RESPONSE OF THE BANK VOLE *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780) TO THE ODOUR AND PRESENCE OF HETEROSPECIFICS AS MEASURED BY SCENT MARKING BEHAVIOUR AND TRAPPING IN DOUBLE TRAPS IN AN ALDER FOREST

ABSTRACT: The paper addresses the following issues: (1) does the bank vole response to odours of other rodent species by urine and faeces marking (2) does this reaction depend on the species, (3) does the amount of odour influence the marking, and (4) the response of bank voles to the presence of heterospecifics, and its comparison with the response of marking the odour deposited by these species. The study was conducted in a *Ribo nigri-Alnetum* swamp located in the Kampinos National Park, central Poland (52°20’N and 27°25’E). To observe scent marking, white paper sheets (15 × 21 cm) supplied with sponges (1 cm³) soaked in odour of particular rodent species were exposed in the forest along a line ca 1200 m long. Odour donors were countryside species: a) phylogenetically close to the bank vole, such as *Microtus agrestis* (L.) and *M. oeconomus* (Pallas), b) sympatric, such as *Apodemus flavicollis* (Melchior) and *A. sylvaticus* (Melchior), or occupying a different habitat *A. agrarius* (Pallas), and allopatric species such as *Meriones unguiculatus* (Milne-Edwards), *Mesocricetus auratus* (Waterhouse), and *Octodon degus* (Bennet). Also sheets with the odour of bank vole and control sheets without odour were exposed. Marking was analysed basing on the number of marked sheets (*marking extensity*), and on the number of urine and faeces marks on sheets (*marking intensity*). During the three study years, a high marking extensity was observed for the odours of phylogenetically close species. The odours of sympatric species were marked less frequently and with a higher variability in successive years. The lowest marking extensity was found for geographically alien (allopatric) species. The mean number of marks per sheet did not differ significantly between the species.

To examine the effect of odour quantity on marking, a line (ca 630 m long) made up of sheets provided with 1, 3, and 5 sponges with *M. oeconomus* and *C. glareolus* odour, and of control sheets was established. The increase in the number of sponges with heterospecific odour had no effect on the extensity and intensity of marking. Significant difference in marking extensity, but not in marking intensity, was found in the case of conspecific odour.

The response of bank voles to the presence of heterospecifics was examined based on the number of captures in double-traps with a live individual. In the forest, a line of 30 double-traps placed every 10 m was established, containing single *M. oeconomus*, *A. flavicollis*, or *C. glareolus*. Bank voles were more often captured in traps with conspecifics than with heterospecifics. Thus, bank voles avoid encounters with heterospecifics but they do not avoid marking their odour (marking the heterospecific odour was not lower than marking conspecifics and control). It may suggest that under natural conditions, interspecific communication is largely mediated through olfactory cues.

KEY WORDS: *Clethrionomys glareolus*, heterospecifics, scent marking, olfactory communication
1. INTRODUCTION

Olfactory communication, which is widespread among small rodents, is important not only for intraspecific but also for interspecific interactions (Doty 1986, Krasnov and Khokhlova 1996, Dulac and Torello 2003, Lopucki and Szymroszczyk 2003). Rodents emit and receive olfactory cues due to which they are oriented in space, can find food sources, inform other individuals about their sex, breeding condition, social status, or individual identity (Osipova and Rutovskaya 2000, Andrzejewski 2002, Johnston 2003). Olfactory cues are also used for identification of the species. Many authors have found that rodents can discriminate between their own odour and the odour of heterospecifics (Jannett 1981, Stoddart and Smith 1984, Dempster and Perrin 1990), though the response to the odour of another species can show differences. In the literature, there are examples of avoidance of heterospecific odour, as well as of a similar or greater interest in it than in the conspecific odour. For example, Drickamer (1984) found that sympatric rodents *Peromyscus leucopus* (Rafinesque) and *P. maniculatus* (Wagner) were captured significantly more frequently in traps marked with conspecific odour than with the odour of a sympatric species. In an experiment performed by Stoddart and Sales (1985) also Apodemus sylvaticus more often selected traps marked with conspecific odour and avoided those with odour of other rodent. A similar interest in conspecific and heterospecific odour was noted by Andrzejewski et al. (1997). In a forest population of bank voles they were trapped with the same frequency in snap-traps marked with conspecific odour and *A. sylvaticus* odour. Drickamer et al. (1992) found that *Mus musculus* (L.) showed preference for conspecific odour, were neutral to *Microtus ochrogaster* (Wagner) odour, and avoided traps marked with *P. leucopus* and human odour. The cases when heterospecific odour increased attraction are rarely described in the literature (Sokolov et al. 1983 in Krasnov and Khokhlova 1996).

Olfactory discrimination among species was tested by different methods, and referred to different behaviour types of rodents. In laboratory experiments we measured the time that rodents spent at an odour, or the first choice, for example in the Y apparatus (Krasnov and Khokhlova 1996, Gouat et al. 1998). The field methods were based on the trappability of individuals in traps marked with heterospecific odour (Drickamer et al. 1992, Gurnell and Little 1992). The response to heterospecific odour includes also deposition of the own scent marks near the marks of another rodent. Few studies conducted as yet focused on olfactory responses to scent marks of other species and mainly under laboratory conditions. Rozenfeld and Rasmont (1987, 1991) found that bank voles deposited scent marks not only in the presence of conspecifics or scent marks left by them but also in the presence of heterospecifics or their odour.

Under natural conditions, Owadowska (1999) and Krywko (2003) observed scent marking in the bank vole. The method used for the observation of scent marking in a natural bank vole population was based on exposing different requisites that could be marked by these animals. This method made it possible to investigate the olfactory response by bank voles to different habitat components (Krywko 2003) and to odours of other individuals in the population (Owadowska 1999). The same method was applied in the present study to analyse the marking response of the bank vole to odour depositions of other rodent species.

As rodents often live in multi-species communities (Hansen et al. 1999, Gliwicz 1981) using the same space and food resources, it may be interesting to know the role of direct contacts among individuals in interspecific interactions as opposed to indirect contacts mediated through olfactory cues left in the habitat. The papers by Andrzejewski and Olszewski (1963), Kalinowska (1971), or Jonge (1980) show that rodents avoid direct contacts with heterospecific individuals. But responses to odour marks of other species suggest that olfactory cues of one species provide information that can be recognised to some extent by individuals of another species. Thus, information transfer by marking scent marks deposited by another rodent can serve as a form of interspecific communication.
The objectives of this paper were:

(1) to test whether bank voles respond to odour deposited in the habitat by other rodent species by marking them with urine and faeces;

(2) to test whether bank voles can recognize other species of rodents, based on olfactory cues, which can be expressed in differential frequency of marking these cues;

(3) to test whether the amount of odour affects marking;

(4) to examine the response of bank voles to the presence of heterospecifics, and to compare it with the marking response to the odour deriving from these species.

2. STUDY AREA

The study was conducted in forest complex of the Kampinos National Park located near Warsaw, central Poland. The Park covers an area of 38 544 ha. Because of its natural and social value, this Park has been recognized as a Biosphere Reserve by UNESCO. The experiments were conducted in western part of the Park (52°20'N and 20°25'E) in a natural forest community represented by a Ribo nigri-Alnetum swamp 110 years old. This community covers an area of about 8 km. The tree stand is dominated by Alnus glutinosa (L.) with a small admixture of Betula pendula (L.). The undergrowth consists mainly of Prunus padus (L.), Frangula alnus (Mill.), and Ribes nigrum (L.). The dense herb layer comprises abundant sedges, ferns, and Urtica dioica (L.). The forest bottom only to a small extent preserved the hummock-hollow structure typical of alder swamps. Also no stagnant water is observed in spring as a consequence of the lowering of water level, progressing across the Park for 20 years (Solon 2003). Numerous rotting stumps and complex root systems of alders, as well as diverse vegetation of the forest bottom create suitable conditions for the bank vole.

The study was conducted in Septembers of 1999–2001 and 2003–2004, when bank voles complete their breeding cycle. Observations of the density and species composition of small rodents indicate that bank voles are the dominant species in this area. Based on the number of captures in 1999–2001, 2003 and 2004, the following species composition and percentage contribution of different species were found: C. glareolus (95–99%), Apodemus flavicollis (Melchior) (1–5%), and A. agrarius (Pallas) (0–1%).

3. MATERIAL AND METHODS

3.1. Reaction to odour of different rodent species – scent marking

To find out whether bank voles scent mark odour of heterospecific rodents, a method was used that makes it possible to find scent marks deposited in the habitat. For this purpose, white sheets of xerographic paper with sponge soaked with the odour of a rodent species were exposed in the habitat. Urine stains and faeces pellet left on the paper around the sponge were clearly visible and easy to count (Owadowska 1999, Krywko 2003).

The deposited marks were counted only on rainless days to know their exact number. Based on the number of captures of bank voles (95–99%), it was assumed with a high probability that the marks on paper sheets were deposited by this species.

Paper sheets of a size of 15 × 21 cm were placed every 3 m in line. The line comprised 400 sheets and was about 1200 m long. A piece of polyurethane sponge (1 cm³) soaked with the odour of a rodent species or without odour was fastened in the middle of each sheet. The sheets without odour served as a control. The sheets were placed in random order. The line was surveyed once a day before afternoon. The sheets marked by bank voles were counted (marking extensity), as well as urine marks and faeces pellet deposited per sheets (marking intensity). At the same time, the checked sheets were replaced by new ones.

Native species of rodents and alien species, not occurring in Poland, were used as the donors of odours. The selection of species was based on their taxonomy and co-occurrence with the bank vole. Among Murinae these were Apodemus flavicollis and A. sylvaticus, the species commonly co-occurring with bank voles, and A. agrarius, the species occurring in a different habitat. Among Arvicolinae these were Microtus oeconomus and M. agrestis, and also...
C. glareolus. Alien species were represented by *Meriones unguiculatus* occurring in Mongolia, *Mesocricetus auratus* from Syria, and *Octodon degus* from Chile. The alien species derived from a laboratory. The native species were trapped in the Kampinos National Park, except for *A. sylvaticus* and *M. agrestis*, caught in the Słowiński National Park. This park is located at the Baltic coast, northern Poland. The rodents were captured in a grassland overgrown with shrubs in the buffer zone of the Park. All rodents were kept in the laboratory for at least one day and night before their odour was taken. They were fed *ad libitum* on oats, apples, and dandelion leaves. Only the adult males, and at least two individuals of each species were used as the odour donors.

Odours were collected using the method proposed by Andrzejewski and Owadowska (1994). Individuals were placed singly in 3-l jars with 50 pieces of sponge. The jars were covered with a wire screen to allow the inflow of air for the animals inside. Rodents were kept in them for 3 hours and then transferred to terrariums, whereas other individuals of the same species were placed to the jars for the next 3 hours. For 6 hours, the rodents deposited on sponges enough odour, most of all urine and faeces, and also such substances as saliva and excretions of skin glands. With this method it was possible to obtain the odour of the whole animal, and the polyurethane sponge served as a durable carrier of odours, easily used in the field. To prevent the decomposition of the odour and, as a consequence, the loss or change in the properties of odour, sponges were frozen (Drickamer et al. 1992). The sponges soaked with odour were fastened to paper sheets by means of a stapler. Separate staplers and tweezers were used for odour of each species. Paper sheets were prepared in the laboratory shortly before placing them in the forest.

The same method was used in each of three years of conducting experiment. Differences between them related to the species of rodents. Odour donors in the first year were native species: *A. agrarius*, *A. flavicollis*, *A. sylvaticus*, *M. oeconomus*, *M. agrestis*, and *C. glareolus*, and one alien species, *M. unguiculatus*. In that year preliminary characteristics of the response of voles was gained. In the following two years *A. sylvaticus* and *M. agrestis* were omitted but two alien species *O. degus* and *M. auratus* were added.

The experiment designed in 1999 and 2000 were conducted for 10 days, and in 2004 for 8 days. Each day, 50 paper sheets baited with the odour of a single species, and the same number of control sheets were exposed. In total, 500 samples were obtained for each species, and 450 control samples in 1999 – marks on 50 sheets being difficult to read. In 2004, a total of 400 samples were obtained for each species and the control. In sum, 11 150 sheets were exposed, of which 2109 were marked by bank voles that deposited 7619 urine marks and faeces pellets.

3.2. The effect of differential amount of odour on scent marking.

An experiment was designed to test whether an increase in the amount of odour left by conspecifics and heterospecifics could affect extensity and intensity of marking. The method applied was the same as in the first experiment. A total number of 210 paper sheets were placed every 3 m along a line that was about 630 m long. Each sheet was supplied with 1, 3, or 5 sponges soaked with rodent odour. Control sheets were supplied with one sponge without odour. The sheets were placed in random order. They were monitored once a day to determine the number of marked sheets and the number of marks per sheet, then the sheets were replaced by new ones.

The adult males of *M. oeconomus* and *C. glareolus* were the odour donors. The odours were obtained by using the Andrzejewski and Owadowska (1994) method. The rodents were captured in the Kampinos National Park (see Section 3.1).

The experiment was conducted for 14 days. Each day, 30 sheets with each number of sponges with the odour of each species, and 30 control sheets were exposed. The sample size for each category of odour was 420. In total, 2940 sheets were exposed, of which 433 were marked by bank voles that deposited 1052 urine marks and faeces pellets.
3.3. The response to the presence of conspecifics and heterospecifics

In the forest, 30 double-traps were placed every 10 m in a line about 300 m long. Each trap consisted of two parts. In one part of the trap, a live individual (resident) was placed to serve as a lure, and another part functioned as a live-trap. Both parts had a large common space made of a wire net where the resident was still separated but the net enabled its contact with the trapped rodent and the surrounding (Kalinowska 1971). Single individuals of *M. oeconomus*, *A. flavicollis* and *C. glareolus* were enclosed in the traps. These species were selected with respect to the intensity of marking their odour by bank voles (see Section 3.1) and possible co-occurrence with the bank vole. These were adult males captured in the Kampinos National Park. Each trap was supplied with food (oat grains, and a piece of apple) for both the resident and the trapped individual. Traps formed a line in random order. They were monitored once a day. The captured animals were marked by clipping, sexed, and then released. The places of traps were changed after each survey as they were shifted by one position on the line.

The experiment was conducted for 12 days. The line was made of 10 traps with individuals of each species. The sample size for each species was 120. During 360 trap-days, 136 captures of bank voles and 2 captures of *A. flavicollis* were noted. In total, 39 bank voles (20 females and 19 males) and one *A. flavicollis* were captured. The latter species was excluded from the analysis because of its low number.

3.4. Statistics

The analysis of scent marking involved: (1) marking extensity, expressed as the percentage of marked sheets with the odour of each species; and (2) marking intensity, expressed as the mean number of urine and faeces marks per marked sheet, and its standard deviation.

The extensity evaluated for the odour of each species was compared with the marking extensity of (1) control sheets to test whether the odour of rodents was marked in a different way than was the requisite without odour, (2) bank vole odour to test whether bank voles can discriminate between conspecific and heterospecific odour, and (3) heterospecific odour to test whether bank voles can discriminate between different heterospecifics.

To analyse marking extensity and the frequency of captures of bank voles in the double-traps, chi-square test ($\chi^2$) was applied. One-way analysis of variance (ANOVA) was used to test the marking intensity. To determine relationship between the density of bank vole population and the number of scent marks deposited on sheets, Pearson correlation coefficient was calculated. All analyses were performed using STATISTICA 6.0.

4. RESULTS

4.1. Response to odour of different rodent species – scent marking

In the first study year, bank voles marked 19% (N = 3950) of all the sheets exposed.

Differences in marking extensity of the species odours and the control were close to the statistical significance ($\chi^2 = 12.85; \text{df} = 7; P = 0.07$). Detailed analysis showed that bank voles significantly more often marked odour deposited by *M. oeconomus* and *A. sylvaticus* as compared with the conspecific odour and control sheets. They also more frequently marked odour deposited by *M. oeconomus* than by the alien species *M. unguiculatus*. The marking extensity of odour of the other species, *M. agrestis*, *A. flavicollis*, *A. agrarius* and *M. unguiculatus*, was similar to that of the conspecific odour and the control (Fig. 1).

In the second study year, bank voles marked 13% (N = 4000) of the sheets exposed. There were significant differences in marking extensity of the species odours and the control ($\chi^2 = 25.9; \text{df} = 7; P = 0.000$). Bank voles significantly more often marked odour deposited by *M. oeconomus* and *A. agrarius* as compared with the control. The marking extensity of *M. oeconomus* odour was significantly higher than those of the conspecifics and the other native species (*A. agrarius* at the marginal significance $\chi^2 =$}
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3.37; \( P = 0.06 \)), and alien species, \( M. \text{unguiculatus} \), \( M. \text{auratus} \) and \( O. \text{degus} \), that were marked at the level of the control and the conspecifics (Fig. 1).

In the third study year, bank voles marked 26\( \% \) (\( N = 3200 \)) of the sheets exposed. As in the preceding year, there were significant differences in marking extensity of the species odours and the control (\( \chi^2 = 18.6; \text{df} = 7; P = 0.009 \)). Among the odour donors, \( A. \text{flavicollis} \), \( C. \text{glareolus} \) and \( M. \text{oeconomus} \) were marked most often. The marking extensity of odours deposited by these species was significantly higher than that of the control and two alien species, \( O. \text{degus} \) and \( M. \text{auratus} \). In this study year, conspecific odour had a high marking extensity (Fig. 1).

To evaluate variation in marking extensity of odour deriving from different species and of the control, frequency distributions of marking extensity obtained in successive years were compared. The medians were found for each distribution (\( M_{\text{med}} = 19\% \) in 1999, 12\% in 2000, and 25\% in 2004), and standardized by converting their values to 0. With respect to this value, each species in a given year was assigned an extensity value ranging from 100\% to \(-100\%\), and the species were categorized into two groups: with marking extensity above the median, between 0 and 100\%, and below the median, between 0 and \(-100\%\) (Table 1). It was found that \( M. \text{oeconomus} \) belongs to the group with a high marking extensity in each study year. Also the \( M. \text{agrestis} \) and \( A. \text{svlyticus} \), odours donors in the first year, also were in this group. The values of marking extensity for these three species were higher than 50\%. The group of species with a low marking extensity in each year comprised two alien species, \( M. \text{auratus} \) and \( O. \text{degus} \), and the control, with marking extensity below \(-50\%\). A large variation in marking extensity between years was found for odours of the mice \( A. \text{flavicollis} \) and \( A. \text{agrarius} \), and also for one alien species \( M. \text{unguiculatus} \). Bank voles also showed a large variation in marking odour of conspecifics.

4.1.2. Marking intensity

In 1999, bank voles deposited 2590 urine and faeces marks on 754 scent marked sheets (mean 3, SD ±3.8). In 2000, they deposited 1219 marks on 531 scent marked sheets, (mean 2, SD ±2.1). In 2004, however, there were 3810 marks on 824 sheets (mean 5 SD ±4.9). No significant differences were found in marking intensity of the species odours and the control in any of the years: 1999 \( F = 1.35, P = 0.2 \); 2000 \( F = 1.74, P = 0.09 \); 2004 \( F = 0.98, P = 0.4 \) (ANOVA test).

The mean number of marks was compared with the bank vole densities in successive years. Population density was defined as the number of individuals captured over 100 trap-days. There were 27 individuals in 1999, 32 in 2004, and 33 in 2004. No relationship was found between the density of bank vole

Table 1. Marking extensity – percentage of marked paper sheets with odour of different rodent species and the control sheets (c) in successive years with respect to the median. Species with a high marking extensity range from 0 to 100\%. Species with a low marking extensity range from 0 to \(-100\%\). aa – \( A. \text{agrarius} \), af – \( A. \text{flavicollis} \), as – \( A. \text{svlyticus} \), ca – \( M. \text{auratus} \), cg – \( C. \text{glareolus} \), ma – \( M. \text{agrestis} \), mo – \( M. \text{oeconomus} \), mu – \( M. \text{unguiculatus} \), od – \( O. \text{degus} \).

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>( M_{\text{med}} )</th>
<th>Species</th>
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<tr>
<td>1999</td>
<td>mo</td>
<td>as</td>
<td>af</td>
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<tr>
<td></td>
<td>100</td>
<td>86</td>
<td>60</td>
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<tr>
<td>2000</td>
<td>mo</td>
<td>aa</td>
<td>mu</td>
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<td></td>
<td>100</td>
<td>39</td>
<td>22</td>
</tr>
<tr>
<td>2004</td>
<td>af</td>
<td>cg</td>
<td>mo</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>72</td>
<td>69</td>
</tr>
</tbody>
</table>
Fig. 1. Marking extensity – percentage of paper sheets with odour of different rodent species and the control sheets (c) marked by bank voles in the years 1999 (N = 500, control N = 450), 2000 (N = 500), and 2004 (N = 400). The significance levels of differences in marking extensity between particular species as well as between the species and the control were presented (chi-square test). aa – *A. agrarius*, af – *A. flavicollis*, as – *A. sylvaticus*, ca – *M. auratus*, cg – *C. glareolus*, ma – *M. agrestis*, mo – *M. oeconomus*, mu – *M. unguiculatus*, od – *O. degus*.
4.2. The effect of differential amounts of odour on scent marking

Bank voles marked any amount of M. oeconomus odour at a similar level, independent of the number of sponges with the odour of this species ($\chi^2 = 0.28$, df = 2, $P = 0.87$). But in response to conspecific odour significant differences were found in the extensity of marking ($\chi^2 = 6.17$, df = 2, $P = 0.04$) that increased with the number of sponges. Paper sheets supplied with 5 sponges were marked significantly more often than the sheets with one sponge. When comparing marking extensity of different amounts of M. oeconomus and C. glareolus odours, it was found that M. oeconomus odour was significantly more often marked only when the amount of the bank vole odour was the lowest (one sponge with odour) (Fig. 2).

No differences were found in making intensity of different number of sponges neither with M. oeconomus ($F = 0.6, P = 0.5$), nor with C. glareolus odour ($F = 1.3, P = 0.3$) (ANOVA test). A slight increase in the number of deposited marks with the increasing number of sponges was observed only in the case of the bank vole odour (Fig. 3).

As compared with the control, the extensity and intensity of marking was significantly higher for each number of the sponges scented by the two species, except for one sponge with C. glareolus odour (Fig. 2 and 3).

Table 2. Number of captures of male and female bank voles in double traps with males of C. glareolus, A. flavicollis and M. oeconomus. N = 120 trap-days.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of captures</th>
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<tr>
<td></td>
<td>Female</td>
</tr>
<tr>
<td>C. glareolus</td>
<td>47</td>
</tr>
<tr>
<td>A. flavicollis</td>
<td>26</td>
</tr>
<tr>
<td>M. oeconomus</td>
<td>21</td>
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</table>
4.3. Response to the presence of conspecifics and heterospecifics

Based on the number of captures of bank voles in the double-traps with males of *M. oeconomus*, *A. flavicollis* and *C. glareolus*, it was found that bank voles were trapped significantly more often in traps with conspecifics than in traps with *A. flavicollis* ($\chi^2 = 6.17; P = 0.01$) and *M. oeconomus* ($\chi^2 = 10.89; P = 0.001$). No difference was found in the number of bank vole captures between traps with *A. flavicollis* and those with *M. oeconomus* ($\chi^2 = 0.69; P = 0.4$) (Table 2).

When comparing the number of captures of male and female bank voles, it was found that females were more often than males captured in traps with conspecific males ($\chi^2 = 19.26; P = 0.000$). Females were also more often captured than males in traps with *A. flavicollis* and *M. oeconomus*, though the difference was significant only for *A. flavicollis* ($\chi^2 = 4.12; P = 0.03$).

The results of experiment show that bank voles avoid encounters with heterospecific individuals, and show preference for contacts with conspecifics.

5. DISCUSSION

The present results show that under natural conditions, bank voles respond to odour deposited by heterospecifics by marking them with their own odour. This response depends on the species of the donor. Statistically significant differences were observed only for the marking extensity, whereas marking intensity was similar for different rodent species. For this reason, the olfactory discrimination ability for odour deriving from different species was evaluated from the marking extensity with respect to the control, conspecific odour, or heterospecific odour.

It was found that the marking extensity of control sheets, that is, unscented requisites, was the lowest. Odours of heterospecifics were marked with a significantly higher or similar extensity as the control, showing little year-to-year variation. In each year, bank voles marked *M. oeconomus* odour significantly more often than the control, whereas allopatric species were always marked at the level of the control (Fig. 1).

Bank voles marked conspecific odour with a variable extensity from year to year. A low extensity of marking was noted in 1999 and 2000, and high in 2004. Consequently, also the ratio of the marking extensity of conspecific odour depositions to depositions of the other species varied. The only exception was *M. oeconomus*, the odour depositions of which were significantly more often marked by the bank vole than the depositions of conspecifics in the first two years, and only in the last year these two species were marked at a similar level (Fig. 1).

When comparing the marking extensity of the different species, significant differences were found only between *M. oeconomus* and allopatric species that were marked by the bank vole at the level of the control each year (Fig. 1).

As the differences in marking extensity between various species were significant only in some cases, it cannot be unequivocally stated that bank voles are able to discriminate between odours of each of them. It is possible, however, to identify groups of species with respect to the degree of bank vole interest in their odour, that is, groups characterised by a high or low marking extensity (Table 1). Bank voles responded most frequently to the odour deposited by species of the same subfamily (*M. oeconomus* and *M. agrestis, Arvicolinae*), thus, evolutionary close, as it is indicated by a high marking extensity in successive years. Bank vole interest in odour depositions of species of the subfamily Murinae (*A. agrarius, A. flavicollis* and *A. sylvaticus*) was lower and more variable. They showed the least interest in the odour of alien species (*M. unguiculatus, M. auratus* and *O. degus*), not occurring in the native fauna and phylogenetically more distant.

The great interest in odour of *M. oeconomus* and small in alien species implies that the marking response may depend on the readability of "chemical information" for bank voles. A higher readability can elicit more frequent marking. It seems thus that the ability of reading the information contained in scent marks has a genetic background, and is related to the similarity of odours within closely related species. Bank
voles marked most often odour of *M. oeconomus*, thus phylogenetically close rodents. This result confirms the results of laboratory experiments designed to discriminate among scent marks of closely related species of the superspecies *Spalax ehrenbergi* (Heth and Todrank 2000), and among mice of the genus *Mus* (Heth et al. 2001). It was found that rodents were more interested in depositions of more closely related species. The authors suggest that rodents recognize other species based on the similarity between conspecific and heterospecific odour. As the bank vole and *M. oeconomus* occupy different habitat types, it is little probable that bank voles encounter scent marks of *M. oeconomus*, but the odour of this species elicited a clear bank vole response. This means that odours of these two species are similar and this facilitates the identification of these odours and, consequently, accounts for their frequent marking.

For rodents of the subfamily Murinae and the bank vole, genetic similarity of odour is smaller, but bank voles can recognise scent marks of *A. flavicollis* and *A. sylvaticus* since they encounter the scent marks of these species in the habitat. The bank vole and mice *A. flavicollis* or *A. sylvaticus* are considered to be competitive species and mice are predominating (Wójcik and Wolk 1985, Fasola and Canova 2000, Andrzejewski and Olszewski 1963) observed that encounters between mice and voles typically were aggressive and they avoided each other. It was found that bank voles marked odour of sympatric species with a high variability in successive years but in any of the years no avoidance of odour of these species was observed. Also Andrzejewski et al. (1997) observed that bank voles did not avoid *A. sylvaticus* odour. Łopucki and Szymrosczczyk (2003) found that bank voles did not avoid the odour of familiar *A. flavicollis* individuals. It seems that what mainly influences the scent marking of odours of phylogenetically distant but co-occurring species are their earlier contacts with the scent marks and the individuals of the species in the habitat.

Odour depositions of alien species, evolutionary and geographically distant, were least frequently marked by bank voles. The probability of odour similarity between the bank vole and alien species is likely to be low, and the acquaintance with scent marks in the habitat impossible. Small readability and lack of acquaintance could account for little interest of bank voles, hence a weaker response to odour depositions and low marking extensity.

It seems interesting that the odour of the own species, as more readable and conveying more important information, was not preferred by bank voles. It is difficult to explain this fact, especially that the literature data are not unequivocal. Most studies indicate preference for conspecific odour (e.g. Drickamer et al. 1992), but there are examples when rodents show a similar interest in heterospecific odour and their own odour (e.g. Andrzejewski et al. 1997), or less interest in their own odour (e.g. Sokolov et al. 1983 in Krasnov and Khokhlova 1996). Based on the genetic background of odour discrimination, it can be suggested that the odour of closely related species gives rise to more interest because of its great similarity to the odour of conspecifics.

The analysis of marking intensity of odours deposited by various species showed no significant differences in the number of scent marks deposited by bank voles. The studies on marking odour depositions of conspecifics (Johnson et al. 1997, Thomas and Wolff 2002) show that the marking intensity is important for intraspecific relations. The number of scent marks plays part in competition for mates, in demonstration of the breeding condition, or signalling the presence in the area. In the present experiment no quantitative effect of marking was found. This means that detailed information conveyed through marking intensity is not important to interspecific communication.

The results of the experiment concerning the effects of differential amounts of heterospecific odour on the extensity and intensity of marking confirm this conclusion. Quantitative differences in *M. oeconomus* odour depositions had no effect on more frequent marking of larger amounts of their odour, nor on the deposition of a higher number of marks. In the case of conspecific odour depositions, an increase in the amount of
odour was followed by a significant increase in the frequency of marking, and a small increase in the number of marks.

The last step was the investigation of the response of bank voles to the presence of heterospecifics, and comparison with the marking response to their odour depositions. It was found that the lowest number of bank voles was caught in traps with *M. oeconomus*, contrary to the result of the scent marking response, scent marking of the odour of this species being most extensive. Bank voles also avoided *A. flavicollis*, that is, a sympatric species, and most often they were captured in traps with conspecifics (Table 2). Differences in the response to the presence of other species were also pronounced in the number of trapped males and females of the bank vole. Bank voles avoided contacts with heterospecific individuals but they did not avoid their odours. Thus, interspecific communication mediated by scent marks deposited by rodents can be more important than communication during direct encounters between individuals of different species.

The response of bank voles to odours deriving from heterospecifics provides evidence for an important role of odour and scent marking in interspecific communication. At the stage of the study presented in this paper, it is not possible to explain all the aspect of this behaviour. A question is open why rodents mark heterospecific odour depositions, what kind of information they convey, and what means a specific frequency of marking conspecific and heterospecific odour depositions in rodent communication. It is possible to predict advantages conferred to rodents through olfactory cues in developing such interactions as competition, cooperation, or predation in multi-species systems. But these issues need empirical tests, and make way for further investigations.

6. CONCLUSIONS

1. Bank voles mark odours of other rodent species, and the frequency of marking depends on the species of odour donor:

- bank voles often mark odour of *M. oeconomus* as the information conveyed by closely related species is more readable for them;

- marking of the odour of mice is weaker and more variable as it depends on the contacts with their odours or with individuals of these species in the habitat;

- a low extensity of marking the odours of allopatric species results from geographical distance and lower genetic proximity;

2. The amount of odour is of no importance in the interspecific communication:

- heterospecific odour has no effect on the number of scent marks left by bank voles;

- an increase in the amount of heterospecific odour has no effect on the extensity and intensity of marking by bank voles;

3. Bank voles avoid direct contacts with heterospecific individuals, but they do not avoid their odours and mark its with their own scent marks.

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7. REFERENCES


Andrzejewski R., Olszewski J. 1963 – Social behaviour and interspecific relation in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber 1780) – Acta Theriol. 7 (10): 155–168.


Jonge G.De. 1980 – Response to con- and heterospecific male odours by the voles Microtus agrestis, Microtus arvalis and Clethrionomys glareolus with respect to competition to space – Behav. 73: 277–303.

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