Intraspecific behavioural interactions in *Apodemus microps*: a peaceful mouse?

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Social interactions of captive *Apodemus microps* Kratochvíl et Rosický, 1952 were studied in dyadic encounters. In neutral-cage conditions both sexes showed exceptionally high proportion of amicable behaviour (on average ca 30% of the total time) and very low proportion of agonistic behaviour (up to 2.1%), when compared to patterns reported in other *Apodemus* species. The high share of amicable behaviour cannot be simply explained by decreased aggression. Mice actively offered amicable acts to their unfamiliar conspecifics even during the short-time (ten-minute) encounters. This phenomenon may be interpreted as a cooperative strategy. However, the near absence of aggression in *A. microps* could be altered by specific social contexts: males, but not females, became mutually agonistic when tested in a home-cage or in the presence of a female.

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Introduction

The herb field mouse *Apodemus microps* Kratochvíl et Rosický, 1952 is the smallest species of the subgenus *Sylvaemus,* recently synonymized with *A. uralensis* from Russia and Middle East by some authors (Mezhzherin 1990, Mezhzherin and Zykov 1991, Mezhzherin *et al.* 1992, Vorontsov *et al.* 1992, Filippucci *et al.* 1996, Orlov *et al.* 1996). In spite of its wide geographical distribution, most data concerning the biology of *A. microps* come from Slovakia (Stanko 1993), southern Moravia (Holišová *et al.* 1962, Pelikán 1964, 1966, 1967, 1970, Zejda and Nesvadbová 1996) and neighbouring territories in Austria (Steiner 1966, 1968, Spitzenberger and Steiner 1967, Obrtel and Holišová 1983).

So far, only limited research effort has been devoted to the behaviour of this species (eg, data on home ranges: Demeter 1984, exploratory behaviour: Frynta 1994). However, the available anecdotal evidence suggests that the behaviour of this species apparently differs from that of its well-studied congeners. When

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compared to *A. sylvaticus* and *A. flavicollis*, *A. microps* is less active and shy, and when handled it shows a low tendency to bite (Steiner 1978). According to our experience with captive *A. microps*, it seems to be unusually placid and amicable. Even sexually active males were mutually non-aggressive. Consequently, as in *A. sylvaticus*, *A.microps* can be housed and even bred in groups consisting of unrelated individuals. Therefore, the presence of low intraspecific aggression in *A. microps* is worth of study.

We tested the following hypotheses concerning behaviour of *A. microps*: (1) apparent tolerance is an active process; non-aggressive interactions are characterised by the presence of amicable acts, not just by mutual avoidance; (2) aggression, as an element of male reproductive strategy, is considerably elevated in male-male interactions in the breeding season; and (3) aggression in this species is not generally reduced, but it is confined to specific social contexts.

Material and methods

Experimental animals (17 males and 23 females of *A. microps*) were captured near the village of Dyjákovičky (district of Znojmo, southern Moravia, Czech Republic) in December 1994. They were housed in heterosexual pairs (or groups consisting of a single male and two females) in standard plastic cages (30 × 15 × 15 cm). Each cage contained sawdust bedding, nesting material and a shelter. Cages were placed in a light-controlled room (12L : 12D). Mice were provided with *ad libitum* water and food (mouse and rat breeder diet, wheat). At the time of testing, all individuals were sexually mature, females were neither pregnant nor lactating.

Neutral-cage experiments

A standard neutral-cage procedure (with minor changes adopted from Gurnell 1977 and Montgomery 1978, for details see Čiháková and Frynta 1996) was used. Encounters between mice were studied in a 50 × 30 × 35 cm glass cage illuminated with a single 40W red-light bulb. The cage was divided by a thick card partition into two equal parts. 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 started. The camera was stopped ten minutes after the moment when one or both animals paid attention to the other for the first time (eg oriented head movement, approaching, sniffing the opponent). The cage was thoroughly cleaned using 96% ethanol after each session.

One set of neutral-cage experiments was performed in winter (January–February 1995) when all the animals were in naturally induced non-breeding condition (evident from testes regression in males). The other one was carried out in summer (June 1995), ie after the spontaneous spring recovery of reproduction.

Overall, 24 male-male, 33 female-female and 17 male-female encounters were performed in the winter set, and 24 male-male, 32 female-female and 15 male-female encounters in the summer set. Each animal was tested with different opponents three or four times in each set (male-female dyad being the last). Repeated testing of the same dyad (a unique combination of animals) in one experimental set was avoided. Testing of the same individual occurred no earlier than 24 hours after the preceding test.

Video records were subsequently observed and quantified, using the computer program package ACTIVITIES (Vrba and Donát 1993). The following categories of behaviour were distinguished: (1) agonistic behaviour (sum of aggressive, neutral and defensive behaviours; note: aggressive behaviours includes aggressive threat, attack, aggressive upright, and chase), (2) amicable behaviour (social grooming and body contact), (3) introductory behaviour (attend, approach, sniffing and/or

following the opponent), and (4) exploratory behaviour. For description and grouping of behavioural elements see Čiháková and Frynta (1996). Sums of time spent by both animals of a dyad by particular categories of behaviour were computed (total time of each observation is 1200 seconds, ie 10 minutes for each of two opponents) and further compared between dyads of different sex and season. Non-parametric statistics were used to avoid deviations from normal distributions (most apparent in the case of agonistic behaviour). Significant comparisons which passed the requirements of Bonferoni correction (α was divided by the number of comparisons concerning single data set) were further considered. Calculations were carried out using Statgraphics version 5.0 (1991).

Social-context experiments

In August–September 1995 we performed additional experiments to assess effects of social context on behavioural interactions. For this purpose we used the individuals previously subjected to neutral--cage experiments. Due to limited number of experimental animals, repeated testing could not be avoided and, therefore, sequence bias (possible learning) and uncertain independence of individual records should be considered. Because of these methodological constraints, the social-context experiment should be understood as more or less preliminary.

We used the following modifications of the above testing procedure:

"H o m e - c a g e" d e s i g n: One of the tested animals ("territory owner") was introduced to the experimental cage 24 hours before the beginning of an experiment. The cage floor was covered with sawdust coming from the animal's home-cage, ie containing the odour of both sexual partners. At the beginning of the experiment an unfamiliar animal ("intruder") was released into the cage and video recording started.

"F e m a l e p r e s e n c e" d e s i g n: The cage floor was covered with clean sawdust, and a plastic box imprisoning a female was placed in one corner of the cage. The plastic box ($14 \times 9 \times 9$ cm) was divided with a transverse wire grill into equal parts. One half of the box imprisoned a female, while the other was accessible to the tested males. The males were either both unfamiliar to the imprisoned female ("unfamiliar female" design) or their familiarity to the female was asymmetric ("familiar female" design). In the former design both males were released into the experimental cage simultaneously. In the latter design one of the males ("female owner") was previously housed with the female for several months. The "female owner" was allowed to recognise the female during 5 minutes before the opponent ("intruder") was released and video-recording started.

Tested males were subsequently exposed to different situations: "home-cage", "familiar female" and "unfamiliar female" designs (12 dyads for each design) were followed by "neutral-cage control" (10 dyads) and by replication of the first three designs in an inverse order (10 dyads for each design). Females were subjected to "home-cage" design (12 dyads) followed by the "neutral-cage control" (10 dyads).

The total duration of both agonistic and amicable behaviour met the requirements of ANOVA. Therefore, these data were treated by ANOVA (factor: grouping according to the combination of design, sex and repetition, df = 9, 87) and showed significant ($p < 0.0001$) variation between groups (agonistic: $F = 4.61$, amicable behaviour: $F = 9.40$). Comparison between individual groups was performed by Scheffe multiple-range tests (Sokal and Rohlf 1981). In addition, in asymmetric designs ("home-cage" and "familiar female"), differences between the behaviour of "owners" and "intruders" were evaluated by non-parametric matched-pair tests (Statgraphics version 5.0. 1991). For this purpose, the scores of aggressive behaviour (ie offensive elements of agonistic behaviour) were also included.

Results

Neutral-cage behaviour

Most interactions performed by mice in a neutral-cage, irrespective of season and combination of sexes, were apparently characterised by a common behavioural pattern (Table 1). Mice showed extremely low incidence of agonistic behaviour

Table 1. Mean duration (in seconds) of particular behavioural categories displayed by *Apodemus microps* during ten-minute encounters in a neutral-cage. Means are calculated per dyad (total time of each observation is 1200 seconds, ie ten minutes for each of two opponents). Explanations: M-M – male-male, F-F – female-female, M-F – male-female interactions, W – winter period, S – summer period, *n* – number of dyads.

Behaviour	Sex: Season: n:	M-M W 24	M-M S 24	F-F W 33	F-F S 32	M-F W 17	M-F S 15
Agonistic		3.5	24.6	2.1	2.2	3.9	8.1
SE		1.3	7.0	0.8	0.5	1.4	4.8
Amicable		349.0	338.3	355.7	350.8	333.1	344.1
SE		20.5	26.5	24.6	25.2	29.0	30.3
mutual groom		33.9	15.1	24.8	17.9	25.3	22.8
body contact		315.1	323.3	330.9	332.9	307.8	321.4
Introductory		79.1	95.8	64.0	75.5	75.1	75.8
SE		5.6	7.7	8.0	6.1	9.2	10.0
Exploratory		194.5	167.1	199.2	183.7	200.1	184.9
SE		16.6	19.1	23.2	17.6	19.5	18.0

(means ranging from 0.2 to 2.1% of total time of observation) and, simultaneously, high proportion of amicable behaviour (27.8–29.6% of total time). Moreover, even the most active form of amicable behaviour, ie social grooming occurred regularly (1.3–2.8% of total time).

Although still at low level, agonistic behaviour was intensified in male-male dyads in the reproductive season (the summer set). Mean duration of agonistic behaviour in this group was significantly longer than in both the male-male interactions in winter (Mann-Whitney: $U = 3.41$, $p = 0.0006$) and female-female interactions in summer ($U = 4.09$, $p < 0.0001$).

In intersexual dyads, males spent longer time than females in carrying out introductory behaviour and also by amicable behaviour (Wilcoxon matched-pair test: $Z = 2.25$, $p = 0.02$ and $Z = 2.01$, $p = 0.04$, respectively; $n = 32$ dyads, seasons pooled).

Effects of social context

The duration of agonistic behaviour in male-male dyads in this experiment was higher compared to the previous data set (Fig. 1). In contrast, female-female dyads were not agonistic. Thus, all the Scheffe comparisons between groups of opposite sex were significant (female-female interactions in neutral-cage or home-cage designs vs all male-male groups, $p < 0.05$).

Although neutral-cage controls interposed into the sequence of male-male encounters showed high scores of agonistic behaviour, they still differed from male-male interactions in different social contexts by markedly and significantly
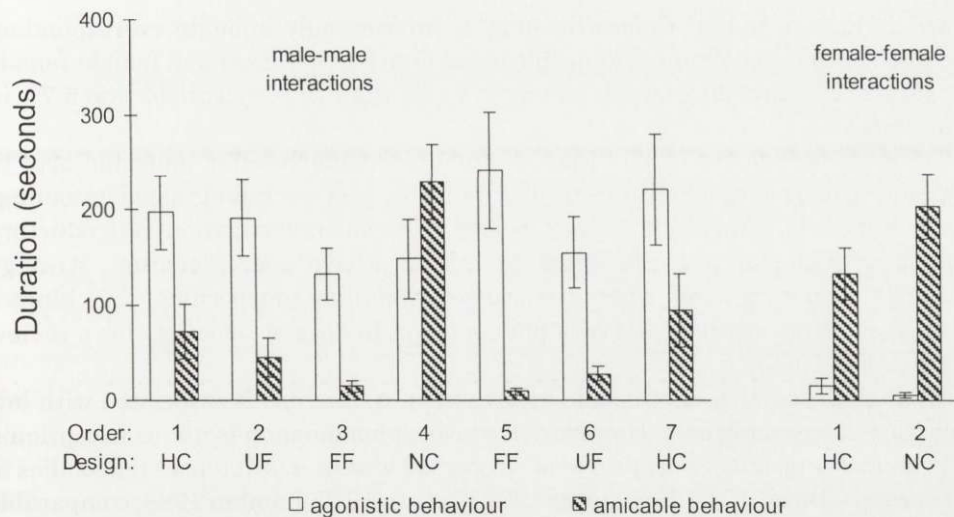
Fig. 1. Mean ± SE duration of agonistic and amicable behaviours displayed by *Apodemus microps* in ten-minute encounters in different social contexts. Means are calculated per dyad. HC – "home-cage" design, UF – "unfamiliar female" design, FF – "familiar female" design, NC – "neutral-cage" control.

higher levels of amicable behaviour (Scheffe test: $p < 0.05$ for all comparisons). Moreover, the mean duration of amicable behaviour in neutral-cage conditions considerably exceeded that of agonistic behaviour.

"Home-cage" and "familiar-female" designs were asymmetric, and therefore, enabled us to test differences between behaviour of "owners" and "intruders". Behavioural asymmetry was most apparent in the "familiar-female" experiment: "owners" spent more time by aggressive (Wilcoxon matched pair test: $Z = 3.04$, $p = 0.0023$), introductory ($Z = 3.18$, $p = 0.0015$) and surprisingly also by amicable behaviours ($Z = 3.15$, $p = 0.0016$) than "intruders". In the "home-cage" design, "owners" spent more time by introductory behaviour (significant for males only: $Z = 2.49$, $p = 0.0124$) and by exploratory behaviour (males: $Z = 2.30$, $p = 0.0211$; females: $Z = 2.86$, $p = 0.0042$) than "intruders".

Discussion

We found that neutral-cage interactions in *A. microps* are usually not only peaceful, but also apparently amicable. Mean proportion of amicable behaviour in *A. microps* (27.8–29.6% of total time of observation) is markedly higher than in other murids previously subjected to identical procedure (Frynta *et al.* 1995, Čiháková and Frynta 1996, Frynta and Čiháková 1996, Suchomelová *et al.* 1998). Considering male-male encounters, the mean values found in *A. microps* (29.1 and 28.2%) exceeded 13–146 times those found in their closest congeners *Apodemus*

sylvaticus (2.2%) and *A. flavicollis* (0.2%). Interestingly enough, corresponding difference in the proportion of amicable behaviour is evident even in female-female encounters (29.6 and 29.2% in *A. microps* vs only 8.2% in *A. sylvaticus* and 5.7% in *A. flavicollis*).

The most surprising fact is that *A. microps* regularly offer amicable acts to unfamiliar conspecifics of either sex. The amicable acts (including social grooming) usually appeared after only a short period of social investigation (introductory behaviour). Thus, *A. microps* seem to exhibit active peace-keeping strategy involving "cooperate first" when exposed to unfamiliar conspecifics. This kind of active cooperative strategy is a rare phenomenon in animal societies (for a review see Dugatkin 1997).

The high proportion of amicable behaviour in *A. microps* is associated with low proportion of agonistic acts. However, the latter phenomenon is not as exceptional as the former one, and it was previously reported also in *A. sylvaticus* (eg studies of social groups: Bovet 1972, Hoffmeyer 1973, Garson 1975, Lambin 1988; comparable results obtained by neutral-cage procedure: Gurnell 1977, Montgomery 1978, Čiháková and Frynta 1996). Nevertheless, comparison of the above neutral-cage studies with our results concerning *A. microps* suggests that both sexes of *A. sylvaticus* are still much more agonistic than *A. microps*. Mean proportion of agonistic behaviour was 9.9% in *A. sylvaticus* males and 4.8% in females (Čiháková and Frynta 1996) while the highest mean value obtained in *A. microps* was 2.1% (Mann-Whitney test: $U = 4.2$, $p < 0.0001$ for between-species comparison of male-male interactions in breeding season). Moreover, our results concerning neutral-cage behaviour of *A. microps* were supported by analysis of six male-male and six female-female dyads that were carried out, using identical procedure and mice from the same region, two years earlier in July 1993 (J. Čiháková-Sádlová and D. Frynta, unpubl.). Mean ($\pm$ SE) durations were 20.2 ± 16.5 of agonistic, 298.8 ± 62.9 of amicable, 115.5 ± 19.8 of introductory, and 280.1 ± 45.8 seconds of exploratory behaviours in male-male dyads. Corresponding values for female--female dyads were 0.3 ± 0.3, 357.2 ± 76.2, 134.8 ± 27.3, and 270.5 ± 61.2 seconds. Thus, also in that experiment *A. microps* exhibited only low proportion of agonistic behaviour (1.7% in males and 0.03% in females) and high share of amicable behaviour (24.9% in males and 29.8% in females).

We can conclude that neutral-cage behaviour of *A. microps* seems to be different from that of related species. Although the relevance of the experiments performed in an artificial environment to the behaviour in nature may be questioned, the above phenomenon might indicate a different social and/or reproductive system in this species. The only available information on mating system in *A. microps* is unfortunately indirect. The small size of their testes (Huminski 1969, Kratochvíl 1971) predicts low incidence of multiple male mating (cf Heske and Ostfeld 1990 in North American voles, Harcourt *et al.* 1981, Kappeler 1997 in primates). Therefore, the reduction of agonistic behaviour cannot be simply explained by the allocation of

investment in favour of activities enhancing mating success (eg sperm competition, searching for females).

In most *Apodemus* species, male-male interactions performed in neutral-cage conditions are usually more agonistic than those female-female (Montgomery 1978, Frynta *et al*. 1995, Čiháková and Frynta 1996), and a slight effect of season on male-male interactions was also reported (Gurnell 1978). We found these phenomena also in *A. microps,* however, the effects were too small to suggest any substantial relation between agonistic behaviour in a neutral cage and male reproduction.

Our social-context experiments were designed to assess whether the presence of putative resources (territory, female) determines the social behaviour of *A. microps*. While the female-female encounters were not substantially affected by the "home-cage" design, males have changed their behaviour dramatically. They became clearly more agonistic when compared to previous neutral-cage condition, and this pattern has remained unchanged in successive experiments (both unfamiliar- and familiar-female defence designs). The proportion of agonistic behaviour in these encounters reached the level comparable to that found in other *Apodemus* species in neutral-cage experiments (Frynta *et al*. 1995, Čiháková and Frynta 1996). Although a sequence bias could not be avoided (ie learning of repeatedly tested mice affected particular comparisons between different designs), it is apparent that agonistic behaviour in *A. microps* is substantially related to the specific contexts of "ownership" and interactions outside these contexts are basically amicable. However, the "ownership" simulated in our experiments should not be interpreted as territorial defence of the entire home range. As repeatedly demonstrated in closely related species *A. sylvaticus,* male home ranges overlap considerably and the role of social spacing is limited (Tew and Macdonald 1994, cf Montgomery *et al*. 1997).

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