SOCIAL BEHAVIOR OF THE JAPANESE WOOD MOUSE, APODEMUS SPECIOSUS (TEMMINCK ET SCHLEGEL), IN THE FIELD

Takaki Kondo, Department of Zoology, Faculty of Science, Kyoto University, Kyoto 606.

Synopsis


Social behavior of the Japanese wood mouse was studied by trapping and by direct observation at two artificial feeding sites during the early part of the breeding season. Meetings were classified into the following five types: aggressive meeting, meeting with retreat, meeting with mutual flight, tolerant meeting and amicable meeting. Amicable meetings and meetings with mutual flight were observed only between opposite sexes. Males always expelled other males from the feeding site when they met, and a straight dominance hierarchy was observed, although their ranges overlapped rather randomly. The subordinate males had somewhat different activity rhythms from those of the dominant. On the other hand, ranges of females tended to be mutually exclusive, but females permitted other females to stay near the feeding site. All females had similar activity rhythms. The social order seemed to be related to the body weight, but males were dominant over females, even if the male was smaller than the female. Although males often took the bait together with females, no evidence that a male associated with a particular female was obtained.

Introduction

Because of the difficulty of observing small nocturnal rodents directly in the field, their social behavior is studied indirectly by the spatial distribution of animals (Blair, 1951; Brown, 1966, 1969; Getz, 1961; Metzgar, 1971), by using nest boxes (Nicholson, 1941; Howard, 1949), or by laboratory experiments on the aggressiveness of animals (Sadleir, 1965; Turner & Iversen, 1973). A few investigations on the social behavior by direct observation have been carried out in the field (Andrzejewski & Olszewski, 1963; Izumi, 1973; Garson, 1975), but there have been no studies connecting the observed social behavior with the distribution and the activity of animals.

As a part of some work on a natural population of the Japanese wood mouse, Apodemus speciosus, I observed the social interaction between individuals directly at artificial feeding sites in the summer of 1975. In this paper, I attempt to relate the observed social interaction to the home ranges and activity rhythms revealed by trapping.

I am grateful to the following persons for their help during the preparation of this paper: Drs. Masaaki Morisita, Hiroya Kawanae, Messrs. Okimasa Murakami, Akio Taki, and all the postgraduate students at the Laboratory of Animal Ecology, Department of Zoology, Kyoto University. I also wish to thank all the staff of the Ashu Experimental Forest, Kyoto University, for their kindness, and Mr. Minoru Onchi for his help in the present study.

Study Area and Methods

This study was carried out in the Ashu Experimental Forest of Kyoto University, Kyoto Prefecture from July 26 to August 12, 1975. The vegetation of the study area consists mainly of Fagus crenata, Quercus mongolica and Cornus controversa. The lower layer of the woods consists mainly of Cephalotaxus harringtonii, Lindera umbellata and Euonymus atatus. The dominant species of herbs are Miscanthus sinensis and Polygonum cuspidatum.

In the study area (72×48 m) seventy trap stations were arranged in a grid with a spacing of 8 m, and one or two Sherman live-traps baited with soybeans were set at each trap station. Trapping was continued for six nights (July 26–Aug. 1) before, and for three nights (Aug. 9–12) after, direct ob-
Observation. Traps were visited every two hours from 18:00 to 6:00, sunset being at about 19 o'clock and sunrise at about 5 o'clock. However, on the night (July 31–Aug. 1) before the direct observation traps were visited only once, in the morning. All captured animals were individually marked by toe-clipping; they were weighed, sexed, their reproductive condition examined and released at their capture sites. All animals caught on the morning of August 1 were brought to the laboratory, and a colored ear tag was attached to each animal in order to identify individuals at a glance; afterwards they were released at their capture sites.

Two artificial feeding sites were pre baited for two nights (Aug. 1–3), and direct observation was carried out for three nights (Aug. 3–6) at feeding site A and for three nights (Aug. 6–9) at feeding site B. The total time spent on direct observation was 1441 minutes (866 min at feeding site A and 475 min at feeding site B). A handful of soybeans, linked together as a rosary by a piece of fine wire to prevent them from being carried away by mice, was placed on the ground at both feeding sites every night except during the period of trapping.

The animals were observed using a normal white light provided by a small portable electric torch, which was placed about 1 m above the bait. The observer sat about 2 m from the bait. The observation indicated that animals were aware of light, but this did not prevent them from appearing to feed on the bait.

Results

Composition of the population

Six adult males and four females were caught in the study area (Table 1). All the males had descended testes, but all the females had imperforate vaginas.

In the study area a population census was carried out for about five nights a month from May to October in 1974 and 1975, using a marking-and-recapture method. Each month the number of mice captured was almost equal to the number estimated by Hayne's regression method (Kondo, unpublished), so that probably nearly all mice living in the study area were caught. One male (♂36) seemed to be a wanderer, because he was caught only once during the present investigation. Another male (♂18) was not caught between September 1974 and June 1975. Probably he had emigrated from the study area and came back just before the time of the present study. One male (♂38) and three females (♀37, ♀39 and ♀40) were newly marked, so that they were new immigrants at that time. The other four mice were residents of the study area.

Types of meeting

Four males (♂5, ♂18, ♂35 and ♂38) and two females (♀39 and ♀40) were observed at both feeding sites. One female (♀34) was observed only at the feeding site B. One male (♂30) was not observed at the feeding sites, although they lay within his range. One female (♀37) was not observed either, probably because her range was far from the feeding sites (Fig. 1).

Forty meetings were observed during the period of direct observation (28 meetings at the feeding site A and 12 meetings at the feeding site B). Only once was it observed that three mice (♂5, ♀39 and ♀40) met at the same time, and this case was counted as three meetings (one was as amicable meeting

<table>
<thead>
<tr>
<th>Individual number</th>
<th>Body weight (g)</th>
<th>Month of initial capture</th>
<th>Month of final capture</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂5</td>
<td>44.7 (+)</td>
<td>June, 1974</td>
<td>October, 1975</td>
</tr>
<tr>
<td>♂18</td>
<td>47.5 (+)</td>
<td>July, 1974</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♂30</td>
<td>49.8 (+)</td>
<td>May, 1975</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♂35</td>
<td>38.5 (+)</td>
<td>June, 1975</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♂36</td>
<td>36.5 (+)</td>
<td>July, 1975</td>
<td>July, 1975</td>
</tr>
<tr>
<td>♂38</td>
<td>33.2 (+)</td>
<td>July, 1975</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♀34</td>
<td>45.8 (−)</td>
<td>June, 1975</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♀37</td>
<td>28.2 (−)</td>
<td>July, 1975</td>
<td>October, 1975</td>
</tr>
<tr>
<td>♀39</td>
<td>30.0 (−)</td>
<td>July, 1975</td>
<td>August, 1975</td>
</tr>
<tr>
<td>♀40</td>
<td>40.3 (−)</td>
<td>July, 1975</td>
<td>September, 1975</td>
</tr>
</tbody>
</table>

* +: in reproductive condition
  −: in non-reproductive condition

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between $\varphi 5$ and $\varphi 40$, the other tolerant meetings)  
the meetings were classified into five types:  
1. Aggressive meeting—a mouse attacks the oth-
er, with the latter fleeing out of sight of the ob-
server.  
2. Meeting with retreat—two mice face each oth-

![Diagram of home ranges]

Fig. 1. Map of home ranges. Open circles, figures and capital letters represent trap stations, the individuals' numbers and the feeding sites respectively. Small letters represent the capture sites of each mouse, and small letters in square indicate the sites where he mouse was observed only.  
(a) males: a- $\varphi 5$, b- $\varphi 18$, c- $\varphi 30$, d- $\varphi 35$, e- $\varphi 38$.  
(b) females: a- $\varphi 34$, b- $\varphi 37$, c- $\varphi 39$, d- $\varphi 40$.  

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er at a distance, and one of the mice retires without being attacked by the other.

3. Meeting with mutual flight—a mouse attacks the other, but both mice run rapidly away in different directions.

4. Tolerant meeting—a mouse attacks the other, but both remain, taking the bait together before or after the attack.

5. Amicable meeting—two mice meet and feed on the bait side by side. No aggressive behavior is displayed.

**Social interaction between individuals**

Meetings between males were relatively few (Table 2), and males never tolerated the presence of other males at the feeding site. No upset of the social order between males was observed (Table 3), and the dominance-subordination relationship between males is clear, thus $\varphi 5 > \varphi 18 > \varphi 35 > \varphi 38$.

Meetings between females were observed only twice, between $\varphi 39$ and $\varphi 40$. Although $\varphi 40$ attacked $\varphi 39$ when they met, the former did not expel the latter from the feeding site, and they took the bait together side by side.

All types of meeting were observed between the opposite sexes, the most frequently observed being amicable. This type of meeting was not observed between the same sex. In tolerant meetings the male always attacked the female. Meetings with mutual flight were observed only twice, between $\varphi 38$ and $\varphi 40$, and the latter attacked the former in both cases. Except in these two cases males were always dominant over females.

Among males, $\varphi 5$ came in contact with females most frequently (Table 4). He most frequently took the bait together with $\varphi 40$, but spent more time with

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**Table 2. Frequencies of each type of meeting between the same and the opposite sexes.**

<table>
<thead>
<tr>
<th>Type of meeting</th>
<th>$\varphi-\varphi$</th>
<th>$\varphi-\varphi$</th>
<th>$\varphi-\varphi$</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggressive meeting</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Meeting with retreat</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Meeting with mutual flight</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Tolerant meeting</td>
<td>0</td>
<td>7</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Amicable meeting</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Totals</td>
<td>8</td>
<td>30</td>
<td>2</td>
<td>40</td>
</tr>
</tbody>
</table>

**Table 3. The dominance-subordination relationships between individuals.** A "score" a+b indicates the number of aggressive encounters at the feeding site A (a) and at the feeding site B (b).

<table>
<thead>
<tr>
<th>Dominant</th>
<th>$\varphi 5$</th>
<th>$\varphi 18$</th>
<th>$\varphi 35$</th>
<th>$\varphi 38$</th>
<th>$\varphi 40$</th>
<th>$\varphi 39$</th>
<th>$\varphi 34$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subordinate</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 5$</td>
<td>$\varphi 18$</td>
<td>$\varphi 35$</td>
<td>$\varphi 38$</td>
<td>$\varphi 40$</td>
<td>$\varphi 39$</td>
<td>$\varphi 34$</td>
<td>$\varphi 39$</td>
</tr>
<tr>
<td>$\varphi 5$</td>
<td>2+0</td>
<td>1+0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 38$</td>
<td>2+0</td>
<td>0+1</td>
<td>2+0</td>
<td>0+1</td>
<td>3+0</td>
<td>3+0</td>
<td>1+1</td>
</tr>
<tr>
<td>$\varphi 39$</td>
<td>2+0</td>
<td>0+3</td>
<td>2+0</td>
<td>1+1</td>
<td>3+0</td>
<td>3+0</td>
<td>3+0</td>
</tr>
<tr>
<td>$\varphi 34$</td>
<td>0+1</td>
<td>0+1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>* mutual flight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 4. Number of each type of meeting for every combination of individuals.** A "score" a-b-c-d indicates the numbers of aggressive meetings (a), meetings with retreat (b), tolerant meetings (c) and amicable meetings (d). Figures in parentheses represent the time (minutes) spent alone or with each partner at the feeding sites (Data from both feeding sites are pooled).

<table>
<thead>
<tr>
<th></th>
<th>$\varphi 5$</th>
<th>$\varphi 18$</th>
<th>$\varphi 35$</th>
<th>$\varphi 38$</th>
<th>$\varphi 40$</th>
<th>$\varphi 39$</th>
<th>$\varphi 34$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\varphi 5$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 18$</td>
<td>1-1-0-0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 35$</td>
<td>2-0-0-0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 38$</td>
<td>0-2-0-0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 40$</td>
<td>1-3-3-4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 39$</td>
<td>0-1-1-1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varphi 34$</td>
<td>0-0-1-1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* including two meetings with mutual flight

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♀ 39 than with ♀ 40 at the feeding sites. One male (♂ 18) did not meet any females at the feeding sites. So far as was observed at the feeding sites, no males associated with any particular females.

Spatial distribution of home ranges

The home range of each individual was defined as being bounded by the lines connecting the outermost sites of capture or observation (Fig. 1). For determining whether home ranges tended to overlap randomly or not, the \( I_s \) index value (Morisita, 1959) was calculated from the distribution obtained by counting the number of stations at which 0, 1, 2, ..., mice were recorded. It was supposed that in theory a mouse could be caught at all stations in its range, even if in practice it was not caught at some stations in its range. The \( I_s \) index is unity when ranges overlap randomly, and zero when ranges do not overlap. The calculated \( I_s \) index values were 0.86 for males, 0.49 for females and 0.97 for both sexes together, taken over the whole observation period. Thus, ranges of males tended to overlap rather randomly, whereas those of females tended to be mutually exclusive.

Traps were visited every two hours (seven times a night) for eight nights, allowing \( I_s \) index values to be calculated each night (Table 5). The \( I_s \) index for males fluctuated from night to night, but that for females was always zero. This indicates that the daily ranges of females were completely exclusive.

There were five cases in which all individuals (except ♀ 36) were trapped at the same time. From these data the distance between pairs was calculated for all pairs (Fig. 2). The frequency distribution of the distance between males and between males and females was random, but that of the distance between females was uniform.

Activity rhythms of individuals

From the capture data of the eight nights when traps were visited every two hours, the activity rhythm of each mouse was represented by the number of times of capture at a given time of night (Fig. 3). Although traps were also set during the daytime, the number of captures before sunset were only 4 (1.6%) out of a total of 253 captures. In a 1965 study of a natural population of this species at Mt.

Table 5. The dispersion pattern of home ranges each night calculated by Morisita's \( I_s \) index. (See text for details).

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>26–27 27–28</td>
<td>30–31 9–10</td>
</tr>
<tr>
<td>Males</td>
<td>4.9 1.7 0.9</td>
<td>0.2 0.9 0.5</td>
</tr>
<tr>
<td>Females</td>
<td>0 0 0</td>
<td>0 0 0</td>
</tr>
<tr>
<td>Both sexes</td>
<td>3.3 0.9</td>
<td>0.4 0.6 0.2</td>
</tr>
</tbody>
</table>

Fig. 2. Frequency distribution of the distance between two individuals. Open circles indicate the theoretical bivariate normal distribution. (a) between males \( (\chi^2=1.72, \ d.f.=4, \ P>0.7) \). (b) between females \( (\chi^2=6.29, \ d.f.=2, \ P<0.05) \). (c) between the male and the female \( (\chi^2=0.95, \ d.f.=5, \ P>0.95) \).
ranges of two males (♂5 and ♂20) overlapped with the other males’ at 22:00, when they were most active. When the other three males were most active, their range tended to overlap only slightly with the other males’.

Fig. 6 shows the activity at the feeding sites. The activity is represented as time (minutes) spent at the feeding site during the observation period of ten minutes. Animals were most frequently observed between 20:30 and 22:30. It is clear that the intervals in which males appeared at the feeding site are separate from each other, but no such tendency is clear in females.

Discussion

ANDRZEJEWSKI & OLSZEWSKI (1963) distinguished three types of meeting in natural populations of Apodemus flavicollis and Clethrionomys glareolus. In a laboratory study on the social behavior of A. sylvaticus, BOVET (1972a) distinguished six types of meeting (Table 6). In the present study five types of meeting were distinguished as mentioned before, one of which, meeting with retreat, was not recognized in other studies. ANDRZEJEWSKI & OLSZEWSKI (1963) observed such meetings, but ignored them because they were not accompanied by any direct contact between individuals, such as attack, chase and so on. But such a meeting may reflect the social relation between individuals; the subordinate mouse always retired in my observation. Therefore, it is improper to ignore this type of meeting.

In a natural population of the Norway rat (Rattus norvegicus), IZUMI (1973) observed the following change in the social order in relation to their meeting site: one rat chased the other, the latter ran away toward its nest about 5 m, then counterattacked and chased the former. But no such change in the social order was observed in the present study: ♂5 was dominant over ♀35 at the feeding site B, nevertheless the feeding site B was placed in the ‘trap-revealed’ range of ♀35, but outside of ♀5’s (Fig. 1). The same situation was observed between ♀39 and ♀40. The distance between the feeding sites was short, and both the feeding sites were placed on the margins of all ranges except ♀30’s, but he was never observed at a feeding site. Therefore, it remains unclear for A. speciosus whether the social order between two individuals changes according to the spatial relationship of their home ranges.

Between individuals of the same sex the social
order seems to be related to the body weight, i.e., the heavier the body weight, the higher the social order. However this can not apply to the relation between ♀5 and ♂18. In the study area ♀5 had lived for a year, while ♂18 came back just before the present study, so that the dominance of ♀5 may be due to prior residence, a situation which has been reported in experimental studies of lizards, fish and so on (Evans, 1936; Braddock, 1949; etc.). Except for two meetings with mutual flight males were always dominant over females, even if the male was smaller than the female.

Home ranges of males overlapped rather randomly, and the distribution of the distance between pairs of males was random. These results indicate that males did not avoid each other in space. However males always expelled other males from the feeding site when they met. The subordinate males (♂18, ♀35 and ♀38) tended to be active earlier than the others, and when they were most active their ranges overlapped only slightly with other males' (Fig. 5). In other words, they tended to be more active when there was little chance to meet with other males, i.e., the so-called Fujimoto effect (Bover, 1972b) was observed between males. Different males may utilize the same place at different times. Home ranges of females tended to be mutually exclusive, and meetings between females rarely occurred. Meetings between females were observed only twice, and in these cases females did not expel

Fig. 4. Nocturnal change of ranges of males described by connecting the capture sites at each given capture time. Symbols are same as in Fig. 1.
Fig. 5. Comparison between the degree of range overlap (open circles) and the activity (closed circles) of males at each given capture time. (See text for details).

Fig. 6. Activity rhythm of each mouse at the feeding sites. Capital letters represent the observed feeding site. Time (minutes) spent at the feeding site during the observation period of ten minutes is on the ordinate. The shaded areas represent periods in which no observations were made. Open and closed symbols indicate males and females respectively.

other females from the feeding site, but fed on the bait together at the feeding site. BURT (1940) regarded mutually exclusive ranges as territories. In this sense, ranges of females may be regarded as territories. But no territorial behavior was ob-

Table 6. Comparison of classifications of meeting in three studies.

cf: aggressive encounters, d: defensive encounters, a: amicable encounters.

<table>
<thead>
<tr>
<th>ANDRZEJSKI &amp; OLSZEWSKI (1963)</th>
<th>Present study</th>
<th>BOVET (1972)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggressive meeting</td>
<td>Aggressive meeting</td>
<td>cf only</td>
</tr>
<tr>
<td>Meeting with mutual flight</td>
<td>Meeting with mutual flight</td>
<td>d+cf only</td>
</tr>
<tr>
<td>Tolerant meeting</td>
<td>Tolerant meeting</td>
<td>cf+a only</td>
</tr>
<tr>
<td>Amicable meeting</td>
<td>Amicable meeting</td>
<td>a only</td>
</tr>
</tbody>
</table>

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erved at the feeding site, so in the present study, it
can not be strictly affirmed that females of *A. spec-
isus* have territories.

Male and female ranges overlapped randomly
and did not correspond closely, as would be expect-
ed if they formed typical pair bonds. Although ami-
cable meetings were most frequently observed be-
 tween the opposite sexes, no evidence of pair bonds
was obtained in the present study. **Garson** (1975)
observed in *A. sylvaticus* that each male fed to-
gether with a particular female more often than
with the other females at the feeding site. The re-
productive condition of the animals in **Garson**’s
work was the same as the present study. This dif-
ference between his study and mine is probably due
to the difference between species, which tends to be
confirmed by other studies: in *Peromyscus leucopus
noveboracensis*, **Nicholson** (1941) found no par-
ticular pairs of adults to be consistently associated
in nest boxes, but in *P. maniculatus bairdii*, **Howard
(1949)** reported that the particular pairs lasted for
the duration of a breeding season.

The results obtained in the present study indicate
that the social behavior of males is different from
that of females. This difference suggests that males
and females regulate their number through different
mechanisms, as shown by **Metzgar** (1971) who
found that in *P. leucopus* females appeared to regu-
late their number by limiting the number of immi-
grants, but males did not.

**Summary**

1. Social behavior of the Japanese wood mouse,
*Apodemus speciosus*, was studied by trapping and
by direct observation at two artificial feeding sites
in the Ashu Experimental Forest of Kyoto Univer-
sity, Kyoto Prefecture from July 26 to August 12,
1975.

2. Six adult males and four adult females were
captured in traps. All males had descended testes,
but all females were imperforate. Among four
males and three females, forty meetings were ob-
served, and they were classified into the following
five types: aggressive meeting, meeting with ret-
reat, meeting with mutual flight, tolerant meeting
and amicable meeting.

3. Between opposite sexes all types of meeting
were observed. Amicable meeting and meeting with
mutual flight were observed only between opposite
sexes. Meetings between the same sex were rela-
tively few. When males met at a feeding site, one
was always expelled. Although meetings between
females were observed only twice, these females
took the bait together at the feeding site.

4. A straight dominance hierarchy was observed
among males. The social order seemed to be relat-
ed to the body weight, i.e., the heavier the body
weight, the higher the social order. Except in meet-
ings with mutual flight males were always dominant
over females, even if the male was smaller than the
female.

5. Ranges of males overlapped rather randomly,
but those of females tended to be mutually exclu-
sive. Male and female ranges overlapped randomly
and did not correspond closely, as would be ex-
pected if they formed typical pair bonds. In the
present study no evidence that a male associated
with a particular female was obtained.

6. Activity of the Japanese wood mouse is mostly
restricted to the night. All females, and males in
the high social rank had similar activity rhythms,
but males in the low social rank had somewhat
different activity rhythms from the others.

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