We monitored the population biology of the Edible dormouse over three years (1999–2001) by monthly checks of nest boxes. The study took place in a semi-natural montane forest of beech *Fagus sylvatica* and fir *Abies alba* in the Dinaric Alps of south-central Slovenia. This report is based on 440 captures of 316 individual dormice. Only 29.4% of specimens were re-captured, 78.5% of which were obtained only once after they were marked and released. The highest annual densities (given as a number of individuals per 100 nest boxes) of adults were in July or August: 23.5 (1999), 25.8 (2000), and 47.8 (2001). Reproduction was recorded in 1999 and 2001, but not in 2000, which makes the high density in the subsequent summer of 2001 surprising. Autumn juvenile densities were much higher than adult ones: 86.7 (1999) and 123.2 (2001). The sex ratio of adults tended to be male skewed in the first half of the season and female skewed later. Juvenile sex ratio was mainly balanced (1:1), however the predominance of males was significant in early October 1999. Litters of young varied between 1–10 per nest box (mean = 4.9, N= 24) in early September. Communal nesting was not recorded.

Key words: *Glis glis*, nest boxes, capture-mark-recapture, population density, reproduction, sex ratio

Leaving aside the fact that the Edible dormouse is an interesting animal, with many aspects of its biology remaining little known, the main reason for initiating the present study was the fact that traditional hunting practices for the Edible dormouse in Slovenia hardly meet the most basic requirements of the Bern convention (The Convention on the Conservation of European Wildlife and Natural Habitats). Although Appendix III of the Convention, which deals with the Edible dormouse, does not require strict protection of the species, any exploitation of the population must be sustainable. Besides the restricted hunting season, which is based more on tradition than on the biology of the target species, the Government of Slovenia has not so far undertaken any other steps to fulfil its legal obligations. Our study is thus intended as a long term monitoring study that is expected to provide basic information on the life history and population dynamics of the Edible dormouse. We also aim to standardise the method for further population studies in Slovenia. These would form a basic step in undertaking wide scale monitoring and in developing the action plan on which a sustainable exploitation of the species should be based (Krystufek & Haberl 2001). Results on the population biology after the initial three years of field work are reported in this paper.

MATERIAL AND METHODS

Study area

The study took place on Mt. Kočevski Rog (south-central Slovenia), which is an isolate of the north-western part of the Dinaric Alps. The bedrock is corroded limestone with an infinite number of fissures and underground caverns. The area belongs to one of the most heavily wooded regions of Slovenia with 82% of the area forested. Since the forestry practice of selective cutting mimics natural disturbances (Yahner 1995), the entire forest ecosystem is in a semi-natural condition. The climate is humid continental with warm summers and cool winters. Mean July temperature in the town of Kočevje (altitude 460 m) is 17.8°C, mean January temperature is –1.6°C, and the annual average is 8.4°C. Precipitation is abundant (annual average of 1,523 mm) and fairly evenly distributed through the year; February, the driest month, receives 91 mm of precipitation and November, as the wettest, receives 168 mm. The growing season is consequently long (228 days). Snow cover lasts for 4–5

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months, from November to April, and temperatures are below freezing for an average of 62 days per year.

We selected two study sites: Pogorelec (altitude 590–620 m above sea level) and Komolec (740–780 m). Both sites are mainly under mixed beech *Fagus sylvatica* and fir *Abies alba* forest. Both used to be small villages, ruined during the Italian occupation in the summer of 1942 and never repopulated since. As a consequence, there are still present small abandoned orchards as well as single orchard trees, particularly in Pogorelec. Small meadows also continue to be maintained as part of a large game management system and the forest edges are densely overgrown by hazel *Corylus avellana*.

Wooden nest boxes of several designs were irregularly dispersed over an area of 5 ha in Pogorelec and were arranged in a line of 600 m in Komolec. They were placed >3 m above the ground, on suitable trees, with the entrance facing the tree trunk. Their number is evident from Table 1. Nest boxes were checked at monthly intervals. Dormice were anaesthetised using di-ethyl ether, sexed and weighed to the nearest gram. Ear tattoos were used to mark new animals individually (7 mm high characters produced by HAUPTNER HERBERHOLZ). In sex ratio calculations we also included specimens trapped during traditional dormouse hunting in September and October. Statistical tests were performed using the software Statistica software (Release 5.5, 1999).

**RESULTS AND DISCUSSION**

*Nest box survey*

Results of the nest box surveys are summarised in Table 1. Among those nest boxes that were checked at least 10-times, only three never contained a single dormouse, although two of these had either a characteristic nest inside or dormouse excrement on the roof.

The proportion of nest boxes found occupied on each visit varied between 6 and 53%. It was evidently lower in a non-reproductive year (2000), and was highest in October 1999 and 2001 (53.5 and 43.3% respectively; Table 1). On average, approximately one fifth of the nest boxes contained dormice (mean = 24.1%, median = 18.8%), and up to about one third of them were occupied by adult animals in July and August 2001. VIETINGHOFF-RIESCH (1955) and GAILSER et al. (1977) report a maximum of about 25% of nest boxes occupied. JUŠKAITIS (2000) found 30–60% of nest boxes occupied in Lithuania in September surveys and MILAZZO et al. (2002) reported 34–80% in Sicily. TVRTKOVIĆ et al. (1996) recorded even higher autumn occupation of nest boxes (= 80%) in north-western Croatia during the peak year of 1995.

The proportion of nest boxes with dormice increased from spring to autumn in all three years, but, in the non-reproductive year of 2000 it was lower in September than in August (Fig. 1). Contrary to this, the mean number of adults per occupied nest box was highest in spring and then decreased towards autumn, when it
Table 1. Summary statistics of the occurrence of Edible dormouse in nest boxes on Mt. Kočevski Rog over three years. NB – number of nest boxes; NB* – number of nest boxes occupied by dormice; NB% – percentage of occupied nest boxes; NM – number of adult males; NF – number of adult females; NT – total number of adults (this number can be higher than the sum of adult males and females since some animals escaped before being sexed); NJ – number of juveniles (* – juveniles present but not handled); R% – percentage of adults recaptured.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Day</th>
<th>NB</th>
<th>NB*</th>
<th>NB%</th>
<th>NM</th>
<th>NF</th>
<th>NT</th>
<th>NJ</th>
<th>R%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>July</td>
<td>3</td>
<td>34</td>
<td>5</td>
<td>14.7</td>
<td>3</td>
<td>2</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>30</td>
<td>34</td>
<td>5</td>
<td>14.7</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>40.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sept.</td>
<td>5</td>
<td>47</td>
<td>11</td>
<td>23.4</td>
<td>6</td>
<td>5</td>
<td>11</td>
<td>20</td>
<td>18.2</td>
</tr>
<tr>
<td></td>
<td>Oct.</td>
<td>2</td>
<td>60</td>
<td>32</td>
<td>53.3</td>
<td>3</td>
<td>3</td>
<td>52</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>June</td>
<td>3</td>
<td>68</td>
<td>4</td>
<td>5.9</td>
<td>8</td>
<td>9</td>
<td></td>
<td>62.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>22</td>
<td>70</td>
<td>8</td>
<td>11.4</td>
<td>12</td>
<td>4</td>
<td>16</td>
<td>56.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aug.</td>
<td>11</td>
<td>31</td>
<td>6</td>
<td>19.4</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>75.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sept.</td>
<td>3</td>
<td>70</td>
<td>7</td>
<td>10</td>
<td>5</td>
<td>4</td>
<td>9</td>
<td>33.3</td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>May</td>
<td>2</td>
<td>71</td>
<td>13</td>
<td>18.3</td>
<td>11</td>
<td>2</td>
<td>13</td>
<td>38.5</td>
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</tr>
<tr>
<td></td>
<td>June</td>
<td>2</td>
<td>71</td>
<td>9</td>
<td>12.7</td>
<td>7</td>
<td>6</td>
<td>13</td>
<td>38.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>7</td>
<td>71</td>
<td>26</td>
<td>36.6</td>
<td>23</td>
<td>11</td>
<td>34</td>
<td>44.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aug.</td>
<td>4</td>
<td>71</td>
<td>25</td>
<td>35.2</td>
<td>16</td>
<td>8</td>
<td>25</td>
<td>*</td>
<td>54.2</td>
</tr>
<tr>
<td></td>
<td>Sept.</td>
<td>8</td>
<td>82</td>
<td>32</td>
<td>39</td>
<td>11</td>
<td>13</td>
<td>24</td>
<td>101</td>
<td>66.7</td>
</tr>
<tr>
<td></td>
<td>Oct.</td>
<td>7</td>
<td>83</td>
<td>36</td>
<td>43.4</td>
<td>2</td>
<td>16</td>
<td>18</td>
<td>61</td>
<td>55.6</td>
</tr>
</tbody>
</table>

Fig. 1. Changes in the percentage of nest boxes with dormice (broken line; right Y-axis) and of mean number of adult dormice per occupied nest box (solid line; left Y-axis) over three years according to month.
was lowest (Fig. 1). The tendency of adult dormice to aggregate in spring possibly reflects social interactions prior to the start of reproductive activities.

**Recaptures**

We marked a total of 316 specimens and 29.4% of them were recaptured between one and eight times. The proportion of recaptures was slightly higher in Pogorelec than in Komolec (Table 2), but the difference was not significant. Thus, our results do not suggest that a linear arrangement of nest boxes is less suitable in population studies as compared to a grid arrangement. The majority of recaptures (= 78.5%) were obtained only once. Only two dormice were recaptured more than three times: one male five times and one female eight times. The recapture rate was thus surprisingly low with about half the animals seen in regular monthly checks being already marked (monthly mean = 52.5%; 2000 and 2001 samples pooled). More surprisingly, the proportion of marked animals did not increase with time (r = 0.08, not significant; samples 2000 and 2001 pooled).

Following four months of marking dormice in 1999, recaptured individuals formed between 33.3–75.0% of the adult population in monthly samplings in the consecutive years 2000 and 2001 (median = 54.2%, quartile range = 24.0%, N = 10; Fig. 2). The median was higher in 2000 (57.7%) than in 2001 (49.8%), the difference however was not significant (Kruskal-Wallis H = 0.183).

Considering the long life expectancy of the Edible dormouse (up to 7 years in central Slovenia; PISTOTNIK 2002), such a low recapture rate is puzzling. Moreover, the relatively low numbers of occupied nest boxes (i.e. about one quarter, see above), left plenty of nesting places available but unused. Compared to the home ranges of adult edible dormice (up to 2.4 ha; PROPERZI et al. 2002a), our study plot (5 ha in Pogorelec) was fairly small. However, BIEBER (1998), who worked on even smaller grids than we did (1 ha), had 955 recaptures of 224 dormice over two years of study.

**Table 2.** Results of monitoring of the Edible dormouse population on Mt. Kočevski Rog over three years according to the site. N – number of individuals; Nc – total number of captures; Nr – number of recaptures; %Nr – percentage of recaptures; R – percentage of dormice recaptured once (R1), twice (R2), or more than twice (R>2). See text for further details.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Nc</th>
<th>Nr</th>
<th>% Nr</th>
<th>R1</th>
<th>R2</th>
<th>R&gt;2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pogorelec</td>
<td>176</td>
<td>252</td>
<td>54</td>
<td>30.7</td>
<td>79.6</td>
<td>13.0</td>
<td>7.4</td>
</tr>
<tr>
<td>Komolec</td>
<td>140</td>
<td>188</td>
<td>39</td>
<td>27.9</td>
<td>76.9</td>
<td>23.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Total</td>
<td>316</td>
<td>440</td>
<td>93</td>
<td>29.4</td>
<td>78.5</td>
<td>17.2</td>
<td>4.3</td>
</tr>
</tbody>
</table>

*Acta zool. hung. 49 (Suppl. 1), 2003*
Population density

Population density is given here as the number of individuals per 100 nest boxes (ind. per 100 NB). The two localities have been pooled in order to increase sample size. Density of adults was lowest in October 1999 (5 ind. per 100 NB) and highest in July 2001 (47.8 ind. per 100 NB). Maximum densities recorded in 1999 and 2000 were surprisingly similar, namely 23.5 (July 1999) and 25.8 ind. per 100 NB (August 2000), respectively (Fig. 3). Thus, the intense reproduction in 1999 had no perceived effect on animal density in the subsequent year. Even more surprising is the high density recorded in 2001 (47.8 ind. per 100 NB in July), in the year following the reproductive failure of the previous season (see also below).

Mean monthly densities of adults varied, both between months (Fig. 3) and between years (Fig. 4). Coefficients of variation over months of the same year were 52.8% in 1999, 35.5% in 2000, and 38.5% in 2001, thus indicating density estimates to depend heavily on the month. The highest densities were recorded in July (1999 and 2001) or August (2000), however variances over the three years were also high for these two months (Fig. 4).

It is clear that our density estimates suffer from a bias. In 2001, a 2.4-fold increase was recorded from June (19.7 ind. per 100 NB) to July (47.8 ind. per 100 NB). The lack of spring reproduction in the Edible dormouse means that this increase cannot be genuine, but must reflect some noise in the data set which remains unknown to us. Assuming that migrations did not significantly affect the popula-

![Fig. 2](image_url)

**Fig. 2.** Percentage of recaptured adult dormice in monthly samples of 2000 and 2001. Total number of adults is in parentheses.
Fig. 3. Changes in number of edible dormice (per 100 nest boxes) according to month over three seasons. Adults are shown as shaded columns and animals born in the same year as empty ones.

Fig. 4. Box plot of variation in density estimates of the Edible dormouse (animals per 100 nest boxes) according to month over a three year period. Adults are shaded and juveniles are blank columns. Mean (bar) and standard deviation (whiskers) are given for each month. Coefficients of variation are given for adults above the whiskers. Number of seasons is in parentheses.
tion structure under study, we evidently did not sample the entire population. Perhaps the semi-natural forest structure, with abundant hollow trees, and because plenty of underground spaces exist due to corroded karstic bedrock, secure nesting places may not be a resource of limited availability. Perhaps many dormice find alternative nest sites and do not always use the nest boxes?

Seasonal changes in sex ratio, as well as a variable time of emergence from hibernation and its start clearly suggest that the entire population is not active simultaneously over the entire active period. This is possibly further exacerbated by summer torpor. Although records of lethargic animals are all from nest boxes (MORRIS 1997b, NOWAKOWSKI 2001; own observations), such a dormancy is likely to occur also in the karstic underground, even more so as this micro-cavernicolous environment is characterised by high humidity and low, but stable temperature (c. 8°C in central Slovenia; MIHEVC 1996).

Observations from central Slovenia suggest that copulatory activities take place in July (KRYŠTUFEK 2001). Presumably, the largest number of adult dormice is simultaneously active in this month, which roughly agrees with the present results. Accordingly, July seems to be the most suitable period for undertaking density estimates. A similar conclusion has been reached by SCHLUND & SCHARFE (1997).

Juvenile density was lowest in September 1999 (42.6 ind. per 100 NB) and highest in September 2001 (123.2 ind. per 100 NB), while no juveniles were recorded in autumn 2000. In 1999 the density was higher in October (86.7 ind. per 100 NB) than in September, but the opposite occurred in 2001, with 73.5 ind. per 100 NB in October. Juveniles strongly outnumbered adults in both reproductive seasons, by a factor ranging from 1.8:1 in September 1999 to 17.3:1 in October of the same year. The October ratio is evidently biased due to the earlier start of hibernation of adults removing them from the active population earlier than the juveniles.

We attempted to estimate density in absolute terms for 2001 in the plot at Pogorelec. From May to October 29 adults were identified on 5 hectares, which gives an adult density of c. 6 per ha. Including juveniles also (78 in total), the maximum density was c.15.5 per ha, approximately a 2.5-fold increase due to reproduction. Various densities have been reported previously for the Edible dormouse: 0.6–1.8 ha⁻¹ in England (HOODLESS & MORRIS 1993), between 1 ha⁻¹ (PILASTRO 1990) and 3.0–34.4 ha⁻¹ in Italy (PROPERZI et al. 2002b), ≥1 ha⁻¹ in Moravia (GAISLER et al. 1977), 0.7–5 ha⁻¹ in Germany (VIETINGHOFF-RIESCH 1955), 1–11 ha⁻¹ in Poland (JURCZYSZYŃ 1995), 30 ha⁻¹ in the Caucasus (OGNEV 1963), and 80.7 ha⁻¹ (c. 40 adults per ha⁻¹) in Croatia (TVRTKOVIĆ et al. 1996). Putting aside the very high estimates given by TVRTKOVIĆ et al. (1996), our results suggest the density in Kočevski Rog to be modest.
Sex ratio

Among 14 monthly samples, the sex ratio deviated significantly from a balanced 1:1 in five of them (Fig. 5). It tended to be male biased between May and July and female biased in October. This accords with the observations of BIEBER (1998) and KRYŠTUFEK (2000). The sex ratio of juveniles was balanced in 2001, but slightly male biased in October 1999 (Table 3). Reasons for skewed sex ratios are not known.

Reproduction

Reproductive activity was recorded in 1999 and 2001, but not in 2000. Males with scrotal testes and females with vaginal plugs were first recorded on July 3, 1999, and July 7, 2001, respectively. The reproductive gap in 2000, which coincided with the lack of beech mast, fits earlier observations from Germany (LÖHRL 1955, VIETINGHOFF-RIESCH 1955, BIEBER 1997) and England (BURGESS et al.

Table 3. Sex ratios in young Edible dormice from different seasons. Specimens obtained during traditional dormouse hunting are also included. $\chi^2$ denotes significant deviation from a balanced sex ratio 1 : 1. **$p < 0.01$, n.s. not significant. N – total sample

<table>
<thead>
<tr>
<th>Sample</th>
<th>N</th>
<th>Males (%)</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>October 6th, 1999</td>
<td>139</td>
<td>55.1</td>
<td>8.813**</td>
</tr>
<tr>
<td>September 8th, 2001</td>
<td>97</td>
<td>56.7</td>
<td>1.742n.s.</td>
</tr>
<tr>
<td>October 7th, 2001</td>
<td>172</td>
<td>51.1</td>
<td>0.087n.s.</td>
</tr>
</tbody>
</table>

Fig. 5. Temporal changes in sex ratio in monthly samples of the adult Edible dormouse over three seasons. Significant deviation from 1 : 1 ratio is indicated by an asterisk: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Males are shaded

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Two hypotheses were formulated to explain lack of litters under conditions of no mast availability. VIETINGHOFF-RIESCH (1955) believed this to be due to resorption of embryos, while BIEBER (1998) suggested that males do not invest energy in reproduction during years of low food availability. Like BIEBER (1997, 1998) and BURGESS et al. (2002), we did not record a single male with scrotal testes in June or July 2000 (N= 20) which inclines us towards the belief that no sexual activity occurred at all. It is noteworthy, however, that adults tended to aggregate in spring 2000 to the same extent as was the case in the two non-reproductive years (cf. Fig. 1).

In the sample of July 7, 2001, twelve males were found with enlarged/scrotal testes and another eleven had abdominal testes. The two categories of males did not differ in body mass (t= 0.308, not significant). Scrotal males were still recorded on August 4, 2001, when six out of seven females were either heavily pregnant (N = 2) or already with newly-born juveniles (N= 4).

The number of young per nest box varied between 1 and 10 in September and 1–7 in October. Juvenile groups were significantly larger in September than in October (Kolmogorov-Smirnov test, p <0.01). Mean litter size in this part of Slovenia, based on counts of embryos and placental scars, is 5.8 (N= 9; KRYŠTUFEK 2001) which is higher than the mean for pooled September samples from nest boxes (= 4.9; N = 24). A very similar average litter size (= 4.7) was estimated from nest boxes by PILASTRO (1992), but values reported from Turkish Thrace (= 6.05; ÖZKAN et al. 2002) and England (= 6.69; BURGESS et al. 2002) are higher.

Although early September juvenile groups presumably represented entire litters, only 58% of them were with adult lactating females, evidently their mother. On the other hand, we did not identify a single communal nesting among 15 September groups. Contrary to this, PILASTRO (1992) found c. 44% of females nesting in communal nests. Communal nesting is said to be common also in mixed montane forest at Tri Kalići, north-western Croatia (i.e. in a region close to our study plot with similar vegetation and climate) during the peak year of 1995 (TVRTKOVIC et al. 1996).

September clusters of young associated with their mothers tended to be larger than those of juveniles found alone (Kolmogorov-Smirnov test, p <0.05). The smallest juvenile, found alone in a nest box, weighed only 32 g and was possibly abandoned. There were no differences in body mass between litters that were together with their mothers and juveniles living alone (t= 0.182, not significant). October groups were significantly smaller than September ones (Kolmogorov-Smirnov test, p<0.05). Ten juvenile groups from October 2001 (number of juveniles 2–4; mean= 3.0) were recaptures from the previous month; six groups were entirely of kin animals and four of them were still together with their mothers.
CONCLUSIONS

Nest boxes, as dens, were not a resource in short supply in our study. On average, only 24% of nest boxes were found occupied by dormice, and this proportion never rose above 53%.

Recapture rate was low (29.4% of marked animals), multiple recaptures were exceptional, and the proportion of recaptured dormice did not accumulate as a function of time. Evidently only a fraction of the whole population used the nest boxes.

Numbers of adults were low in spring and autumn, peaking in July and August. These two months are presumably the most suitable for population density estimates.

Adult population density was estimated as c. 6 dormice per ha in 2001, and the total density at the end of reproduction was 15.5 per ha. Compared to the situation elsewhere, these are modest values.

Sex ratios tended to be male biased in the first half of the season and female biased afterwards. This pattern seems to be widespread. Juvenile sex ratio generally did not deviate significantly from a balanced 1 : 1.

Coinciding with the lack of beech mast in 2000, no scrotal males were recorded and there was no reproduction. Such a response of edible dormice to the life cycle of beech seems to be general where it is the dominant tree species in the deciduous forest ecosystem.

Mean litter size was estimated as 4.9. No communal nestling was recorded, but juveniles were frequently found alone in nest boxes, already at the beginning of September.

Acknowledgements – We are most grateful to the members of the Dormouse Club ‘Polh’ for their enthusiastic help in nest box surveys. Our special thanks are to Mr. STANE KUMELJ for his continuous support and the efficient organisation of the field work.

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