INTRASPECIFIC AND INTERSPECIFIC BEHAVIOURAL INTERACTIONS IN THE WOOD MOUSE (APODEMUS SYLVATICUS) AND THE YELLOW-NECKED MOUSE (APODEMUS FLAVICOLLIS) IN A NEUTRAL CAGE

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Abstract
Intraspecific and interspecific behavioural interactions between captive wild-born mice were video-recorded and subsequently analysed. Altogether, 118 neutral cage dyadic encounters, each lasting 10 minutes, were carried out. In both intraspecific and interspecific tests, male-male interactions were apparently more agonistic than those female-female. A. flavicollis males spent more time performing agonistic behaviour than A. sylvaticus males. In both sexes, the heavier A. flavicollis was the regular winner of interspecific encounters.

Key words: agonistic behaviour, aggression, behavioral ecology, Apodemus

Introduction
The wood mouse, Apodemus sylvaticus (Linnaeus, 1758) and the yellow-necked mouse, Apodemus flavicollis (Melchior, 1834) are closely related species living in great sympatry. In woodlands, they frequently occur even syntopically. Behavioural interactions, especially aggressive, both intraspecific and interspecific, can be expected to play an important role in the ecology of wood mice populations and possibly affect their coexistence.

There are at least two studies comparing levels of aggressive behaviour in A. flavicollis with those in A. sylvaticus. Hoffmeier (1973) observed small groups of animals of both species in 16 m² indoor enclosure. She suggested that A. flavicollis was found to be less aggressive towards members of their own species than A. sylvaticus. Montgomery (1978) did not find significant differences between these species in amounts of aggressive behaviour recorded during short-time experiments in a neutral cage.

There is a strong contradiction between above mentioned results and our experience with captive wood mice. In A. flavicollis, we have never succeeded to form a stable social group including two or more unrelated males. Such attempts led regularly to serious wounding or even killing of the subordinate male. Captive A. sylvaticus, unlike A. flavicollis, seem to be fairly tolerant. This suggestion was supported by both laboratory and field studies on aggressive behaviour in A. sylvaticus (Gurnell 1977, Lambin 1988). According to our experience, which is supported elsewhere (e.g., Bovet 1972b), A. sylvaticus
can be kept and even bred in groups of unrelated animals. Resident animals of this species, especially dominant males, are aggressive against intruders, but finally intruders are usually accepted (Bove et 1972a, Richard-Yris 1979).

The objective of the present study is to compare aggressive behaviour in these two Apodemus species, using dyadic encounters in a neutral cage. In sharp contrast to a corresponding study by Montgomery (1978), our experiments were performed during the reproductive season, when the level of aggressive behaviour in the Wood mouse was reported to be higher (Gurnell 1978) than in winter months. Last but not least, tested mice came from a different part of Europe.

Material and Methods

Twenty individuals (10 males and 10 females) of A. sylvaticus and twenty (10 males and 10 females) A. flavicollis were included in the investigations. They were wild born, sexually mature, animals captured in various localities of Central Bohemia in the autumn 1992 and maintained in the laboratory throughout the subsequent winter and spring until testing. The experiments were performed in July 1993. According to our knowledge of the growth and population structure of these species, the experimental animals were probably born in the late summer 1992. Despite their sexual maturity, females were actually neither pregnant nor lactant at the time of testing.

At the time of testing, the mean body weights of A. sylvaticus were 23.9 g (min. 18.4 g, max. 38.0 g) and 21.7 g (min. 14.0 g, max. 26.9 g) in males and females, respectively. The corresponding values for A. flavicollis were 43.5 g (min. 30.5 g, max. 54.1 g) and 29.4 g (min. 25.3 g, max. 38.4 g).

All the animals were housed in heterosexual pairs in standard plastic cages 42 x 22 x 22 cm or in larger glass cages (60 x 50 x 40 cm). Cages were placed in a light-controlled room (14L: 10D at the time of testing). Ad libitum water and food (mouse and rat breeder diet, wheat etc.) were provided. Each cage contained sawdust bedding, nesting material (hay) and shelters.

Encounters between mice were carried out in a 50 x 30 x 35 cm glass cage. The cage was divided by a thick card partition into two equal parts. During testing, the cage was illuminated by a single 40 W red light bulb suspended in the distance of approximately 1.5 metres. Mice were tested during the dark phase of their light-dark cycle. At the beginning of each experimental session, two mice were placed in the pen, on the opposite sides of the partition, and left for five minutes. The central partition was then removed and video recording by a single VHS-camera started. The video camera was stopped at the end of the session, i.e., ten minutes after the moment when one or both animals paid attention to the other for the first time. After each session, the sawdust covering the floor was changed, and the cage was thoroughly cleaned (using 96% ethanol).

In total, 80 intraspecific encounters (20 for each sex and species) were performed in the first set, while 38 interspecific (18 male-male, 20 female-female) in the second set. Each animal was tested with different opponents 4 times in the first and 2 times in the second set. Repeated testing of the same individual occurred no earlier than 24 hours after the preceding test. No effect of multiple testing was evident.
We distinguished 33 behavioural elements (with minor changes adopted from Gurnell (1977) and Montgomery (1978), for description see Appendix I), which were summarised into 18 categories (Roman numerals) and 5 functional blocks.

Video records of encounters were subsequently observed and analysed. The observed behavioural elements were quantified using the computer program package ACTIVITIES (Vrba & Donát 1993). Data on total duration of each of these elements for a particular session and animal were used as the primary data for further analysis. Duration was expressed in seconds.

The index of dominance was calculated as sum of time spent by dominant behaviour (A/I,II) minus sum of time spent in behaviour considered to be defensive or submissive (IV, VII, VIII, IX, X). In dyads in which non-neutral, agonistic interactions were recorded, the animal displaying higher value of the index of dominance, was classified as the winner of the encounter. The data were compared using the Mann-Whitney or Wilcoxon tests.

Table 1. Mean duration (in seconds) of different behavioural categories. n = number of dyads. Means are calculated per encounter.

<table>
<thead>
<tr>
<th>Species Sex</th>
<th>A. sylvaticus males females n=20 n=20</th>
<th>A. flavicollis males females n=20 n=20</th>
<th>A. sylvaticus versus A. flavicollis males n=18 A.s. A.f. females n=20</th>
<th>A.s. A.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>threat-attack</td>
<td>14.0 9.0 32.9 5.9 13.0 .0 13.0 11.9 .4 11.5</td>
<td>chase</td>
<td>11.2 2.1 6.7 3.9 11.5 .0 11.5 4.3 2.8 1.6</td>
<td>roll-over fight</td>
</tr>
<tr>
<td>AGONISTIC</td>
<td>119.3 57.4 193.7 51.1 111.3 73.4 37.9 84.1 53.1 31.0</td>
<td>S.E.</td>
<td>21.2 18.8 30.7 21.8 19.4 15.0 9.9 27.8 17.2 13.7</td>
<td>attend</td>
</tr>
<tr>
<td>INTRODUCTORY</td>
<td>136.8 95.0 148.8 145.1 138.4 69.4 68.9 84.2 44.7 39.5</td>
<td>S.E.</td>
<td>19.5 7.9 17.6 17.9 16.5 11.9 7.6 9.5 6.5 5.5</td>
<td>AMICABLE</td>
</tr>
<tr>
<td>INDIVIDUAL</td>
<td>593.3 548.3 545.3 655.7 564.6 339.1 225.5 593.3 262.3 331.0</td>
<td>S.E.</td>
<td>39.2 30.0 39.7 46.4 28.8 25.0 20.1 28.3 30.0 30.9</td>
<td>loco-explore</td>
</tr>
</tbody>
</table>
Results

Intraspecific Interactions

Sexual differences were the most apparent (Table 1, Fig. 1). In both species male-male interactions were markedly more agonistic (A. sylvaticus: P = 0.003, A. flavicollis: P < 0.0001) and less amicable (A. sylvaticus: P = 0.019, A. flavicollis: P = 0.002) than those female-female. Moreover, there were significant differences in all agonistic categories (with the exception of chase and avoid-retreat), attend and crouch-sit in A. flavicollis. In A. sylvaticus they were: chase, flee-jump-freeze, attend.

![Graphs showing percentage of time spent in different types of behaviour in intraspecific encounters of A. sylvaticus (top) and A. flavicollis (bottom).](image)

A. flavicollis males spent slightly, but nonsignificantly (P=0.064) more time in agonistic behaviour during male-male interactions than males of A. sylvaticus, whereas the latter species displayed more amicable behaviour (P=0.066). The situation becomes more clear when the individual behavioural categories are
evaluated: *A. flavicollis* males spent significantly more time in five of six categories of contact agonistic behaviour, i.e., roll-over-fight (*P* = 0.031), box (*P* = 0.029), neutral upright (*P* = 0.011), defensive (*P* = 0.008), submissive (*P* = 0.020) as well as in the ambivalent behaviour (*P* = 0.020) and approach (*P* = 0.044) than *A. sylvaticus* males did. On the other hand, the distant elements (chase, avoid-rereat, flee-jump-freeze) representing a considerable proportion of the agonistic behaviour in *A. sylvaticus* males, were less represented in *A. flavicollis* males. However, these differences were not significant.

No substantial difference between behavioural patterns displayed by *A. sylvaticus* and *A. flavicollis* females was found in intraspecific encounters. The latter species displayed more individual (*P* = 0.060) and introductory (*P* = 0.070) as well as less exploratory behaviour (*P* = 0.026). When individual categories were evaluated, they differed significantly in approach (*P* = 0.038), croach-sit (*P* = 0.005) and rear-jump (*P* = 0.002).

**Interspecific Interactions**

Behavioural patterns displayed in interspecific encounters generally resembled those found in intraspecific ones (Table 1, Fig. 2). Sexual differences were similar, but less pronounced than in intraspecific encounters. Significantly more introductory behaviour was found in male-male interactions than those female-female (*P* = 0.015), but the differences in total time spent by agonistic (*P* = 0.072) as well as by amicable behaviour remained non-significant (*P* = 0.114). Attend (*P* = 0.0006) and threat-attack (*P* = 0.030) differed significantly when individual categories were tested.

The heavier *A. flavicollis* was regularly the winner of interspecific male-male dyads. Using the index of dominance, this species was classified as the winner in 16 of 18 encounters. (Wilcoxon test: *P* = 0.009). In addition, *A. flavicollis* expressed more exploratory (*P* = 0.001) and less individual behaviour (*P* = 0.008). Similar, but nonsignificant superiority of *A. flavicollis* was recorded also in female-female interactions. *A. flavicollis* females won in 11 cases and lost only in 6 out of 20 encounters. Neither dominant nor submissive behaviour was recorded in three cases.

![Fig 2](image)

*Fig 2.* Percentage of time spent in different types of behaviour in interspecific encounters between *A. sylvaticus* and *A. flavicollis.*
Discussion

A serious problem is, to what extent aggressive behaviour is species-specific. The results of laboratory studies of aggressive behaviour are dependent upon rearing conditions, prior experience and other environmental factors (Hood & Cairns 1989, Brain & Parmigiani 1990). On the other hand, as clearly demonstrated in laboratory mice, a considerable component of this behaviour is inherited and can be altered by an artificial selection (Cairns et al. 1983, Gariépy et al. 1988, Cairns et al. 1990). In the context of our study, it is interesting that cross-sex inheritance of aggressive behaviour was found in laboratory mice (Hood 1988, Hood & Cairns 1988) and therefore, a correlation between male and female aggression might be expected in interspecific comparisons.

Another methodological problem is that our experiments were performed in a neutral arena of limited size. Therefore, the effects of residence and scent marking affecting the social interaction of mice in more natural situation (Hurst 1993) were ruled out by the experimental design.

Intraspecific Interactions

Female spacing behaviour was proposed to play an important role in the population regulation of several rodents (Gliwicz & Rajaska-Jurgiel 1983, Galindo & Krebs 1987, Parmigiani & Palanza 1994). In A. sylvaticus, presence of this phenomenon is supported by female exclusive home ranges (Wolton 1985, Wilson et al. 1993, Tew & Macdonald 1994) and random distribution of adult females contrasting to aggregate distribution of males and juveniles (Montgomery 1989b). There is no doubt that females of both species were apparently less aggressive than males in our neutral-cage experiments. However, this fact cannot be used as an argument against female spacing. As demonstrated, for example, in house mice (Parmigiani & Palanza 1994), female territorial aggression is highly associated with specific stimuli, and therefore it can be even absent in a neutral-cage conditions.

Having no evidence for greater aggressiveness in A. sylvaticus, we cannot agree with the Hoffmeyer's conclusion that "A. sylvaticus is intrinsically more aggressive than A. flavicollis". Her impression may be an artifact caused by prevalence of more apparent non-contact elements of agonistic interactions in A. sylvaticus. Moreover, we found that A. flavicollis males spent significantly more time in five contact agonistic elements than A. sylvaticus males. These elements frequently occur in the behavioural sequences typical for serious fighting. Therefore, despite the fact that the difference between males of these species in the total time spent in agonistic activities was insignificant, we can conclude that the former species seems to be more aggressive than the latter. This opinion is supported also by greater amounts of amicable behaviour in A. sylvaticus males.

Interspecific Interactions

Our results support previous studies, which suggest superiority of A. flavicollis over A. sylvaticus in aggressive interactions (Hoffmeyer 1973,
Montgomery 1978). Dominance of *A. flavicollis* can be explained simply by the fact that this species is much heavier. However, as reported by several authors for rodents (e.g., Grant 1970), the heavier species is not necessarily the winner of interspecific encounters.

*A. flavicollis* also dominates over its possible competitor in woodlands, the bank vole, *Clethrionomys glareolus* (Andrzejewski & Olszewski 1963, Kalinowska 1971). Unlike *A. flavicollis*, the striped-field mouse, *A. agrarius*, did not show dominance over *Clethrionomys glareolus* (Kozakiewicz & Boniecki 1994), but this species was the regular winner of behavioural interactions with *A. sylvaticus* (Frynta et al. 1995). The Wood mouse was subordinate also in interactions with the house mouse, *Mus musculus*, as reported by Smirin & Shilova (1989), but the taxonomic status of the Russian wood mice used in that experiment is still unclear.

We performed our observations in the neutral cage, while it cannot be excluded that behavioural dominance in nature might be more dependent on residence than on species, as reported by Wolff et al. (1983) in the deer mouse, *Peromyscus maniculatus*, and the white-footed mouse, *P. leucopus*. Therefore, still having no data from direct observations in the field, the relevance of laboratory experiments to natural situation remains unsolved. On the other hand, the superiority of *A. flavicollis* over *A. sylvaticus* found in our experiments fit well with the results of field studies (e.g., Montgomery 1980, 1989a).

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Appendix I. Behavioural elements and their grouping

(A) Agonistic. (1) Threat-attack: (1) Threat, (2) Aggressive upright, (3) Attack; (II) Chase: (4); (III) Roll-over fight: (5); (IV) Neutral upright: (6); (V) Box: (7); (VI) Ambivalent: (8) To-fro, (9) Tail rattling; (VII) Defensive: (10) Defensive upright, (11) Defensive threat; (VIII) Avoid-retreat: (12) Avoid, (13) Retreat; (IX) Flee-jump-freeze: (14) Flee, (15) Jump avoid, (16) Freeze; (X) Submissive; (17) Submissive posture. Note: Categories A/ I - II are denoted as aggressive, A/ III - VI as neutral, and A/ VII - X as defensive. Categories A/ I, III, IV, V, VII, X are further referred to as a contact, while categories A/ II, VIII, IX as a distant agonistic behaviour.

(B) Introductory. (1) Attend: (18); (II) Approach: (19); (III) Nose: (20) Nose-nose, (21) Nose-body, (22) Nose-anal, (23) Follow (usually found as an extension of nose-anal).

(C) Amicable. (24) Mutual groom, (25) Crawl under, (26) Lie on, (27) Block. Note: All the amicable elements were recorded only for that animal of the dyad who initiated or actively participated in the amicable interaction.

(D) Individual. (1) Self groom: (28); (II) Crouch-sit: (29) - This is a composite element that may be associated with various motivations. The mouse is sitting in the cage and interacts with the opponent in a passive way only.

(E) Exploratory. (1) Loco-explore: (30) time spent by non-social loco-exploratory activities (gnawing the field, scratching at the floor or walls with the forepaws, climbing, sniffing, walking and running about the field). (II) Rear-jump: (31) Rear - the mouse by the exploratory behaviour holds up on its hind legs, (32) Rear at the wall - the mouse holds up at the wall of the cage. (33) Jump - the animal springs into the air regardless the impact of the opponent.
LITERATURE


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