Short communication

Response of *Apodemus flavicollis* to conditions at the altitude limit in the Western Tatra Mountains

By Natálie Martínková, D. Žiaj, and L. Kocian

Department of Zoology, Comenius University, Bratislava, Slovakia

Receipt of Ms. 10. 05. 2000
Acceptance of Ms. 09. 11. 2000

Key words: Rodentia, population dynamics, subalpine habitat

The occurrence of a species at the distribution border exhibits a dynamic pattern which sensitively reacts to the changing conditions of the environment as well as the state of the population of the species (Begon et al. 1997). The distribution border is set by at least one environmental factor close to its limiting value. Regardless of the patchiness of suitable habitat within the distribution range, the quality of habitat changes towards the distribution border from optimal through suboptimal to pessimal. Local populations adjacent to the distribution border react to the changes of local conditions and become extinct or are recolonized (Kozakiewicz 1993; Hanski et al. 1996) causing the distribution border to expand and contract (Angelstam et al. 1987).

The distribution border of *Apodemus flavicollis* (Melchior, 1834) includes a wide range of habitats and diverse climatic conditions due to its large distribution range (Niethammer 1978; Lura et al. 1995). The local occurrence and altitude tolerance of the species seems to be affected by the requirements of a continental climate (Lura et al. 1995) and food abundance (Angelstam et al. 1987). The seed abundance appears to be a critical factor affecting the distribution and population dynamics of *A. flavicollis*. Populations are usually non-cyclic but density outbursts occur in years of high seed crop (Gurnell 1985; Angelstam et al. 1987; Pucek et al. 1993; Žiaj and Kocian 1994). Considering habitat, *A. flavicollis* prefers mature deciduous forests with an open ground layer (Gurnell 1985). Therefore, the altitude range stretches from sea-level (Greece, Italy) to about 2000 m (Alps) (Niethammer 1978; Yoccoz 1992).

The aim of this study is to investigate the population response and habitat selection of *A. flavicollis* to conditions at an altitude border in an upper subalpine zone.

The research was conducted in the Western Tatra Mts., Slovakia. The locality in the National Nature Reserve Roháče Lakes (elevation of the trapping grids: 1 570–1 600 m a.s.l.) represents a transition between a subalpine and an alpine zone due to climatic conditions caused by north-western orientation of the mountain range. The habitat is characterized by scattered patches of *Pinus mugo* cover, the occurrence of wet subalpine meadows, and a talus gradient of various rock sizes partially overgrown with vegetation dominated by *Juncus trifidus*.

Small mammal live-trapping was carried out in June, August, and October 1991–99.
with the exception of 1992 and 1994 when trapping was carried out twice, in July and October. In the years 1991–95 two trapping grids were established, one 1 ha in size containing 10×10 live-traps, and the other 0.5 ha containing 6×8 live-traps, both with 10 m spacing. In 1996–99 another 1 ha trapping grid was added, and the trap layout was modified in the previous two grids giving in total two 1 ha grids with 7×7 live-traps at 15 m intervals, one 1.3 ha grid containing 10×13 live-traps at 10 m intervals. The traps were baited with rolled oats, operated for 3–5 consecutive nights, and were checked twice daily. Animals were marked by toe-clipping, data on species, body weight, sex, reproductive status (scrotal testes, open vagina, gravidity, lactation), and body length were recorded.

The habitat characterization was modified from DUESER and SHUGART (1978, 1979), and M’CLOSKEY and FIELDWICK (1975). The habitat at each trap point was characterized for the years 1996–98. The habitat variables were recorded in the summer series 1996–97 in a circle (diameter 10 m, or 15 m) centered on the trap. At each point, the proportion of the area covered by rocks, by rocks smaller and greater than 50 cm in diameter was registered. The vegetation structure was estimated by the proportion of the area covered by litter, herbs, shrubs and trees (including Pinus mugo), and specifically by dominant plant species: Juncus trifidus, Vaccinium myrtillus, Pinus mugo, and grasses other than J. trifidus. The total number of plant species present at the sample was recorded. The vegetation density below or above 50 cm was counted as the number of touches on a stick at 20 check-points forming a cross 10×10 centered on the trap and expressed as percent. The heights of herb, shrub and tree layers were measured at the same intersection depending on the availability of the given layer. Finally, the distance to the nearest patch of Pinus mugo larger than 30 m in diameter was recorded.

Discriminant function analysis was used to explore the microhabitat preferences of A. flavicollis. A qualitative model was chosen where trap points used by at least one resident individual, defined by the time span between first and last capture being at least two days, were referenced against trap points not used by resident individuals.

During the research time span (7200 trap-nights) 12 species of small ground mammals were registered: Sorex araneus, S. minutus, S. alpinus, Neomys sp., Apodemus flavicollis, Clethrionomys glareolus, Microtus nivalis, M. agrestis, M. tetricus, Muscardinus avellanae, Mustela nivalis, and M. erminea (Ziak and KOCIAN 1994; N. MARTÍNKOVÁ, D. ŽIAK, L’ KOCIAN unpubl.). Apodemus flavicollis has only been captured in the years 1993, 1996, and 1998 (Fig. 1). A total of 44 individuals was caught, 30 males and 14 females, a significant deviation from an expected sex ratio of 1:1 (χ² = 5.8, p = 0.016). Except for two individuals, all animals were captured in one trapping series. The first exception was a sexually inactive female trapped in August and October 1993, and the second was a male trapped in August and October 1996, which was in breeding condition in August, but not so in October. No individuals were registered to stay the entire winter at the locality. Recaptures have also been rare with 60% of all individuals captured only one or two times, the average number of captures per individual being 2.3 and the maximum was eight (the sexually inactive female present in series VIII/93 and X/93). Individuals captured five or six times were all trapped in August 1996. No females were found demonstrating perforated vagina, or lactation, but one female may have been pregnant in August 1993. Among males, twenty-two possessed scrotal testes.

The discrimination of the preferred habitat of A. flavicollis was significant at p < 0.001. The discrimination model correctly classified 77% of unused trap points and 76% of used trap points (Tab. 1). Habitat variables that possess the highest absolute values of standardized coefficients influenced to a greater extent the position of samples on the discriminant function axes. This means that the variation of these variables best describes the differences between preferred and non-preferred habitat (LEGENDRE and LEGENDRE 1983). Variables associated with
A. *flavicollis* in subalpine habitat

![Graph showing minimum number of *Apodemus flavicollis* known to be alive each season. Total number of yellow-necked mice being 44 individuals, where one individual was present in series VIII/93 and X/93, and another VIII/96 and X/96. Starting June 1996 methodology was changed so that 228 live-traps on three trapping grids were used instead of 148 on two grids.](image)

**Fig. 1.** Minimum number of *Apodemus flavicollis* known to be alive each season. Total number of yellow-necked mice being 44 individuals, where one individual was present in series VIII/93 and X/93, and another VIII/96 and X/96. Starting June 1996 methodology was changed so that 228 live-traps on three trapping grids were used instead of 148 on two grids.

**Table 1.** Discriminant function analysis coefficients characterizing habitat occupied by resident (time span between first and last capture being at least two days) individuals of *A. flavicollis* (*p* < 0.001). Habitat variables are ordered with regard to their importance in discriminating preferred and non-preferred habitat based on the absolute value of standardized coefficients.

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Standardized coef. of DFA</th>
<th>Average</th>
<th>Stand. Dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation density above 50 cm</td>
<td>-0.819</td>
<td>0.31</td>
<td>0.22</td>
</tr>
<tr>
<td>Distance from <em>Pinus mugo</em> patch</td>
<td>0.813</td>
<td>8.69</td>
<td>22.84</td>
</tr>
<tr>
<td><em>Pinus mugo</em> cover</td>
<td>0.789</td>
<td>0.35</td>
<td>0.28</td>
</tr>
<tr>
<td>Area covered by rocks less than 100 cm in diameter</td>
<td>-0.417</td>
<td>0.06</td>
<td>0.14</td>
</tr>
<tr>
<td><em>Juncus trifidus</em> cover</td>
<td>-0.399</td>
<td>0.07</td>
<td>0.17</td>
</tr>
<tr>
<td>Herb height</td>
<td>-0.393</td>
<td>35.05</td>
<td>15.28</td>
</tr>
<tr>
<td><em>Vaccinium myrtillus</em> cover</td>
<td>-0.263</td>
<td>0.36</td>
<td>0.25</td>
</tr>
<tr>
<td>Grass cover</td>
<td>-0.246</td>
<td>0.43</td>
<td>0.31</td>
</tr>
<tr>
<td>Shrub height</td>
<td>-0.242</td>
<td>24.13</td>
<td>9.37</td>
</tr>
<tr>
<td>Vegetation density below 50 cm</td>
<td>-0.240</td>
<td>0.81</td>
<td>0.14</td>
</tr>
<tr>
<td>Area covered by rocks more than 100 cm in diameter</td>
<td>-0.180</td>
<td>0.06</td>
<td>0.11</td>
</tr>
<tr>
<td>Number of plant species</td>
<td>-0.125</td>
<td>8.06</td>
<td>2.98</td>
</tr>
<tr>
<td>Litter cover</td>
<td>0.071</td>
<td>0.09</td>
<td>0.16</td>
</tr>
<tr>
<td>Tree height</td>
<td>-0.060</td>
<td>148.40</td>
<td>61.55</td>
</tr>
<tr>
<td>Total area covered by rocks</td>
<td>0.031</td>
<td>0.12</td>
<td>0.22</td>
</tr>
</tbody>
</table>
Pinus mugo cover showed a strong indication that Apodemus flavigollis preferred a habitat dominated by P. mugo. However, the raw data show that no used trap was located within the dwarf pine cover (neither trap point had negative values of distance to the nearest P. mugo patch). This would characterize the habitat of occurrence of A. flavigollis as the edge of P. mugo stands. The typical habitat of Apodemus flavigollis is described as open mature forests, preferably deciduous with open ground level. Its occurrence at ecotones, grasslands or shrubby habitat is considered atypical (Niethammer 1978; Gurnell 1985). Yet, the ecotone of dwarf pine and subalpine meadows is the habitat preferred by this species in the subalpine zone in western Tatras. Here, large seeds forming the base of A. flavigollis diet (Niethammer 1978; Smettan 1996) are in short supply as well as in coniferous forests in general. These are usually considered suboptimal habitats or serving as corridors (Angelstam et al. 1987; Kotzageorgeis and Mason 1996; Šmaha 1996).

Since the locality does not enable individuals to remain through the winter, but their survival is possible during the vegetation season, it could be considered a suboptimal habitat for this species (Gliwicz 1989, 1993). However, sporadic occurrence of A. flavigollis at the locality indicates that the species is not a regular seasonal resident to this area. This assumption is supported also by the fact that the sexual ratio is deviant from the expected values, which occurs in dispersers (Gliwicz 1988), i.e., most individuals were present at the locality exclusively in a single trapping series and by low number of captures per individual. In a habitat in which reproduction per individual is low, population density has a tendency to decline (Gaines et al. 1994) and the population shows a high turnover rate (Mazurkiewicz 1991, 1994) in this type of habitat, is referred to as a “sink” habitat. This is the case for the area investigated in the present study.

The appearance of yellow-necked mice can be explained by high population densities in altitudes below the research area. Apodemus flavigollis tends to occur in “nuclei” within occupied forests, which are relatively stable centers of occurrence, and spatially oscillate depending on the population density (Gurnell 1985). If we assume a positive correlation between population density in a given nucleus and the effort that the dispersers make to travel from the nucleus (distance × number of dispersers), then population density at our study plots indicates the culmination phases at lower altitudes. A crowded habitat would force subdominant individuals to seek vacant space and they will appear at our study plots. If such a situation occurs, the population probably exhibits a three year cycle.

Acknowledgements

The research in the National Nature Reserve was carried out with the permission of the Slovak Ministry of Environment. We are indebted to Mr. Halák and Mr. Hudáček (Tatra National Park), their support is acknowledged. Financial support of the research provided by VEGA (grant number: 1/4140/97, assigned to L. Kocian).

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Authors’ addresses:
NATÁLIA MARTÍNKOVÁ, Department of Zoology, Charles University, Vinohradná 7, 12844 Praha 2, Czech Republic (e-mail: natalia@natur.cuni.cz); DÁVID ŽIAK, and L’UDOVIT KOČIAN, Department of Zoology, Comenius University, Mlynská dolina B1, 84545 Bratislava, Slovakia.