1 Aspects of demography in three distinct populations of garden 2 dormouse, *Eliomys quercinus*, across Italy and Spain

3 Abstract

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

14 Key words

15 Rodents; demography; population size; Mediterranean

16 Introduction

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

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

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

32 **Study areas**

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

35 Northern Italy (Alps)

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

39 Central Italy (Appennines)

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

44 Spain

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

50 **Data collection**

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

55 Northern Italy (Alps)

56 Garden dormice were trapped using 144 Sherman live-traps, placed at 20 m intervals in a grid of 8 lines
57 with 17-20 traps each, covering an area of 4.68 ha. Traps were placed on the ground, baited with hazelnuts,
58 cheese and carrots. They were set in the evening and inspected in the morning. A trapping session of 6 days
59 was planned monthly from May to September, when garden dormice are active in alpine habitats. During
60 1995, the field work stopped at the end of August, because of bad weather conditions. In 1996, the
61 trapping was carried out every month. However, in August, when juveniles became trappable, two trapping
62 sessions were performed: one in the first half of the month and one in the second half. We trapped in June
63 1997 to monitor winter survival. The dormice were individually marked with passive integrated
64 transponder (PIT) tags. We did not implant juveniles that weighed less than 35-40g; this lower limit of body
65 weight assured us that animals developed properly and were fully viable. In fact, juveniles caught in August
66 (mean weight 34.5 ± 5.0 g) were provisionally marked by fur-clipping, while September captures were
67 implanted with transponders (mean body weight 47.3 ± 4.9 g). At each capture the animals were weighed
68 (by means of a spring balance, accurate to 1g), aged, and the reproductive condition recorded.

69 Central Italy (Appennines)

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

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

81 Spain

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

92 Statistical methods

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

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

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

98 (b) "Schnabel-Petersen model (Schnabel ML, M_t)" (Krebs 1989). This model provides that the probability of
99 capture of individuals at each sampling event remains the same, but can differ between one event and
100 another sample.

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

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

106 (e) "Both individual and temporal differences in capture probability (M_{th})". This model assumes that the
107 probability of capture varies depending on the temporal parameters and individual parameters (Chao et al.
108 1992).

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

119 of survival, temporary emigration from the trapping area, and immigration of marked animals back to the
120 trapping area.

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

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

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

132 **Results**

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

135 The distribution of capture histories was similar across study areas, showing that the great majority of
136 specimens were captured no more than 2 times (Figure 1). Indeed, the distribution of capture histories
137 were significantly correlated in Northern and Central Italy ($r^2= 0.989$, $P < 0.001$), Central Italy and Spain ($r^2=$
138 0.911 , $P < 0.001$), as well as between Northern Italy and Spain ($r^2= 0.935$, $P < 0.001$).

139 The summarized dataset for the three study areas are given in Appendix 1 (Northern Italy), 2 (Central Italy),
140 and 3 (Spain), for both closed and open population models. The most long-lived individual in our study was
141 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

166 study areas, in both short and long term trapping protocols. A possible explanation may be that these
167 rodents are very short lived. However, this is probably not the case as we determined for the Spanish
168 population a maximum lifespan reaching well over 2 years. In addition, literature data also reported that
169 wild animals may live longer than 2-3 years (Kahmann and Staudenmayer 1970; Baudoin 1980), with a
170 maximum reported age of 5 years in captivity (Baudoin and Abdi 1981). In Northern Italy, Bertolino et al.
171 (2001) reported a lifespan of about 20 months. Another explanation may be that the garden dormice have
172 large home ranges, thus minimizing the probability of recapture. However, literature data suggest that this
173 species is sedentary, with home ranges lesser than 1 ha (Bertolino et al. 2003), thus making this hypothesis
174 also unlikely. A third hypothesis may be the lack of habituation of dormice and consequent avoidance of
175 traps. Indeed, we suggest that the most likely explanation for the observed pattern is that this species is
176 shy, and the individuals can disperse from their usual core area when over-disturbed (i.e. trapped multiple
177 times). This pattern has already been detected as an outcome of prolonged capture-mark-recapture
178 monitoring in other vertebrates (Gauthier-Clerc et al. 2004; Langkilde and Shine 2006; Fauvel et al. 2012).
179 We urge further and detailed research on this issue, because it may considerably bias the available studies
180 on rodent population demography.

181 Our analyses also revealed that the Robust design gave consistently more reliable population size estimates
182 than open population models. This result mirrors with the statement made by Pollock et al. (1990), showing
183 that it is the most suitable model for long-term studies. Our conclusions also confirm what was stated by
184 Canova et al. (2003), that is a clear advantage of this model that it calculates the estimates for the first and
185 last capture session, whereas they will be excluded from the Jolly-Seber model (Seber 1965).

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

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

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

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277

278

279 **Table 1** Summary data for the three study areas

280

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

281

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

284

	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)

285

286 **Figure 1** Distribution of capture histories across study areas.

287

288

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

291

292

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

295

296 (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			

297

298 (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

299

300

301

24	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	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	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	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			

305

306 (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

307

308

309

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

311

312 (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 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	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	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	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	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	1	3	28																
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	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	3	30															
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	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	3	32														
33	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	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	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	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	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	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	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	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	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	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	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	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

313

314 (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