Aspects of demography in three distinct populations of garden dormouse, *Eliomys quercinus*, across Italy and Spain

Abstract

Comparative aspects of the demography were investigated in three distinct populations of the ecologically poorly studied rodent *Eliomys quercinus*, in Spain and Italy. Maximum longevity was observed in a Spanish female (at least 2 years and 4 months survival). For all the populations under study, various closed populations models and the Robust design model gave similarly reliable estimates for population size, with Jolly-Seber estimates being considerably less reliable. The same result also emerged for survival and capture probabilities estimates, but with less profound differences between Jolly-Seber and the closed models with Robust design. Average density showed considerable oscillations over the years and across localities, being nearly identical in northern and central Italy but considerably higher in Spain. Survival was considerably higher in Spain than in Northern and Central Italy. Conversely, capture probability was higher in Northern Italy than in the other two study areas.

Key words

Rodents; demography; population size; Mediterranean

Introduction

There is considerable scientific evidence that the garden dormouse (*Eliomys quercinus*) is presently declining in wide regions of its distribution (Amori 1993; Amori et al. 1994; Andera 1994; Jusïkaitis 1994; Pilats 1994). For instance, the species is rare in Estonia, Latvia, east Germany, the Czech Republic (Andera 1994) and adjacent Austria (Spitzenberger 2002), and has disappeared completely from Lithuania, Slovakian Carpathians and Croatian mainland (see www.iucnredlist.org). The last record in Romania is over 20 years old (www.iucnredlist.org)).

Unfortunately, it is difficult to evaluate the patterns of, and the reasons behind, this decline and the measures to reverse it because very few studies are available on the population ecology and demography of this rodent species (Amori et al. 1994).

In recent years, some garden dormouse populations have been studied by trapping methods in three different contexts in southern Europe, i.e. in Spain and in Northern and Central Italy. Therefore, we have considered that a comparative analysis of these data would have been of some interest for improving the knowledge of the demography of this poorly studied and declining rodent species. Therefore, in the present work, we compare the demographic data for three garden dormouse populations from Northern, Central Italy, and Spain, with emphasis on population estimates, survival, and capture probabilities.

Study areas

The summarized data (place name, altitudes, geographic coordinates and research period) of the three study areas are given in Table 1.

Northern Italy (Alps)

The study was carried out at a mountain site in the Val Troncea Natural Park, located in the Italian Western Alps. The study site had an eastern exposure. Snow cover is present for 4-6 months (IPLA, 1982). The garden dormouse was studied in an area of fragmented larch (*Larix decidua*) woodland, growing on a scree.

Central Italy (Appennines)

The study was carried out at a mountain area, Campo Felice, characterized by a karst plateau-alluvial site located in the Abruzzo region of central Italy in the province of L'Aquila. The area is partly lying within the Regional Natural Park Velino-Sirente. Snow cover is present for 3-5 months. The trapping area was inside a beech (*Fagus sylvatica*) forest.

Spain

The study was carried out at a lowland area of Doñana National Park, located on the South-West coast of the Iberian Peninsula, on the right bank of the mouth of the Guadalquivir river. The climate is Mediterranean. The study area was characterized by Mediterranean scrublands (mainly *Halimium* spp., *Cistus* spp., *Ulex* spp., *Stauracanthus ginestoides* and *Rosmarinum officinalis*), and is typical habitat for most small mammal species (Camacho and Moreno 1989).

Data collection

The data for the three study areas were obtained through capture, marking and recapture (CMR, Flowerdew, 1976). Details are presented below. In all study areas, the new born individuals were identified by their pelage and small body size; males with enlarged testes and females with an open vagina or visible signs of pregnancy or lactating were considered sexually active.

Northern Italy (Alps)

Garden dormice were trapped using 144 Sherman live-traps, placed at 20 m intervals in a grid of 8 lines with 17-20 traps each, covering an area of 4.68 ha. Traps were placed on the ground, baited with hazelnuts, cheese and carrots. They were set in the evening and inspected in the morning. A trapping session of 6 days was planned monthly from May to September, when garden dormice are active in alpine habitats. During 1995, the field work stopped at the end of August, because of bad weather conditions. In 1996, the trapping was carried out every month. However, in August, when juveniles became trappable, two trapping sessions were performed: one in the first half of the month and one in the second half. We trapped in June 1997 to monitor winter survival. The dormice were individually marked with passive integrated transponder (PIT) tags. We did not implant juveniles that weighed less than 35-40g; this lower limit of body weight assured us that animals developed properly and were fully viable. In fact, juveniles caught in August (mean weight 34.5 ±5.0g) were provisionally marked by fur-clipping, while September captures were implanted with transponders (mean body weight 47.3 ±4.9g). At each capture the animals were weighed (by means of a spring balance, accurate to 1g), aged, and the reproductive condition recorded.

Central Italy (Appennines)

Data were collected from July to November 2011 and in the months of July and September 2012. The monthly trapping sessions were set up to 5 consecutive days each. The animals were trapped using two types of live traps: one type at single capture (LOT type; Locasciulli et al. 2015) and one at multiple capture (Ugglan type). The traps were baited using cereals, anchovy paste and hazelnut cream. The traps were placed along two transects of 100 m each, arranged in two areas of interest, the beech forest and meadow - pasture. In total, 60 traps were used, 30 for each habitat type (20 at single capture and 10 at multiple capture), arranged along the transect and spaced apart 10 m from one another. The two transects were approximately 300 m apart in linear distance. The overall surface was 3 ha.

Traps were checked every morning. Each individual was processed to determine its sex (with external reproductive signs also being noted) and weight (by means of a spring balance, accurate to 1g). Individuals were marked by ear-tagging (cf. Amori et al. 2015).

Spain

The field study was performed from March 1978 to March 1981. Capture-recapture sessions were performed monthly (one or two times/month for about 4 consecutive months). A grid of 64 live traps (similar to Sherman type) was located in 8 rows of 8 traps each (15 meters separated). The total surface was 1.44 ha. Traps were baited with bread soaked with used fish-oil and placed at each grid intersection. Traps were set just before sunset and checked within 2 h after sunrise the following morning. Captured small mammals were marked (using ear tagging, see Moreno 1988), weighed (by means of a spring balance, accurate to 1g), measured to body length and sexed (with external reproductive signs also being noted). Animals were immediately set free in the same place as they were captured and were available for recapture on subsequent nights. Individuals weighing less than 60 g were considered as young animals (Moreno 1988).

Statistical methods

To estimate the density of the various populations, several demographic models, applicable to both closed and open populations, were applied.

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

(a) "Equal Catchability (M_0) " (Pollock et al. 1990), or null model. This 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 model (Schnabel ML, M_t) (Krebs 1989). This model provides that the probability of capture of individuals at each sampling event remains the same, but can differ between one event and another sample.

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

(d) "Heterogeneity Model (M_h)" (Chao 1988). In this 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, age and social dominance.

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

As open population models (thus subject to immigration/emigration, birth/death), we applied to our data the Cormack-Jolly-Seber model (Seber 1965) and the Robust design (Pollock 1982). This latter model is a combination of the Cormack-Jolly-Seber and the closed capture models. The key difference of Robust design with Cormack-Jolly-Seber model is that, instead of just 1 capture occasion between survival intervals, multiple (>1) capture occasions (named ‘trapping sessions’) are used. These capture occasions are close together in time, allowing the assumption that no mortality or emigration occurs during these short time intervals. Each trapping sessions is analyzed as a closed capture survey. The power of this model is derived from the fact that the probability that an animal is captured at least once in a trapping sessions can be estimated from just the data collected during the session using capture-recapture models developed for closed populations (Otis et al. 1978). The timespan between different trapping sessions allows estimation of survival, temporary emigration from the trapping area, and immigration of marked animals back to the trapping area.

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

We used the determination coefficient (r^2) to evaluate the presence of any statistically significant relationship between the estimates of relative densities obtained with the various models. The same type of analysis was also performed to determine whether the estimates obtained with the open population models approached the estimates obtained with models for closed populations.

Estimates for demographic models were generated by the softwares "Simply Tagging" and "Mark" (Colorado State University) , and the software ‘’PAST’’ (Paleontological Statistics) was employed for all other statistical analyses. The best fitting model was selected using the software “Capture”.

Results

In northern Italy, 169 individuals were captured for 326 times in total. In central Italy, 17 individuals were recaptured for a total of 26 times. In Spain, a total of 181 individuals was captured 597 times.

The distribution of capture histories was similar across study areas, showing that the great majority of specimens were captured no more than 2 times (Figure 1). Indeed, the distribution of capture histories were significantly correlated in Northern and Central Italy (r^2= 0.989, $P < 0.001$), Central Italy and Spain (r^2= 0.911, $P < 0.001$), as well as between Northern Italy and Spain (r^2= 0.935, $P < 0.001$).

The summarized dataset for the three study areas are given in Appendix 1 (Northern Italy), 2 (Central Italy), and 3 (Spain), for both closed and open population models. The most long-lived individual in our study was a Spanish female that was captured for the first time in May 1978 (when she had already reached the adult age) and for the last time in June 1980. Thus, considering that sexual maturity is reached at 3 months age (Santini, 1983), this female would have survived for at least 2 years and 4 months.

The summary of the various demographic parameters for the three studied populations is given in Table 2. For all populations under study, the various models for closed populations and the Robust design model gave similarly reliable estimates for population size (in all cases, Delta AICc < 5), with Jolly-Seber estimates being considerably less reliable (in all comparisons, Delta AICc > 24). The same result also emerged for survival and capture probabilities estimates, but with less profound differences between Jolly-Seber and the closed models with Robust design (in all cases, 17>Delta AICc >10).

The average estimated density, although with considerable oscillations over the years, was nearly identical in Northern and Central Italy, but considerably higher in Spain (Figure 2).

Survival was consistently estimated to be considerably higher in Spain than in Northern Italy and Central Italy by all models, with comparatively similar associated errors (Table 2). Conversely, capture probability was consistently estimated to be considerably higher in Northern Italy than in the other two study areas that appeared very similar by all models, with comparatively similar associated errors (Table 2).

Discussion

First of all, we acknowledge that a considerable heterogeneity of the datasets (in terms of experimental protocols, habitat types, study areas, and temporal distribution of the data including relative length of each sampling design) may have partially biased the results. However, we have also discovered some aspects of demography that may be interesting because of the declining status of the study species that has experienced a population collapse especially in Spain (Moreno 1984, 1988).

Interestingly, some aspects of population biology of the garden dormouse have been similar across study areas, despite the above-mentioned heterogeneity of datasets. For instance, in all study areas we detected a similar trend in strong reduction of recapture probability of the various individuals after the first two capture events. This pattern is unlikely to be by chance, because it was found with no exception in all the study areas, in both short and long term trapping protocols. A possible explanation may be that these rodents are very short lived. However, this is probably not the case as we determined for the Spanish population a maximum lifespan reaching well over 2 years. In addition, literature data also reported that wild animals may live longer than 2-3 years (Kahmann and Staudenmayer 1970; Baudoin 1980), with a maximum reported age of 5 years in captivity (Baudoin and Abdi 1981). In Northern Italy, Bertolino et al. (2001) reported a lifespan of about 20 months. Another explanation may be that the garden dormice have large home ranges, thus minimizing the probability of recapture. However, literature data suggest that this species is sedentary, with home ranges lesser than 1 ha (Bertolino et al. 2003), thus making this hypothesis also unlikely. A third hypothesis may be the lack of habituation of dormice and consequent avoidance of traps. Indeed, we suggest that the most likely explanation for the observed pattern is that this species is shy, and the individuals can disperse from their usual core area when over-disturbed (i.e. trapped multiple times). This pattern has already been detected as an outcome of prolonged capture-mark-recapture monitoring in other vertebrates (Gauthier-Clerc et al. 2004; Langkilde and Shine 2006; Fauvel et al. 2012). We urge further and detailed research on this issue, because it may considerably bias the available studies on rodent population demography.

Our analyses also revealed that the Robust design gave consistently more reliable population size estimates than open population models. This result mirrors with the statement made by Pollock et al. (1990), showing that it is the most suitable model for long-term studies. Our conclusions also confirm what was stated by Canova et al. (2003), that 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 the Jolly-Seber model (Seber 1965).

Concerning the density estimates, it appeared that the two Italian populations had lower densities than the Spanish population. Interestingly, the estimated density of the Spanish population resembled somehow the densities observed in France (Baudoin et al. 1986; Vaterlaus-Schlegel 1997). We tentatively interpret these differences in relation to the relative altitude of the various sites, with French and Spanish sites being low altitude and high density, and the Italian sites being high altitude and low density.

We also detected a higher survival in the Spanish population. We suggest that this fact may be due to the larger body size of the Spanish individuals (*E. quercinus lusitanicus*; Moreno 2002), as it has been observed in rodents that there is a positive correlation between probability of survival and body mass (Korslund and Steen 2006). The higher survival of Spanish individuals may be due to the fact that these populations do not hibernate (Moreno 1984), as it is well known that hibernating animals often suffer high mortality rates during this inactive period (e.g. Arnold 1990; Blumstein and Arnold 1998). Using our Jolly-Seber estimates of survival, it resulted that all our populations had considerably higher survival than conspecific populations from France and Switzerland (Schaub and Vaterlaus-Schlegel 2001).

Considering that the knowledge of garden dormice demography is still fragmentary and incomplete, we strongly urge to collect more detailed datasets in different areas of their range in order to achieve a better information of potential conservation interest for this declining rodent species.

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Table 1 Summary data for the three study areas

Region	Northern Italy	Central Italy	Spain
Place name	Val Troncea Regional Park	Campo Felice	Donana
Latitude	44.95561 N	42.24086 N	37.00377 N
Longitude	6.95601 E	13.34595 E	-6.33316 E
Elevation (m a.s.l.)	1690-1760	1650	0-100
Research period (years)	1995-1997	2011-2012	1978-1981

Table 2 Summary of the various demographic parameters, with respective dispersion measures, for the three dormouse populations studied in this paper.

	Northern Italy	Central Italy	Spain
Jolly-Seber			
Population estimate ± SD (SE)	26.18 ± 15.65 (5.22)	4.12 ± 2.87 (0.796)	31.70 ± 22.83 (3.75)
Survival ± SD (SE)	0.884 ± 0.0001 (0.058)	0.684 ± 0.0005 (0.0021)	0.926 ± 0.49 (0.076)
Capture probability ± SD (SE)	0.685 ± 0.073 (0.032)	0.263 ± 0.0007 (0.0006)	0.291 ± 0.036 (0.017)
Petersen-Schnabel			
Population estimate ± SD (SE)	67 ± 2.28 (0.019)	36 ± 10.55 (0.128)	21.3 ± 10.53 (0.0006)
Survival ± SD (SE)	0.778 ± 0.031 (0.048)	0.675 ± 0.053 (0.102)	0.924 ± 0.077 (0.048)
Capture probability ± SD (SE)	0.229 ± 0.100 (0.03)	0.025 ± 0.025 (0.0047)	0.034 ± 0.025 (0.038)
M_t			
Population estimate ± SD (SE)	92 ± 11.7 (0.022)	28 ± 6.62 (0.036)	24.3 ± 17.62 (0.0005)
Survival ± SD (SE)	0.778 ± 0.031 (0.048)	0.675 ± 0.053 (0.102)	0.924 ± 0.077 (0.048)
Capture probability ± SD (SE)	0.167 ± 0.73 (0.05)	0.031 ± 0.032 (0.006)	0.030 ± 0.022 (0.0033)
M_h			
Population estimate ± SD (SE)	102 ± 19.3 (0.197)	37 ± 11.67 (0.06)	24.8 ± 22.93 (0.0006)
Survival ± SD (SE)	0.778 ± 0.031 (0.048)	0.675 ± 0.053 (0.102)	0.924 ± 0.077 (0.048)
Capture probability ± SD (SE)	0.202 ± 0.09 (0.027)	0.024 ± 0.025 (0.005)	0.034 ± 0.024 (0.0045)
Robust design			
Population estimate ± SD (SE)	24.79 ± 9.07 (0.028)	18 ± 1.62 (0.111)	21.1 ± 0.25 (0.0002)
Survival ± SD (SE)	0.778 ± 0.031 (0.048)	0.675 ± 0.053 (0.102)	0.924 ± 0.077 (0.048)
Capture probability ± SD (SE)	0.642 ± 0.043 (0.031)	0.48 ± 0.049 (0.009)	0.34 ± 0.025 (0.004)

Figure 1 Distribution of capture histories across study areas.

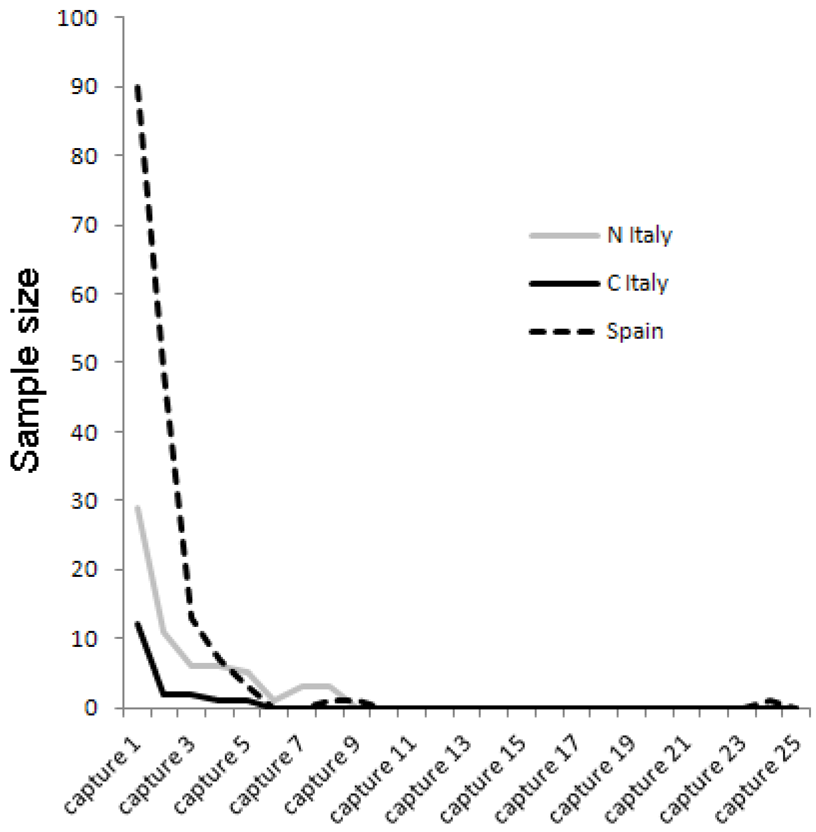
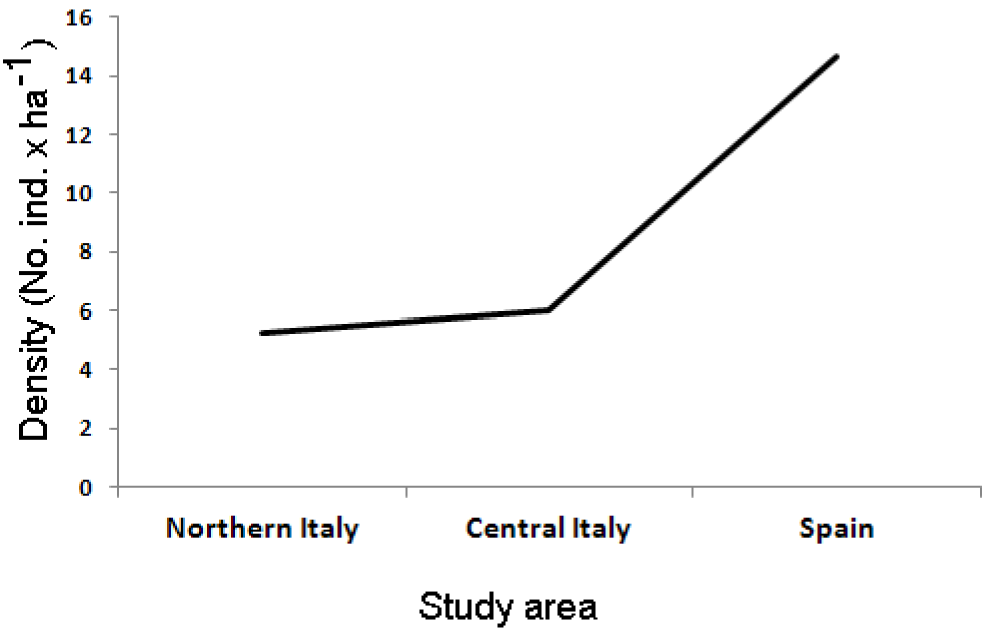


Figure 2 Variation in the average density (estimated by the robust design model) of the three studied populations of garden dormouse.



Appendix 1 Summarized tables for open and closed populations model for the garden dormouse population in Northern Italy.

(A) tables of recaptures

Sample i											
1	1										
2	3	2									
3	4	10	3								
4	0	0	10	4							
5	0	0	1	11	5						
6	0	0	0	4	11	6					
7	0	0	0	0	3	15	7				
8	0	0	0	0	0	2	12	8			
9	0	0	0	0	0	1	7	13	9		
10	0	0	0	0	0	0	0	1	7	10	
11	0	0	0	0	0	0	0	1	6	13	11
Z(i-1)+1	4	0	1	4	3	3	7	2	6		

(B) closed population summary

Sample number i	1	2	3	4	5	6	7	8	9	10	11
Animals caught N(i)	7	6	14	29	11	15	18	12	23	19	15
Marked animals in population M(i)	0	7	10	14	33	33	37	40	40	50	62
Newly caught animals U(i)	7	3	4	19	0	4	3	0	10	12	2
Capture Frequencies f(i)	29	11	6	6	5	1	3	3	0	0	0

Appendix 2 Summarized tables for open and closed populations model for the garden dormouse population in central Italy.

(A) tables of recaptures

Sample i																							
1	1																						
2	0	2																					
3	0	0	3																				
4	0	0	0	4																			
5	0	0	0	0	5																		
6	0	0	0	0	0	6																	
7	0	0	0	0	0	1	7																
8	0	0	0	0	0	0	0	8															
9	0	0	0	0	0	0	0	0	9														
10	0	0	0	0	0	0	0	0	0	10													
11	0	0	0	0	0	0	0	0	0	0	11												
12	0	0	0	0	0	0	0	0	0	0	0	12											
13	0	0	0	0	0	0	0	0	0	0	1	1	13										
14	0	0	0	0	0	0	0	0	0	0	0	0	1	14									
15	0	0	0	0	0	0	0	0	0	0	0	0	0	1	15								
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16							
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17						
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18					
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19				
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20			
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21		
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	22	
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	23

24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24			
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25		
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	27
Z(i-1)+1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	2		

(B) closed population summary

Sample number i	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Animals caught N(i)	1	2	1	0	0	0	0	1	0	0	0	0	2	2	0	0	1	0	0	0	1	5	5	1
Marked animals in population M(i)	0	1	2	2	2	2	2	2	2	2	2	2	2	3	4	4	4	5	5	5	5	6	9	12
Newly caught animals U(i)	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	3	3	0
Capture Frequencies f(i)	6	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3 Summarized tables for open and closed populations model for the garden dormouse population in Spain.

(A) tables of recaptures

Sample i																						
1	1																					
2	1	2																				
3	0	2	3																			
4	0	2	2	4																		
5	0	0	0	0	5																	
6	0	0	0	0	0	6																
7	0	1	2	2	3	4	7															
8	0	0	0	1	1	1	2	8														
9	0	0	0	0	0	0	0	7	9													
10	0	0	0	0	0	0	0	1	3	10												
11	0	0	0	0	0	0	0	0	0	5	11											
12	0	1	1	1	1	1	1	1	1	1	1	12										
13	0	0	0	0	0	0	0	0	0	4	6	6	13									
14	0	0	0	0	0	0	0	0	0	1	1	1	4	14								
15	0	0	0	0	0	0	0	0	0	2	2	2	4	6	15							
16	0	0	0	0	0	0	0	0	1	1	1	1	1	3	5	16						
17	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	5	17					
18	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	4	5	18				
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	11	19			
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	20		
21	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	3	21	
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	22

23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	23																				
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	24																			
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25																		
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	26																	
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	27																
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	28															
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	2	2	4	29														
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	30													
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	2	2	3	6	31												
32	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	32											
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	2	3	33										
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	34									
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	35								
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	36							
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37						
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38					
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	4	4	6	39				
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	40			
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	3	4	41		
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	7	7	11	42	
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	3	3	3	6	43
Z(i-1)+1	0	4	3	4	5	2	1	2	2	10	11	6	7	9	6	7	7	5	4	5	5	5	4	7	6	7	6	4	5	2	2	1	2	2	6	7	8	4	13	10	3		

(B) closed population summary

Sample number i	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Animals caught N(i)	2	12	4	5	7	1	5	11	7	20	9	2	13	13	6	7	10	18	13	10	4	3	2	5	2	3	3	3	6	4
Marked animals in population M(i)	0	2	13	15	18	25	26	27	36	36	53	57	58	65	74	74	76	81	94	96	101	102	104	105	107	108	109	110	110	112
Newly caught animals U(i)	2	11	2	3	7	1	1	9	0	17	4	1	7	9	0	2	5	13	2	5	1	2	1	2	1	1	1	0	2	1
Capture Frequencies f(i)	90	49	13	7	3	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Sample number i	31	32	33	34	35	36	37	38	39	40	41	42	43
Animals caught N(i)	6	3	3	6	10	4	3	6	25	3	7	12	13
Marked animals in population M(i)	113	113	113	113	117	122	125	128	134	153	154	157	158
Newly caught animals U(i)	0	0	0	4	5	3	3	6	19	1	3	1	7
Capture Frequencies f(i)	0	0	0	0	0	0	0	0	0	0	0	0	0