ABSTRACT: Social behaviour of the bank vole was video recorded during direct encounters between individuals under natural conditions. The apparatus consisted of miniature video cameras, a system of image processing and recording, and infrared emitters. This device enabled continuous 24-h observations at several sites simultaneously. The study was conducted in an alder swamp *Ribonigri-Alnetum* located in the Kampinos National Park, central Poland (52°20’N, 20°25’E). Observations were made in the late summers of 2002 and 2003 at six independent baited sites for 10 days and nights per each site. Rodents visiting the sites were individually marked by fur clipping. In sum, 13 053 visits to the sites and 1868 encounters between two marked individuals of *C. glareolus* were video recorded during 1440 hours of observation. It has been found that under natural conditions, bank voles most often avoided each other (55% of the encounters). In the case of close contacts they were aggressive (30%), rarely tolerant (7%), and during the remaining encounters they showed a mixed behaviour. The voles met mainly in the night (94% of the encounters) despite of 25% of their daily activity ran during the day. The frequency and character of encounters depended on the sex, age, and the origin of individuals. Encounters between males were more aggressive than between females (*P* < 0.01). In encounters between opposite sexes, males were dominants (*P* < 0.001). Individuals with a larger body mass were dominant in access to food (*P* < 0.000). Cases of the dominance of juveniles over adults were interpreted as a result of the site of their origin. Social relations between individuals were characterised by persistence and repeatability in time. The results are compared with the literature describing experiments with animals kept in the laboratory or in enclosures, and field observations based on trapping techniques and telemetry.

KEY WORDS: social relationships, dominance, direct observation, *Clethrionomys glareolus*, rodents

1. INTRODUCTION

Social relationships among individuals are of basic importance to such population processes as spatial distribution of individuals (Mazurkiewicz 1971, Bujalska and Saitoh 2000), sexual selection (Bateson 1978, Barnard *et al.* 1991, Smadja and Ganen 2002), dispersal (Mazurkiewicz and Rajska-Jurgiel 1975, Wolff 1993), sexual maturation (stimulation of the hormonal system) (Getz *et al.* 1983, Kawata 1987, Prévot-Julliard *et al.* 1999), or differential survival of various categories of individuals, for example, age groups or migrants (Walkowa 1964, Wolff 1993, Ylönen and Horne 2002). By influencing these activities...
of rodents, social relationships directly or indirectly determine population dynamics and composition (Krebs 2003).

Social organisation of small rodent populations is difficult to study, especially under field conditions (Gliwicz and Rajska-Jurgiel 1983, Bujalska 1990). The major difficulty lies in the fact that the hierarchy among individuals is established as a result of direct encounters, and a direct observation of such interactions under natural conditions is difficult, if not impossible (Chełkowska 1978, Andrzejewski 2002). The reason is that rodents are small animals with a secretive mode of life (often underground), they can be largely dispersed and often active only at night.

To overcome habitat restrictions, observations of interactions between individuals were conducted mainly under artificial conditions (in the laboratory) or in semi-natural enclosures (e.g. Lidicker 1976, Schadler 1990, Marchlew ska-Koj 2000). Such experimental conditions (a small closed space) facilitate observations, enable the organisation of contacts between selected individuals, interfere in their physiology (the level of hormones), but at the same time they can change the behaviour of the experimental animals, and elicit unnatural behaviour (Creel 2001).

The methods used in the field studies on the social status of individuals (or hierarchy in a group) typically provided data for indirect conclusions, most often based on the priority of access to resources such as space or food (Novak 1983, Gipps 1985). They include trapping (Bock 1972, Bujalska and Saitoh 2000), telemetry (Madison 1978, Erlinge et al. 1990) and, on rarer occasions, fluorescent powder (Dickman 1988, Kaufman 1989). With these methods it was possible to avoid difficulties involved in direct observations of rodents. A measure of their social status was the frequency of captures or the size of an area searched by them (so called home range analysis). These methods serve for observation of the consequences of social interactions, for example, the distribution of individuals in space. They cannot replace, however, the method of observing direct contacts between individuals due to which social behaviour of these mammals can be examined at the stage of both the formation of relationships between them and the maintenance of these relationships.

Field works with the application of direct observations of the behaviour of rodents in their natural habitats are very scarce (Andrzejewski and Olszewski 1963, Gipps 1981, Lambin 1988). Moreover, the material collected (that is, the number of encounters observed) is poor and fragmentary, so that a quantitative description of social behaviour is not possible, and attempts at the analysis in sex or age groups are based on the number of data insufficient for statistical examination, for example, two encounters of adult males in Gipps (1981).

With respect to this situation, the present paper is focused on: (1) developing a method for the direct observation of rodents interacting under natural conditions, (2) description of the social behaviour of rodents in their natural environment, and in particular frequency and character of encounters with respect to sex and body mass (age), and persistence and repeatability in time of the observed behaviour.

The experimental species was the bank vole Clethrionomys glareolus (Schreber, 1780) – a model species in the population ecology of small mammals (Bujalska and Hansson 2000).

2. MATERIAL AND METHODS

The study was conducted in an alder swamp Ribo nigri-Alnetum (Solinska-Gornicka, 1975) located in the Kampinos National Park (52°20’N, 20°25’E). This community covers an area of about 8 km². A characteristic plant cover and a high soil moisture provide suitable habitat conditions for bank voles, which account for 90–99% of all the rodents captured there (Owadowska 1999). The experiment was conducted in three steps:

Step 1. Trapping and marking of rodents in the study area.

Trapping was carried out at six sites for five successive days and nights. The distance between trapping sites was 100 m. At each site, 10 live-traps were placed. The traps were checked four times in the daily cycle: at 7:00,
Social relationships in a bank vole population

The captured rodents were described in terms of their sex, sexual activity, and body weight, then they were uniquely marked by fur clipping on the back and body sides. Each clipping pattern was assigned a number. In total, 87 individuals of *C. glareolus* were captured and marked, including 55 females and 32 males (Table 1). On the average, 14.5 ± 3.9 bank voles were trapped per site.

Step 2. Observation of bank vole behaviour at baited trap sites.

After the 5-day period of trapping, the traps were removed and replaced with portions of bread (ca 100 g) fastened to the substrate as a bait. A miniature video camera (monochrome camera with a variable focus, lens 3.6 mm, 1/3" image sensor, 300 TV lines resolution, min. illumination 0.1 lux, power supply of 12V/80mA) and infrared light-emitting diodes (28 diodes LED) were placed about 50 cm above the bait. The application of infrared diodes made it possible to conduct continuous 24-h observations even in a complete darkness.

To delimit precisely the area observed by the camera, four plexiglass sheets measuring 30 cm × 30 cm were placed around the bait so that they did not touch each other at the corners. In this way, a square area surrounded with walls, a box, was formed of a size of 40 cm × 40 cm, with four entrances about 7 cm wide in the corners, and with the bait in the centre.

With this structure of the box, the site preserved the character of an open area. Although in close vicinity to the bait it was restricted, facilitating the observation, a rodent had four ways to escape from the box. The camera placed above the box enabled observations of the inner space and the entrances, so that both the rodents in the box and those entering it or peeping were visible.

The image from the camera placed above the bait was transmitted by a coaxial cable to the quad processor (VP-3000) placed in the forest and video tape recorder for a simultaneous image recording from several cameras on a single video tape. The image was recorded at a speed of 25 frames × sec⁻¹.

All the components of this device (cameras, infrared emitters, quad processor and video tape recorder, also cables and power sources) are used in so called systems of Closed Circuit Television (CCTV) for monitoring and protection of objects. Due to the choice of suitable models, it was possible to use them for the observation of animals under field conditions. The basic properties that this device should have involved: the maximum miniaturisation (enabling their easy concealment), easy assembling and disassembling (easy to move), high sensitivity (that enables filming by dim or infrared light), appropriate image resolution (to get a high quality image for the identification of individuals), possibility of a continuous work and without breaking-down (24-h recording, without gaps for any number of days),

Table 1. Video records of *Clethrionomys glareolus* behaviour at 6 baited sites for 10 days and nights. Number of marked females and males at particular trapping sites.

<table>
<thead>
<tr>
<th>Number of site</th>
<th>Number of marked females</th>
<th>Number of marked males</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10</td>
<td>7</td>
<td>17</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>9</td>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>6</td>
<td>21</td>
</tr>
<tr>
<td>5</td>
<td>8</td>
<td>6</td>
<td>14</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>55</strong></td>
<td><strong>32</strong></td>
<td><strong>87</strong></td>
</tr>
</tbody>
</table>
low energy intake (an important parameter when batteries are the source of energy), safety (device prone to destruction, supplied with 12V current), and relatively low costs of the components.

At each site, records were taken continuously for 10 days and nights, that is, for 1440 hours. The experiment was conducted in late summers of two seasons: between 20 August and 15 September of 2002 and 2003. In 2002, data were collected at five sites (sites 1, 2, 3, 4, and 5) and in 2003, at one site (site 6).

Step 3. Reviewing the records, description of rodent behaviour, and analysis of data.

When reviewing tape recordings, the time of the appearance of each bank vole (to the nearest second) and its number (the pattern clipped in the fur) were noted. Marked individuals appeared on 13 053 occasions and unmarked individuals on 3 434 occasions, in total 16 487 visits. When two individuals appeared at the same time, their behaviour was described and assigned to one of the five categories:

1. Avoidance: one or two of them ran away immediately – the time they spent at the site was shorter than 5 seconds.
2. Aggression: expressed in aggressive postures (attacking, biting, chasing, pursuit) and submission (escape). All these behaviours lasted for a short time, several to a dozen seconds, and terminated with fleeing of one or both individuals.
3. Tolerance: two individuals stayed together at the site longer than 30 sec., ate the bait together, remained close to each other, sniffed each other, did not show aggressive behaviour.
4. Aggression-tolerance: during a single encounter, individuals displayed aggressive as well as tolerant behaviour, for example, they stayed together at the site, tolerated the presence of the other individual, ate together, but after some time they also showed aggression, attacked each other, bit, chased from the bait.
5. Tolerance-avoidance: the appearance of another individual did not result in a rapid escape of one or both individuals. During the joint stay they strove to maintain the greatest possible distance between them, and the most frequent cause of escape was an excessive reduction of this distance by one of them. Lack of the behaviour characteristic of tolerance, for example, approaching and sniffing, as well as lack of aggression.

In total, during the ten-day recording period at six independent sites, 3168 encounters between two bank voles were noted and described. As the sites were visited by marked and unmarked individuals, three combinations of encounters were observed: (1) between two marked individuals – 1868 cases, (2) between two unmarked individuals – 276 cases, and (3) between one marked and one unmarked individual – 1024 cases. As the sex and age of unmarked individuals were unknown, their encounters are excluded from the analysis.

The χ² test was used for analysing data in the nominal scale (e.g. types of behaviour in sex and age groups). Logistic regression or the Spearman rank correlation coefficient (Rₛ) was applied to analyse changes in behaviour with time. Mean values are given with standard deviation (SD).

3. RESULTS

3.1. Frequency of visits to baited sites and encounters of C. glareolus individuals during the 24 h cycle

Marked individuals visited the baited sites with a relatively fixed frequency in the daily cycle. On the average, marked bank voles visited observation sites 1305 ± 143 times per 24 h. No increasing or decreasing tendencies in the frequency of visits were noted during the ten-day observation period (Rₛ = 0.18, P = 0.17), implying that the additional food supply over this period had no effect on the preference of these sites by marked rodents.

Bank voles visited the sites most often in specified hours, with preference for the night time (75% of the visits occurred between 19:00 and 6:00). Based on the frequency of visits, a pattern of the daily activity of rodents was determined (Fig. 1 – grey line). Although, in general, their activity was higher at night, three periods can be distinguished when the baited sites were visited most often (activity peaks): about 21:00 h, at midnight,
and at dawn between 4:00 h and 5:00 h. During the daylight only one small activity peak occurred about 10:00 h. During the remaining part of the day, rodents visited the baited sites with a steady frequency and rather rarely. In sum, 25% of the visits noted for 24 hours occurred during the day.

Each marked bank vole visited the sites many times in the 24-h cycle, with a mean of 16.7 ± 14.6 visits. The duration of the visit of a single individual typically did not exceed one minute (73% of the cases), rarely more (1–2 min in 12%, 2–3 min in 6%, 3–4 min in 4%, 4–5 min in 2%, and 5–13 min in 3%). The longest recorded visit lasted for 12 min and 17 sec.

At each site, there were 2.2 ± 2.9 encounters per hour, on the average. This value largely fluctuated, depending on the time of the day. At night (between 19:00 and 6:00), direct contacts between individuals took place 4.5 ± 2.8 times per hour per site, or every 13 minutes. During the daylight, however, two individuals could be seen together at 4–5-h intervals, as the mean number of encounters was 0.22 ± 0.25 per hour per site. In sum, night encounters accounted for 94% of all observed, and the remaining 6% occurred during the daylight. The number of encounters recorded every hour is shown in Fig. 1 (black line).

3.2. Description of encounters between individuals

During the 10-day observation period, marked bank voles had 1868 encounters, with participation of 84 out of 87 marked individuals. It was calculated from the known number of encounters recorded for each individual that a "statistical" bank vole encountered another individual 4.4 ± 3.6 times per 24 h, on the average.

Summation of the encounters recorded for the marked bank voles provided a general picture of the behaviour in the whole population (Fig. 2). More than a half (55%) of the encounters, or 1020 cases, involved avoidance and ended with fleeing of one or both rodents. In these 738 out of 1020 cases (72%) only one individual fled, and in the remaining 282 cases (28%), both fled. Avoidance was rarely preceded by a close sniffing of individuals. In most cases, the escape was an immediate response caused by the appearance of another individual, without ap-
approaching and without signs of a close olfactory identification.

The second most often behaviour was aggression (558 cases). It was recorded in 30% of the recorded encounters (Fig. 2). Aggressive encounters always ended with fleeing of one or both individuals. It was, thus, possible to enrich this analysis by introducing the category of winners and losers (Volodin and Goltsman 2003). The winner was defined as an individual remaining in the site after the encounter, and the loser as an individual that escaped from the site. The cases when both individuals fled simultaneously were classified as ties.

The third of the possible interactions, tolerance, was relatively rare (aggression was four times more frequent) (Fig. 2). During encounters of this type, close contacts and mutual sniffing were frequent. Most often, the animals were eating together the bait for a relatively long time (even up to several minutes). The individuals stayed close to each other and did not display visible signs of aggression.

The other types of behaviour (aggression-tolerance and tolerance-avoidance) were rare, about 4% each (Fig. 2). Encounters of these types represented a transition form between tolerance and aggression, or between tolerance and avoidance, and they comprised components characteristic of both these categories, rendering difficulties in their interpretation. Because of their rare occurrence and difficulties in interpretation, they are excluded from the analysis in sex and age groups.

3.3. The effect of sex on encounters between individuals.

Among the encounters, 162 involved two males, 776 two females, and 930 a male and a female. First, it was analysed whether the frequency of encounters between individuals of a given sex was proportional to their respective numbers, or there was a tendency to more frequent or less frequent encounters between particular sex combinations. As encounter took place in groups of animals visiting a given site, it was calculated from Table 1 that males could form 73 different pairs*, females 250 pairs, and males and fe-

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Fig. 2. Video records of Clethrionomys glareolus encounters at 6 baited sites for 10 days and nights. Proportion of different categories of behaviour during encounters of marked individuals; N = 1868.

* At site 1, there were 7 males (n = 7), thus the number of possible combinations (C) between them was 21 [C = n (n – 1)/2]; at sites 2 and 3 there were 4 males – 6 possible combinations; at sites 4 and 5 there were 6 males, thus, 15 different combinations were possible at each of them; at site 6 there were 5 males – 10 possible pair combinations. In sum, all the observed males could meet in 73 different pair combinations (21+6+6+15+15+10 = 73). Similar calculations were performed for females.
males 302 different combinations of individuals. A comparison of these values with the number of recorded encounters for each sex combination (162 male-male, 776 female-female, and 930 male-female) showed that two males visited the site at the same time significantly less often than did two females ($P < 0.05, \chi^2 = 4.5, df = 1$) and also less often than pairs of opposite sexes ($P < 0.05, \chi^2 = 4.45, df = 1$). No differences were found in the frequency of encounters between female-female pairs and male-female pairs ($P < 0.9, \chi^2 = 0.006, df = 1$). This implies that differences in the number of encounters between sexes were due not only to differences in numbers of males and females, but they also depended on the character of relationships between individuals of a given sex.

This result indicates that under natural conditions, males avoid being close to each other. But when an encounter took place (two males visited the experimental site at the same time), one or two individuals fled immediately (the response classified as avoidance) in 58% of the cases (Fig. 3A). The males that did not use this tactics, most often showed aggression (33% of the cases) – they were fighting for an access to food. Tolerance was an extremely rare behaviour, only six such cases, or 4%, being recorded (Fig. 3A).

The results of the encounters between females (Fig. 3C) were characterised by a smaller proportion of avoidance response (52%) and aggression (28%), and a higher tolerance (10%). A comparison of the frequency distributions of behaviour types for males (Fig. 3A) with that for females (Fig. 3C) showed a significant difference ($P < 0.01, \chi^2 = 7.93, df = 2$).

Encounters between individuals of opposite sexes (Fig. 3B), taking place in 930 cases, had an intermediate course as compared with those described above. As in the other cases, a tendency to avoidance predominated, accounting for 56% of the cases, and also to aggression, almost 31%. Tolerance was rare (6%). This distribution of behaviours was significantly different from that for females ($P < 0.001, \chi^2 = 15.30, df = 2$), but it was similar to that for males ($P > 0.2, \chi^2 = 1.02, df = 2$). Absence of the difference is indicative of a rather aggressive character of direct encounters between the opposite sexes, male-female interactions being characterised by a similar level of aggression as male-male interactions.

Additional data on interactions between the sexes were provided by observation which of the sexes won or lost the contest. Based on the records of aggressive behaviour

![Fig. 3. Video records of Clethrionomys glareolus encounters at 6 baited sites for 10 days and nights. Behaviour of bank voles during encounters with respect to their sex.](image-url)
Rafał Łopucki

during male-female encounters (286 observations), it has been found that females most often fled, this being the case in 55%. Males fled in 36% of the cases, and 9% of the aggressive encounters ended with a tie, that is, both individuals fled at the same time. Males were significantly more often the winners than the females ($P < 0.001$, $\chi^2 = 11.21$, $df = 1$), chasing thus females from the source of food.

A similar division of individuals into fleeing and remaining at the site can be done when analysing the avoidance reaction. Also during encounters of this type ($N = 520$), the female fled first from the site in 44% of the cases, whereas the male in 31%, the difference being statistically significant ($P < 0.001$, $\chi^2 = 11.9$, $df = 1$). The remaining 25% of the encounters ended with a simultaneous fleeing of both individuals. This provides evidence that mutual avoidance is not a behaviour occurring by chance, but it also reflects relationships between the sexes, in this case the dominant position of males.

3.4. The effect of age (body mass) on encounters between individuals

First, it was tested whether heavier individuals had an advantage over lighter individuals in gaining dominant position. Data from 558 cases of aggressive interactions were used for this analysis. As the body weight of each individual was known, the number of encounters was calculated in which either heavier or lighter individuals were winners. It has been found that lighter individuals were losers chased from the bait in 46% of the cases, whereas heavier individuals were losers in 27%, the difference being significant ($P < 0.000$, $\chi^2 = 26.64$, $df = 1$). The other encounters ended with ties, or both individuals had the same body weight so that it was not possible to distinguish a winner (17%).

An interesting point is that also avoidance behaviour could be classified in a similar way, based solely on individuals fleeing first. Also in this situation, heavier individuals significantly more often remained in place (in this case without fighting) ($\chi^2 = 14.01$, $df = 1$, $P < 0.001$). This means that the mutual avoidance also reflects relationships between bank voles.

For a more detailed analysis of the effect of age on the behaviour of marked bank voles they were assigned to three age groups based on their body weight. The first group consisted of juveniles with a body weight below 15 g. They accounted for 15% of the population. The second group comprised bank voles weighing 15–17g , called subadults, forming 57% of the population. And the third group consisted of adults that weighed 18 g or more. They contributed to 28% of the population.

Adults most often avoided simultaneous visits to a site (avoidance contributed to 66% of the behaviour) and they did not show tolerance (0% of the cases) (Table 2). Subadults exhibited a lower tendency to avoidance (49%) and a higher tolerance (9%) but, at the same time, a high proportion of aggressive behaviour (31%). Juveniles were most tolerant to each other (14%), rather rarely fled from each other (39%), and rarely showed aggression (25%).

During the encounters of adults with younger bank voles, avoidance was the dominant behaviour (over 60%). Moreover, adults were more tolerant towards juveniles (10%) than towards subadults (4%). Encounters between subadults with juveniles were characterised by a lower tendency to avoidance, and by a high proportion of tolerant behaviour, but also by a high proportion of aggressive behaviour.

A comparison of the frequency distributions of different behaviours from Table 2 by using the $\chi^2$ test showed that the highest number of significant differences occurred between the adult-adult pairs and the other combinations of pairs, and also between the adult-subadult pair and the other pairs. Most often no difference was found between pairs from younger age groups.

3.5. Behaviour of bank voles with respect to the joint sex and age effect

As indicated in the previous sections, both sex and age separately affect the behaviour of encountering individuals. The joint effect of these two factors is shown in Table 3. Although the number of records was high (1868 encounters), some combinations of individuals with respect to their sex and age
were not represented (e.g. no two juvenile males were recorded), or underrepresented. In particular, this was the case of juveniles as they represented a small group (15% of the marked individuals). The results of this analysis confirm the previous results and add more details:

- adults of both sexes (rows 1–3, Table 3) most often showed avoidance behaviour and no tolerance,
- among subadults (rows 4–6), males were mutually most aggressive (37%) and they did not show tolerance (0%). Females were much more tolerant to each other (12%) and less aggressive (29%). Encounters between opposite sexes had an intermediate course.
- Encounters between juveniles were rare. Juvenile females were mutually tolerant (25%). Encounters between opposite sexes were characterised by more aggression (30%) and lower tolerance (5%).
- Encounters of adult bank voles with subadults (rows 10–13) were dependent on their sex. The encounter between an adult female and a subadult male was significantly more often aggressive (and less frequently tolerant) than the encounter with a subadult female ($P < 0.02$, $\chi^2 = 8.36$, df = 2). Adult males were also more aggressive to subadult males (34%) than to subadult females (27%), but this difference is not statistically significant ($P = 0.3$, $\chi^2 = 1.79$, df = 2).
- Encounters of adult bank voles with juveniles (rows 14–17) were characterised by a high proportion of avoidance behaviour (ca 70%), low aggression, and a relatively high proportion of tolerance.

Table 2. Video records of Clethrionomys glareolus encounters at 6 baited sites for 10 days and nights. Behaviour of bank vole pairs in different age groups. The last column shows statistically significant differences (comparisons between rows): * $P < 0.02$, ** $P < 0.01$, *** $P < 0.001$ (test $\chi^2$, df = 2).

<table>
<thead>
<tr>
<th>Bank voles pairs – age of individuals</th>
<th>Categories of behaviour (% of cases)</th>
<th>Number of encounters (N)</th>
<th>Statistically significant differences</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>avoidance</td>
<td>aggression</td>
<td>tolerance</td>
</tr>
<tr>
<td>Adult-adult (aa)</td>
<td>66</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td>Subadult-subadult (ss)</td>
<td>49</td>
<td>31</td>
<td>9</td>
</tr>
<tr>
<td>Juvenile-juvenile (jj)</td>
<td>39</td>
<td>25</td>
<td>14</td>
</tr>
<tr>
<td>Adult-subadult (as)</td>
<td>60</td>
<td>30</td>
<td>4</td>
</tr>
<tr>
<td>Adult-juvenile (aj)</td>
<td>62</td>
<td>25</td>
<td>10</td>
</tr>
<tr>
<td>Subadult-juvenile (sj)</td>
<td>49</td>
<td>30</td>
<td>9</td>
</tr>
</tbody>
</table>

3.6. Changes in the behaviour of individuals during the experiment

The analysis of changes in the behaviour of bank voles during the 10-day period of tape recording enabled the evaluation of the method used in this experiment. A question arose whether the permanent food supply at the experimental sites would not cause changes in the behaviour of rodents, for example, an increase in competition. A binomial logistic regression was used for analysing this problem. Changes in the proportion of a specified behaviour (for example, aggression) were estimated with respect to all the other behaviour types considered jointly (avoidance plus tolerance). It was found that the proportion of avoidance and aggression remained at the same level over that period (statistically not significant change: $P = 0.65$ for avoidance and $P = 0.48$ for aggression), but the proportion of tolerance declined ($P = 0.03$). These results imply that relationships between the encountering bank voles underwent slow changes. The rate of these
Table 3. Video records of *Clethrionomys glareolus* encounters at 6 baited sites for 10 days and nights. Behaviour of the bank voles during encounters with respect to sex and age.

<table>
<thead>
<tr>
<th>No</th>
<th>Sex and age of individuals</th>
<th>Categories of behaviour (% of cases)</th>
<th>Number of encounters (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>♀ adult – ♀ adult</td>
<td>avoidance: 58, aggression: 37, tolerance: 0</td>
<td>19</td>
</tr>
<tr>
<td>2</td>
<td>♀ adult – ♀ adult</td>
<td>avoidance: 52, aggression: 43, tolerance: 0</td>
<td>21</td>
</tr>
<tr>
<td>3</td>
<td>♀ adult – ♀ adult</td>
<td>avoidance: 77, aggression: 18, tolerance: 0</td>
<td>39</td>
</tr>
<tr>
<td>4</td>
<td>♀ subadult – ♀ subadult</td>
<td>avoidance: 48, aggression: 29, tolerance: 12</td>
<td>379</td>
</tr>
<tr>
<td>5</td>
<td>♂ subadult – ♂ subadult</td>
<td>avoidance: 52, aggression: 37, tolerance: 0</td>
<td>27</td>
</tr>
<tr>
<td>6</td>
<td>♀ subadult – ♂ subadult</td>
<td>avoidance: 50, aggression: 34, tolerance: 7</td>
<td>335</td>
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<tr>
<td>7</td>
<td>♀ juvenile – ♀ juvenile</td>
<td>avoidance: 50, aggression: 19, tolerance: 25</td>
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</tr>
<tr>
<td>8</td>
<td>♂ juvenile – ♂ juvenile</td>
<td>avoidance: –, aggression: –, tolerance: –</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>♀ juvenile – ♀ juvenile</td>
<td>avoidance: 30, aggression: 30, tolerance: 5</td>
<td>20</td>
</tr>
<tr>
<td>10</td>
<td>♀ adult – ♂ subadult</td>
<td>avoidance: 56, aggression: 39, tolerance: 1</td>
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<tr>
<td>11</td>
<td>♀ adult – ♂ subadult</td>
<td>avoidance: 62, aggression: 26, tolerance: 6</td>
<td>195</td>
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<td>avoidance: 58, aggression: 34, tolerance: 3</td>
<td>71</td>
</tr>
<tr>
<td>13</td>
<td>♂ adult – ♂ subadult</td>
<td>avoidance: 61, aggression: 27, tolerance: 5</td>
<td>278</td>
</tr>
<tr>
<td>14</td>
<td>♀ adult – ♂ juvenile</td>
<td>avoidance: 71, aggression: 21, tolerance: 8</td>
<td>24</td>
</tr>
<tr>
<td>15</td>
<td>♀ adult – ♂ juvenile</td>
<td>avoidance: 47, aggression: 36, tolerance: 11</td>
<td>53</td>
</tr>
<tr>
<td>16</td>
<td>♂ adult – ♂ juvenile</td>
<td>avoidance: 71, aggression: 15, tolerance: 12</td>
<td>34</td>
</tr>
<tr>
<td>17</td>
<td>♂ adult – ♂ juvenile</td>
<td>avoidance: 69, aggression: 20, tolerance: 9</td>
<td>35</td>
</tr>
<tr>
<td>18</td>
<td>♀ subadult – ♂ juvenile</td>
<td>avoidance: 64, aggression: 28, tolerance: 0</td>
<td>25</td>
</tr>
<tr>
<td>19</td>
<td>♀ subadult – ♂ juvenile</td>
<td>avoidance: 52, aggression: 26, tolerance: 11</td>
<td>114</td>
</tr>
<tr>
<td>20</td>
<td>♀ subadult – ♂ juvenile</td>
<td>avoidance: 40, aggression: 34, tolerance: 11</td>
<td>62</td>
</tr>
<tr>
<td>21</td>
<td>♂ subadult – ♂ juvenile</td>
<td>avoidance: 44, aggression: 56, tolerance: 0</td>
<td>9</td>
</tr>
</tbody>
</table>
Social relationships in a bank vole population

changes was so slow that the observed decline in tolerant behaviour was not replaced by a significant increase in the other types of behaviour (aggression and avoidance).

4. DISCUSSION

When summing up the results of this experiment, some specific conditions should be remembered. It was conducted in so called open population (occurring in an alder swamp 8 km² in area) in late summer, when the breeding season the bank vole was coming to an end. Local density of the population was about 14 individuals per site as estimated from the number of individuals caught during five days in 10 traps per site. These are important circumstances because many studies provide evidence that such factors as the season and, consequently, breeding period and population density affect social behaviour of rodents (Gurnell 1978, Saitoh 1981, Karlsson 1988, Nelson 1995, Koskela et al. 1997).

The results of video records have shown that “nose-to-nose” encounters are not a preferred way of information exchange in bank voles. Direct encounters were rare (see Fig. 2 – avoidance behaviour), they were characterised by aggression and short. Vолодин and Gotzsm (2003) called this type of behaviour "the strategy of short and quick interactions". It should also be noted that the observed bank voles had a reason for visiting the same places – the sites with additional food supply. It may be expected that without such a stimulus attracting individuals, they would encounter in the field even less often, that is, they would use the strategy of avoidance even more often. The postulated “reluctance” of bank voles to close interactions with another individual may be characteristic of this species. As indicated in the literature, rodents of other species do not show so strong tendencies to avoidance and are much more tolerant during encounters (Andrzejewski and Olszewski 1963 for A. flavicolis, Lambin 1988 for A. sylvaticus).

Additional information about direct contacts between bank voles is provided by the frequency distribution of encounters in the 24 h cycle. Bank voles were active during the day and at night, which is also known from the literature (Wójcik and Wolk 1985). About 25% of their activity occurred during the daylight, but encounters between individuals took place almost exclusively at night (ca 95% of the cases). It is possible that during the day they can avoid each other more efficiently because they can see other individuals, whereas at night, when light is scarce at the forest floor, they can use mainly auditory and olfactory cues to detect a close presence of another individual. Kalkowski (1968) has found that laboratory mice can identify other individuals from a small distance not exceeding 20 cm. Assuming that bank voles have a similar ability, it means that at night it is easier to record encounters as they occur within a smaller area.

4.1. Encounters between individuals of the same sex

During male-male and female-female encounters, the major parameter determining the social position of an individual was its age – older individuals won access to food. There were, however, some exceptions as it happened that juveniles or subadults were winners in interactions with considerably heavier (even by 10–12 g), thus older individuals of the same sex. This means that the dominant position of an individual depends also on other factors such as the place of origin. Individuals living further away from the baited site can be losers in the interaction with an even much younger resident (Hudgens and MacNeil 1970).

Sex was a factor considerably differentiating the behaviour of bank voles. Males both adults and subadults most often avoided close contacts. Close contacts typically ended with aggression and, consequently, an escape of one of the individuals. This observation confirms the literature data on a high level of aggression between males (Viitala 1977, Ims 1987, Marchlewiska-Koj et al. 1989). Small number of the recorded encounters between males precluded a more detailed analysis of dominance relationships in the form of a graphic representation of the hierarchy postulated by some authors (Viitala 1977, Gustafsson et al. 1980, Viitala and Hoffmeyer 1985).
Social interactions between females were more dependent on the age of individuals. Encounters of adult females were rare, and their contacts were as aggressive as those between males (they did not tolerate each other). A consequence of the behaviour based on aggression and avoidance may be the spatial distribution of adult females. Only one or two females weighing more than 20 g were recorded at each baited site. Such isolating forms of behaviour were described by Bujalska (1985) and Mironov (1990). In this context, avoidance behaviour may be interpreted as a “fixed effect” of aggressive interactions. This confirms a close relationship between social interactions and the spatial distribution of individuals.

Encounters between females from younger groups (subadults and juveniles) were characterised by a high proportion of tolerant interactions. A similar result was obtained by Saitoh (1981) from enclosures. This tolerance may be due to the age of individuals, but it may also be based on close relatedness. Young females often remain near the place of birth (Mazurkiewicz and Rajska-Jurgiel 1975, Viitala and Hoffmayer 1985), and kin recognition in groups of sisters may account for a higher proportion of tolerant behaviour during interactions (Ferkin 1988, Barnard and Fitzsimons 1988).

4.2. Social interactions during male-female encounters

Male-female encounters were characterised by a high level of aggression, like male-male encounters. Typically, males were the dominant sex in these interactions. This finding seems to contradict the literature data for the bank vole stating that females predominate the males (Mihok 1976 for C. garreri, Viitala 1977 for C. rufocanus, Marchlew ska-Koj et al. 1989, Kapusta et al. 1996 for C. glareolus). It should be noted, however, that the encounters between bank voles of the opposite sexes were largely dependent on the age of interacting individuals. Adult males and females avoided each other, and their closer encounters were always aggressive. Much more frequent were encounters between adults and younger individuals of both sexes. During these encounters, older individuals were more aggressive (and less tolerant) towards younger males than females. This difference in the behaviour of adults may be important for the fates of young individuals, and it may be interpreted as a behavioural mechanism forcing the migration of subadults of a specified sex.

It is known that in autumn, when population density is increased, a part of individuals abandon the area they previously occupied, and start migrating (Gliwicz 1986). This migration may be caused by intensified social interactions in the population between adults and their abundant offspring (Wolf 1992). Migrants most often are immature males (Bondrup-Nielsen and Karlsson 1985, Greenwood 1980, Ims 1987, Ims and Andreassen 1991). It is thus possible that the recorded aggressive behaviour of adults towards young males could account for emigration of the latter. This conclusion corresponds to the results obtained by Kozakiewicz (1976), who conducted studies in the same area (Kampinos National Park). He found that the seasonal increase in migration in the bank vole population occurred at the end of September, that is, shortly after the present experiment. This may directly confirm the thesis that the autumn migration of bank voles in the study area had a behavioural background.

Lower aggression of older individuals towards subadult females may explain the philopatry of females, that is, settling near the natal place (Viitala 1977, Yönen et al. 1988, Sandell et al. 1990). This phenomenon occurs especially in periods of increased population density (Bujalska and Grüm 1989), and is known as the “sit and wait strategy” (Bujalska 1990). Staying near the place of birth is less risky than migration, and enables the acquisition of a home range if the territorial individual dies. Remaining among kin and familiar, thus, more tolerant individuals is also important (Viitala and Hoffmeyer 1985, Ferkin 1988, Lambin and Krebs 1991). Such groups of individuals can better survive winter, for example, due to advantage from social thermoregulation (Kłosińska 1994). Closely related and/or familiar females that survived winter in...
the same area (also in the same nest) and inhabit neighbouring areas in spring can have a higher reproductive success than unfamiliar individuals involved in heavier competition for space and other resources (Lambein and Krebs 1993, Mappes et al. 1995).

4.3. Persistence and repeatability of social relationships between individuals

An important finding is that social interactions between bank voles during direct encounters were relatively persistent and repeatable. During the 10-day period, only a small decline in tolerance was observed, whereas the proportion of the other behaviour types remained unchanged. This implies that during this experiment, a relatively steady fragment of the “social life” of the population was recorded, and the additional food supply did not cause a rapid increase in the aggression stimulated by competition for food. This may be due to the fact that point food sources appear rather frequently in a natural way, for example, near trees producing heavy seeds, in the period of seed fall (Jensen 1982, Babińska-Werka 2005). When considering the above arguments, it seems, however, that experiments conducted with the use of bait for a longer time can bring about changes in the behaviour of these mammals grouped in a particular area. This suggests that observations of the social behaviour of rodents should be rather short-term, or attempts should be made to eliminate the need for baiting.

4.4. Prospects of the use of video monitoring in population studies

The method used in this experiment resting on video recordings for observation of the behaviour of rodents, enabled us to overcome difficulties associated with the investigation of social interactions between these mammals under natural conditions. The basic advantage of this method is the possibility of obtaining data on the behaviour of rodents in a direct way. There was no need to capture them repeatedly, or providing them with radio transmitters, and the animals were not scared by the work of these devices or by the presence of an observer (these are the major disadvantages of the trapping and telemetric methods – Gipps 1985, Andrzejewski 2002). Multiplication of the observation sites and the use of infrared light enabled 24-h recording, thus increasing the amount of data. Recording the observed behaviour on the video tape enabled a detailed analysis, including a frame-by-frame review. This is important because interactions between individuals typically occur rapidly so that it is difficult to observe them and take notes without delay (Andrzejewski, Olszewski 1963).

The present results allow many questions concerning the direction of future studies with the use of a similar method. First, there is a problem of the effect of kinship on the behaviour of individuals. Also a series of observations in different seasons, characterised by different food conditions and population densities, would be useful. This could also provide a deeper insight into the consequences of various behaviours, for example, in terms of the breeding success of individuals showing a particular type of behaviour, or this could result in a better understanding of migrations. Also the restriction or abandoning the introduction of additional food to the natural environment seems to be desirable. The use of natural sources of food would enable observations over larger areas, making possible the monitoring of movements of individuals. These and probably many others applications would be available if the tools used in this study were improved, while preserving the general scheme of their work. Especially useful may be the digital data recording and the introduction of a function of motion detection. These would enable the monitoring of even several ten sites simultaneously, would facilitate a review of the data, and, consequently, collection of a sufficient material even without baiting. Moreover, the application of wireless transmission between components of the system (camera-computer) would increase the mobility and facilitate the setting up of the components in the field. With respect to the versatility of such monitoring systems and the possibility of obtaining data difficult or impossible to obtain in a different way, their broader application may be a valuable tool for study-
ing animal behaviour, especially under field conditions.

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