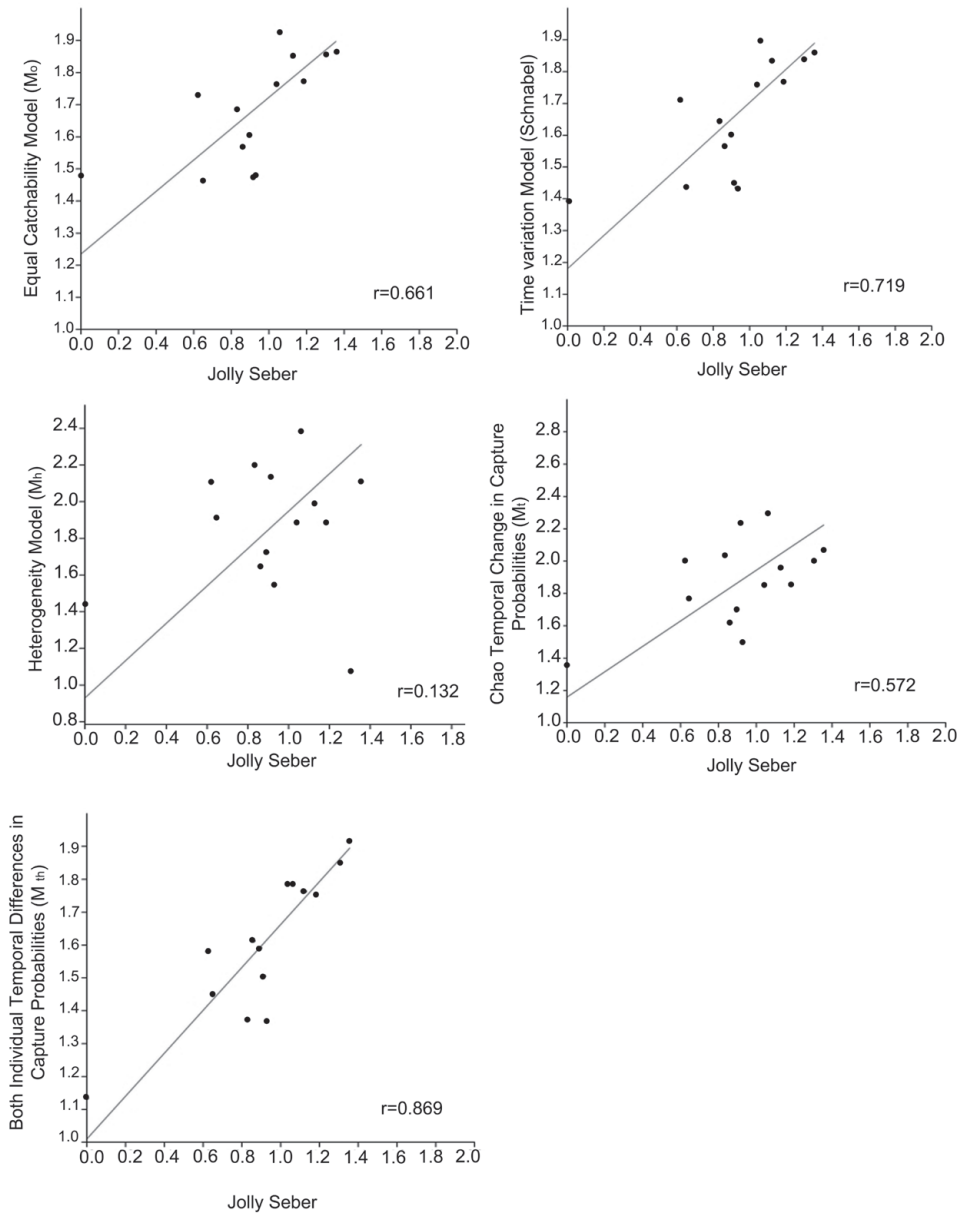


Figure 1. Correlations between the population density estimates (individuals/ha) by Jolly-Seber model versus closed demographic models for *Apodemus flavicollis*. In all cases, $P < 0.05$

(Jolly-Seber) and enumeration methods (MNA) were analysed by Mann-Whitney U-test. Mean annual differences in the capture/recapture ratio (with each sampling period being a separate data entry) were analysed by Student t-test. Heterogeneity of slopes for the general regression between MNA/ha and Jolly-Seber/ha for the two study species was assessed by one-way Analysis of Covariance (ANCOVA).

All demographic models were generated by the software 'Simply Tagging version 2.0.1' (Pisces Conservation Ltd.), available at <http://www.pisces-conservation.com/softtagging.html> and 'Mark' (Colorado State University; Cooch & White 2017). GLM models were performed with PASW statistics ver-

sion 18.0 software (available at <http://www.spss.com.hk/statistics/>). The software 'PAST' (Paleontological Statistics; available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm) was employed for all other statistical analyses. The best fitting model was selected using the software 'Capture' (available at <http://www.phidot.org/software/>).

2. RESULTS

Over the fourteen years of sampling, a total of 2378 individuals were trapped, including the individuals that were captured for the first time ($n = 960$) and those recaptured multiple times

(n = 1418) (Table 1). More in detail, *A. flavicollis* had a similar number of captures \times year⁻¹ (33.5 \pm 15.8 versus 35.1 \pm 27.1) but a much lesser number of recaptures \times year⁻¹ (37.1 \pm 25.3 versus 64.2 \pm 125.1) than *M. glareolus* (Table 1). However, the yearly ratio between 'No. captures/No. Recaptures' did not differ significantly between species (t = 1.149, df = 12, P = 0.261).

The estimates of population density by the various demographic models are presented in Table 2 (*A. flavicollis*) and Table 3 (*M. glareolus*). For *A. flavicollis*, the smaller value of population density was given by Jolly-Seber, with the exception of the year 2004 in which M_h provided an even lower estimate value (respectively 13.982 ind/ha and 8.521 ind/ha) (Table 2). M_h gave higher density estimates than all other demographic models for the period 1988-1995, while in the period 2000-2005 the largest values were given by models M_o , M_t and M_h . Jolly-Seber showed that the minimum and maximum density relative to the sampling period 2000-2005 were lower than those of the period 1988-1995 (Table 2). Moreover, the population density values obtained for 1988-1995 had a much lower variance (values ranging from 5.02 to 15.76) than in the period 2000-2005 (range 0.69 to 13.98) (Table 2). Overall, the inter-annual patterns of population density were similar between

Jolly-Seber (open populations) and M_{th} (closed populations), with higher minimum and maximum values for 1988-1995 than for 2000-2005, and with the width of confidence intervals being lesser in 1988-1995 than in 2000-2005 (Table 4). Considering only the closed demographic models, it appeared that: (i) M_o and ML had a very similar trend; (ii) M_t and M_h were similar in 1988-1995, with density estimates that far exceeded those of all other demographic models in the period 2000-2005 (Table 4).

Concerning *M. glareolus* (Table 3), it resulted that M_o was similar to ML, with a slight difference in the period 2003-2004. The inter-annual patterns of M_t and M_h were also similar (apart that in 2002, when there was a density peak according to M_h). The higher values of density were obtained from M_h , and the lesser values from Jolly-Seber. All the closed demographic models provided inter-annually consistent density values, with short confidence intervals. Jolly-Seber estimates showed that both the maximum (45.62 ind/ha) and minimum (0.76 ind/ha) densities occurred in the period 1988-1995. The densities were relatively stable (around 10 ind/ha), with the exception of the peak recorded in 1995 (Table 3). Overall, estimates were signifi-

Table 1. Raw data on the total number of captured and recaptured rodents by species and by the year of study. No. captures = Minimum Number Alive (MNA)

No. Captures	No. Recaptures	No. captures/ No. Recaptures	No. Captures	No. Recaptures	No. captures/ No. Recaptures
	<i>Apodemus flavicollis</i>			<i>Myodes glareolus</i>	
55	40	1.38	16	9	1.78
52	58	0.9	40	53	0.75
27	26	1.04	42	64	0.66
37	42	0.89	20	14	1.43
36	47	0.77	32	51	0.63
28	46	0.61	24	21	1.14
12	3	4	2	6	0.33
52	91	0.57	117	492	0.24
12	4	3	22	26	0.85
25	42	0.6	51	78	0.65
20	11	1.82	15	13	1.15
22	20	1.1	34	19	1.79
60	70	0.86	31	19	1.63
31	19	1.63	45	34	1.32

Table 2. Estimates of population density (individuals/ha) of *Apodemus flavicollis*, obtained with different demographic models and relating to each year of sampling. For the abbreviations, see the text.

Year	Jolly-Seber	M_0	ML	M_h	M_t	M_{th}
1988	7.961	58.508	55.023	167.152	138	42.361
1989	9.256	49.09	47.312	67.361	62.541	40.277
1990	5.438	28.059	27.79	36.739	34.298	27.083
1991	10.609	41.089	40.838	52.998	49.755	39.583
1992	7.604	40.192	39.97	52.998	49.813	42.361
1993	5.019	25.743	25.722	30.805	29.309	28.472
1994	5.879	20.997	18.896	24.238	22.115	16.148
1995	15.755	50.729	50.416	89.131	80.979	57.638
2000	0.694	20.997	17.19	19.085	15.708	9.462
2001	5.697	20.677	19.613	94.166	119.659	22.222
2002	4.711	33.675	30.372	110.09	74.944	16.372
2003	3.088	20.228	19.065	56.479	40.618	19.444
2004	13.982	49.754	48.031	8.521	70.895	49.305
2005	2.903	37.514	35.5	89	68.84	26.388

Table 3. Estimates of population density (individuals/ha) of *Myodes glareolus*, obtained with different demographic models and relating to each year of sampling. For the abbreviations, see the text.

Year	Jolly-Seber	M_0	ML	M_h	M_t	M_{th}
1988	2.975	21.6	20.456	43.194	35.625	13.425
1989	7.57	30.107	29.828	33.461	31.971	28.472
1990	7.722	35.447	35.162	49.177	46.61	38.888
1991	5.28	26.895	26.622	60.638	52.631	24.305
1992	4.272	32.851	32.631	77.138	69.833	41.666
1993	3.311	20.408	20.086	24.202	22.4522	23.529
1994	0.756	5.319	4.875	11.313	8.897	16.437
1995	45.625	98.69	98.63	141.916	134.576	
2000	6.243	18.059	16.902	24.223	21.326	16.666
2001	9.036	41.515	41.147	62.333	58.105	40.972
2002	2.361	16.066	15.765	119.145	85.479	15.277
2003	5.555	46.01	43.151	53.312	48.263	26.604
2004	5.859	38.82	37.606	54.555	48.427	23.751
2005	7.109	50.809	49.945	74.437	70.687	34.926

cantly different between various demographic models in most of the years (Table 4).

The best fitted model was the Robust design for both species. Concerning *A. flavicollis*, the $\Delta AICc$ of M_0 (3.52) and M_t (4.4) also showed that these two models were quite good, as well M_t for *M. glareolus* ($\Delta AICc = 4.25$) (Table 5).

Comparing the yearly density estimates between the two species by the various demographic models, it resulted that the only significant correlation was relative to M_t ($r = 0.631$, $P = 0.0147$), but the correlation relative to M_h fell just short of statistical significance ($r = 0.495$, $P = 0.0685$). There were also statistically significant positive correlations between Jolly-Seber density estimates and all the density estimates by closed demo-

graphic models (Fig. 2). A heterogeneity of slopes test revealed no differences between Jolly-Seber and enumeration methods (MNA) in terms of the slopes of the among years' regression lines ($F_{1,75} = 0.052$, $P = 0.896$).

3. DISCUSSION

Overall, we observed that the percentage of recapture of *A. flavicollis* was distinctly lower than the percentage of recaptures of *M. glareolus*, and this information may indicate a lower propensity to recapture *A. flavicollis* than *M. glareolus*. Most of the previous studies did not analyse the interspecific differences in recapturability (e.g., Pucek et al. 1993), thus generalizations are

Table 4. Statistical differences of pairwise comparisons between demographic models in terms of their year-by-year estimates for the two-study species. *Apodemus flavicollis* is above the diagonal and *Myodes glareolus* is below the diagonal.

	Jolly-Seber	M_0	ML	M_h	M_t	M_{th}
Jolly-Seber	****	$z = -3.65$; $P < 0.0001$	$z = -3.84$; $P < 0.001$	$z = -3.88$; $P < 0.0001$	$z = -4.11$; $P < 0.0001$	$z = 3.65$; $P < 0.0001$
M_0	$z = -3.65$; $P < 0.0001$	****	$z = -0.62$; $P = 0.536$	$z = -1.91$; $P = 0.06$	$z = -2.27$; $P < 0.05$	$z = -0.76$; $P = 0.447$
ML	$z = -3.56$; $P < 0.0001$	$z = -0.299$; $P = 0.768$	****	$z = -2.18$; $P < 0.05$	$z = -2.27$; $P < 0.05$	$z = -0.53$; $P = 0.6$
M_h	$z = -4.25$; $P < 0.0001$	$z = -2.27$; $P < 0.05$	$z = -2.32$; $P < 0.05$	****	$z = -0.115$; $P = 0.903$	$z = -2.23$; $P < 0.05$
M_t	$z = -4.25$; $P < 0.0001$	$z = -2.37$; $P < 0.05$	$z = -2.41$; $P < 0.05$	$z = 0.07$; $P = 0.944$	****	$z = 2.60$; $P < 0.01$
M_{th}	$z = -4.48$; $P < 0.0001$	$z = -0.67$; $P = 0.508$	$z = -0.67$; $P = 0.511$	$z = -2.72$; $P < 0.01$	$z = -2.82$; $P < 0.01$	****

Table 5. Second order Akaike Information Criterion (AICc) values for the various demographic models used in this paper. $\Delta AICc$ represents the difference between the best fitting demographic model and the candidate demographic model.

Demographic Model	AICc	$\Delta AICc$	W
<i>Apodemus flavicollis</i>			
Robust design	79.81	0.00	0.275
M_0	83.33	3.52	0.151
M_t	84.21	4.4	0.157
M_{th}	84.21	4.4	0.157
Jolly-Seber	159.66	79.85	0.033
ML	171.41	91.6	0.009
<i>Myodes glareolus</i>			
Robust design	71.33	0.00	0.322
M_t	75.58	4.25	0.186
M_0	78.45	7.12	0.164
M_{th}	78.45	7.12	0.164
Jolly-Seber	166.33	95.00	0.021
ML	161.46	90.13	0.034

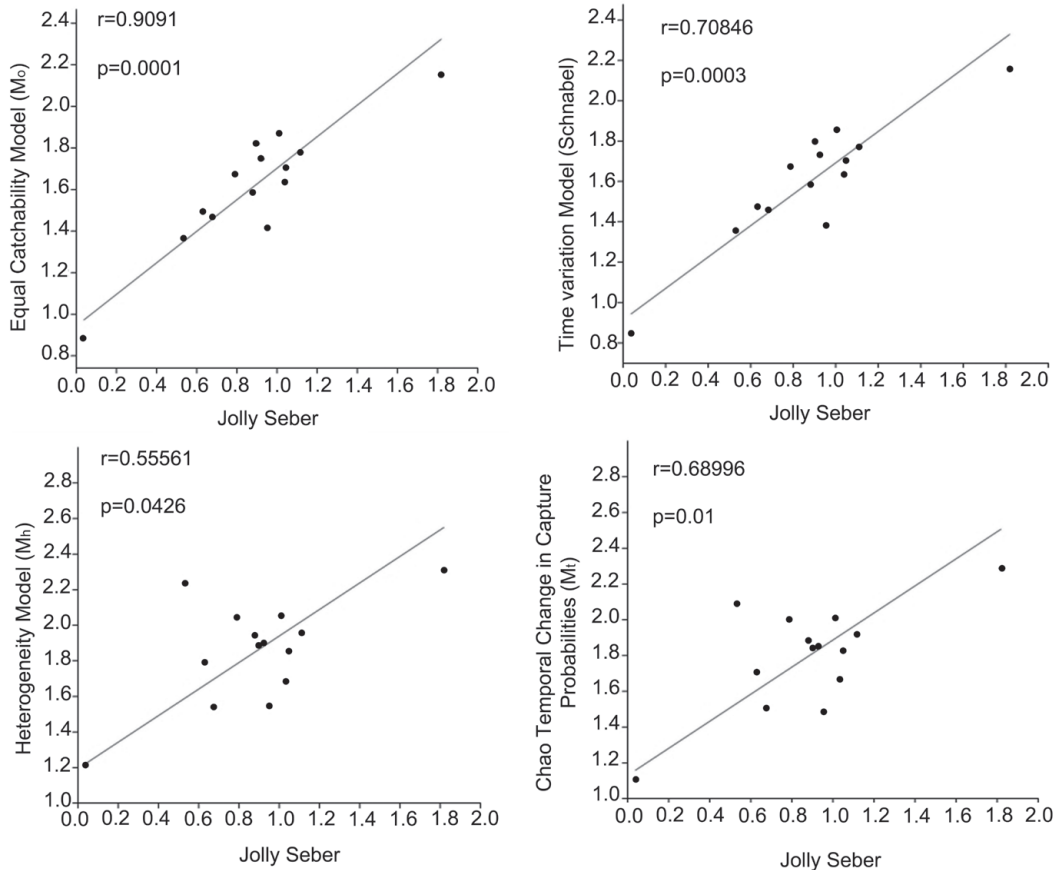


Figure 2. Correlations between the population density estimates (individuals/ha) by Jolly-Seber model versus closed demographic models for *Myodes glareolus*.

difficult. However, a similar trend was already found in Montgomery's (1987) dataset, although with no explicit mention of the pattern by the author himself. We think that the difference in recapturability between species depends on larger home ranges in *Apodemus* than in *Myodes* (e.g., Crawley 1969).

For both species, the Robust Design (Pollock 1982) was found to be the best fitting model. This result is in agreement with the statement made by Pollock (1990), showing that it is the most suitable demographic model for long-term studies. Our conclusions also confirm Canova et al.'s (2003) statement that it is a clear advantage of this model that it calculates the estimates for the first and last capture session, whereas they will be excluded from Jolly-Seber (Seber 1965).

Among all the demographic models used in this study, Jolly-Seber returned the lower values of population density estimates, for both *A. flavicollis* and *M. glareolus*. In most of the years, the differences in population density estimates were very high, pointing out that experimenters should be careful before deciding which demographic model they want to use. Indeed, assuming that the population between samples must be open and knowing that the life of every individual is unlikely to exceed 12 months (Amori & Luiselli 2011a, 2011b), it results that Jolly-Seber model could not be suggested for long-term studies

of small mammal populations. This is also in accordance with Pollock et al.'s (1990) statements. In addition, Hammond and Anthony (2006) recommended to applying this model only in the cases where the number of specimens captured in each sampling session is greater than 100. In our cases, the threshold value of 100 newly captured individuals was not reached in most of the years (despite the remarkable field effort), thus it is likely that the relatively low number of yearly captures may have affected the performance outcome of the various demographic models.

The similar trends of inter-annual population densities that emerged from both M_0 and ML for either species can be attributed to the similarity of the assumptions made by these demographic models. Although M_0 and ML can be used interchangeably, Pollock et al. (1990) recommended that they should not be applied in the studies of population dynamics, since the assumptions are not verifiable in natural populations. The population density values provided by M_h and M_t were very similar for the two species. This pattern can be justified by the fact that these two demographic models consider the time scale and individuality as the factors most influencing the demography of a natural population. For both species, the population density values by M_{th} were lower than both M_t and M_h .

The time factor, or any climatic factor that may affect the catchability of an individual, may amplify in a positive or negative effect the heterogeneity of individuals. In fact, it may increase the probability of capture of a 'trap-happy' individual or decrease the probability of capture of 'trap-shy' individual (Flowerdew 1976).

Finally, a comparison of the population density estimates between Jolly-Seber and the various closed demographic models showed that the values obtained were correlated to each other. Therefore, our study showed that, when using Jolly-Seber for long term studies, the main population density trends (for instance, increases or decreases among years) are uncovered similarly to other demographic models. However, although adequately describing the yearly trends in population density of the two populations, Jolly-Seber model regularly underestimates the population density compared to the robust design and close demographic models, and this underestimation may be statistically significant.

The positive correlation observed in our study between the yearly density of *Myodes* against the yearly density of *Apodemus* may indicate that in the presence of some exter-

nal factors, the two species did not mutually influence each other in terms of density, but there may be environmental factors that affect both these species in a parallel way (Pucek et al. 1993). In Poland, for instance, seed availability was the main factor influencing rodent densities across years in the forest habitat (Pucek et al. 1993). We suggest that the same reason may explain a similar pattern found in our study area, despite this, we did not measure seed productivity in the field for any of the study years.

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